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Multi-factor biotopes as a method for detailed site characterization in diverse benthic megafaunal communities and habitats in deep-water off Morro Bay, California

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ABSTRACT

Here we describe the methods and results for biological characterization of the benthos on a previously unexplored area of central California, USA seafloor. We conducted 40 remotely operated vehicle dives from 371 to 1173 m water depth. Seafloor habitats and megafauna (fish and invertebrates) were documented from 46.8 km of seafloor video footage. Our expanded development and analysis of biotopes from quantitative data allowed us to describe detailed biological communities, along with the physical characteristics and habitat associations within the study area. This method provides a framework for potential monitoring, detection of future environmental change (natural and anthropogenic) and comprehensive comparison to other deep water regions. From 185 h of observational video at 25 sites, nearly 120,000 annotations of organisms, habitat characters, biological detritus and anthropogenic debris were recorded and analyzed. We identified a total of 228 taxa, with 173 of them present on linear quantitative transects. Species richness for transects ranged from 0.04 to 0.28 m^{-2} (8–55 taxa), with densities ranging from 0.07 to 5.20 ind. m^{-2}. Both were highest on hard substrate with greatest surface area. Densities decreased with depth. Within soft substratum zones was a large field of pockmarks, which are seafloor depressions averaging 175 m in diameter and 5 m in depth. Pockmarks have sometimes been associated with seafloor gas seepage, but here we found no biological evidence of chemosynthetic organisms. No significant differences were found in either density nor species richness at pockmark sites vs. non-pockmark sites. Mud draped greenish-black coarse sand occurred only in low oxygen areas, while hummocky, rugose mud supported somewhat different species than flat mud plains. Seventy percent of the transects occurred inside the oxygen minimum zone. We conclude that high rugosity, slope, and the presence of hard substratum were better predictors of species richness and density than oxygen concentration in this specific study. Abundant biological detritus, in the form of dead and dying pelagic pyrosomes and salps, created a large, presumably ephemeral flux of carbon to the seafloor during the study period.

1. Introduction

The need for comprehensive baseline studies of the deep seafloor where none exist are critical for ongoing assessment of change. In addition, an integrated regional understanding of biology and geology are critical for comprehensive marine planning. Offshore central California, state and federal agencies are planning for both conservation and wind energy development areas. Despite these regional planning activities, large portions of the seafloor off central California were unmapped using modern methods and largely unsampled. The need to better understand the regional seafloor resulted in a US West Coast partnership called the Expanding Pacific Research and Exploration of Submerged Systems (EXPRESS). The present study involved the Monterey Bay Aquarium Research Institute (MBARI), the US Geological Survey (USGS), the Bureau of Ocean Energy Management (BOEM), and the National Oceanic and Atmospheric Administration (NOAA) in an effort to first map, and then explore the seafloor in this area. Here we report on efforts conducted in 2019 to explore the biological communities and conduct habitat characterization in deep water offshore of Morro Bay, California (Fig. 1).

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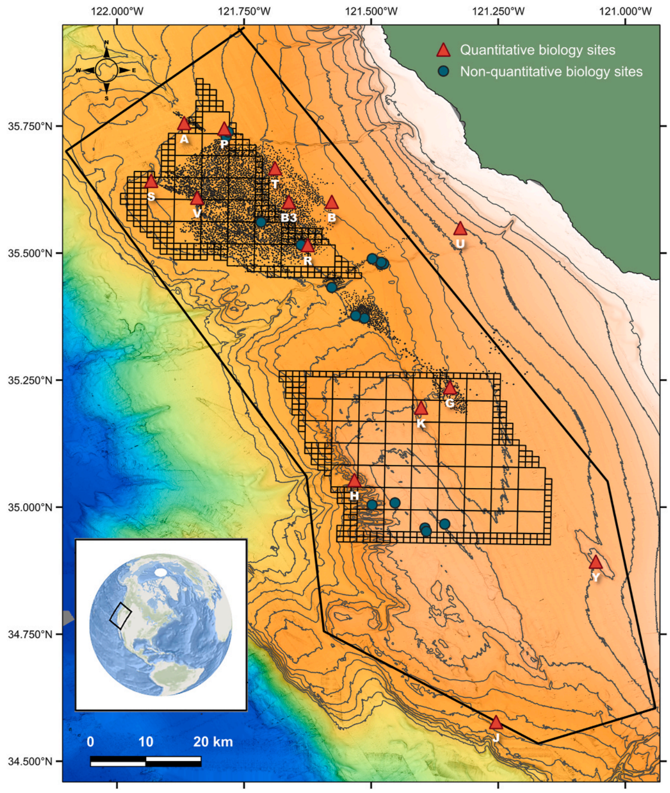

Fig. 1. Region of study offshore of Morro Bay, central California from approximately 400–1200 m depth. The study area from which we subsampled is defined with a black polygon (8424 km^2). Small fields of black dots illustrate the extent of pockmark fields. The gridwork of lines indicate potential wind farm lease block areas as initially identified.

Recently collected bathymetry show areas of both low and high relief bottoms in the study region. The high relief areas, like Santa Lucia Bank and other topographic highs, contain both rock outcrops and boulders intermingled with sandy fill (Walton et al., 2021; Cochrane et al., 2022). Two predominately mud-filled submarine channel systems or shallow canyons (Lucia Chica and San Simeon) have been explored (Maier et al., 2011, 2012, 2013; Dobbs et al., 2020). However, the dominate geologic habitat in the study area is characterized by low to medium relief soft substratum. Within the soft substratum area is a ~1300 km^2 area containing several thousands of seafloor depressions called pockmarks, which average 175 m in diameter and 5 m in depth and have been named the Big Sur pockmark field (Paull et al., 2002, 2020; Lundsten et al., 2022).

Pockmark depressions are enigmatic submarine landforms, which frequently occur on continental slope environments in clusters or fields that contain hundreds of features. Since the publication of a classic book on origin of pockmarks, they have been most commonly attributed to seafloor seepage, usually of gaseous methane (Hovland and Judd, 1988). Pockmarks frequently occur in areas that are likely underlain by hydrocarbon deposits (e.g., Gay et al., 2007) and in some cases fluid venting has been documented (Whiticar, 2002; Hustoft et al., 2009). However, pockmarks also occur in areas where the connection with significant subsurface gas accumulations is unlikely and samplings have found no direct evidence that fluid venting is actively occurring (e.g., Goff, 2019; Michel et al., 2017; Paull et al., 2020; Ussler et al., 2003; Wang et al., 2016; Webb et al., 2009; Wirth et al., 2020; Nickel et al., 2012). A rigorous understanding of the mechanism which seeping or even eruptive venting of fluid form pockmarks remains poorly developed and the one existing mechanism requires large underlying gas columns (Cathles et al., 2010), not seen in seismic data from the Big Sur area (Walton et al., 2020, 2021). Because sites of seafloor gas seepage are potentially unstable, they are considered as potential geohazards (Hovland et al., 2002; Marsset et al., 2010). Moreover, if methane is actively venting from the pockmarks, they might support chemosynthetic biological communities (Sibuet and Olu, 1998). Thus, the fauna within the pockmarks merit careful investigation.

Both modern seafloor mapping data and an understanding of the anthropogenic activities in this region provided context for designing video surveys of benthic biological communities. The greater seafloor region offshore Morro Bay has had multiple past exposures to anthropogenic disturbances with the largest being a major telecommunications cable landing region for the west coast. Commercial bottom trawling occurred in this area and the impact to the seafloor was studied in the more actively fished shallower than 400 m of this region (Lindholm et al., 2015). Oil and gas platforms occur outside the study area to the south and the closest platform is in 74 m water depth. Impacts from platform discharges were studied at three platforms offshore Point Arguello, California from 1986 to 1995, detecting changes in some species from discharges up to 3 km away (Lissner 1993; Coats, 1994; Hyland et al., 1994).

Efforts to characterize benthic biological communities and habitats have long been associated with connecting the species to abiotic physical factors. Attempts to characterize biological communities and habitats in deep-water zones have been largely based on depth boundaries, and are quite large in area (Hartman and Barnard, 1958; McClain and Hardy, 2010; Watling et al., 2013). Depth is typically the primary environmental factor in determining megafaunal communities (Hardin et al., 1994; Levin et al., 2010; Love and Yoklavich, 2006; Duffy et al., 2013). Previous biological investigations to the north (Tissot et al., 2008; Lindholm and DeVogelaere, 2009; Hallenbeck et al., 2012) and south (Love, 2009; Huff et al., 2013; Shester et al., 2017) of the study region show that high relief features such as seamounts, banks, slope reefs and canyons (Yoklavich et al., 2000) are associated with a relatively high diversity of megafaunal species (i.e., benthic fish and invertebrates), as compared to surrounding continental slope soft substratum. Deep-sea corals and sponge habitat suitability was modeled along the US West Coast as an important habitat feature for conservation and fisheries management (Guinotte, 2017; Poti et al., 2020).

Deep-water fish distributions have been explored in the region (Love and Yoklavich, 2006; Keller et al., 2017; Koslow et al., 2011), some with emphasis on commercial fish juvenile habitats (Tolimieri and Wallace-Haltuch, 2020). For macrofauna (i.e., small mostly infaunal invertebrates living in soft sediments) depth is a known driver f community structure, with grain size and latitude also being important correlating environmental factors (Lissner et al., 1989; Hyland et al., 1994; Gillett et al., 2017; Henkel and Nelson, 2018; Henkle and Gilbane, 2020). The Oxygen Minimum Zone (OMZ) shapes both assemblages in deeper waters off the US West Coast (Thompson and MullingsNewton-Vercoutere, 1985; Levin et al., 1991; Levin, 2003) and globally (Gooday et al., 2010; Stramma et al., 2010).

The primary goal in this study was to survey, document, and describe regional benthic megafaunal (fish and invertebrate) community compositions by employing a stratified sampling design covering all depths and major habitat types based on Multibeam Echo Sounder (MBES) data. Because the soft substratum pockmark fields were potentially unique habitats, this study investigated differences in the megafaunal and macrofaunal communities that live within them, as compared to the surrounding traditional soft substratum. We quantified the abundances of fish and invertebrate species by specific depth, distinct surficial geologic environments, and physical environmental parameters (i.e., dissolved oxygen, temperature, salinity, rugosity, and slope), thus we were able to develop multi-factored biotopes to describe species compositions, habitats and their connections more comprehensively. Biotopes are based on the concept that taxa units of a defined community often occur among similar environmental circumstances (Udvardy, 1959). Patterns of biotope associations are useful in other marine environments (Nagelkerken et al., 2000; Olenin and Daunys, 2004) but have not before been applied to deeper waters offshore the US West Coast. Detailed site characterization provides baseline data for a previously unexplored region, data to monitor future change, allows more accurate prediction of what is likely to be present in unobserved areas, enables comparisons with other deep regions, and aids in the definition of marine ecosystems.

In this study we focused on the following aspects of benthic species and their associations with surficial geology, depth, oxygen levels, and temperature:

1. Do megafaunal density and biodiversity significantly differ between a water depth zone of 300–500 m, 501–700 m, 701–900 m, and >900 m?
2. Do megafaunal density and biodiversity significantly differ between areas of soft substratum, within the pockmark fields, and mixed/hard substratum?
3. Do localized biological communities (megafauna and macrofauna) inside individual pockmarks significantly differ from those outside the individual pockmarks?
4. Can the development of multi-factored biotopes more precisely describe the ecosystem of the study area?

2. Methods

Multiple video surveys of the seafloor were combined from three separate cruises to the study area. A joint USGS-BOEM-MBARI cruise, which took place from 19 to 26 September 2019 on the R/V *Bold Horizon*, focused on conducting biological surveys using MBARI's *miniROV* (dives M137–148). Additional surveys were conducted from 02 to 14 February 2019 (dives D1120–1131) and from 01 to 11 November 2019 (dives D1202–1217) using MBARI's R/V *Western Flyer* and ROV *Doc Ricketts*.

2.1. Data collection of video and physical data

Video was recorded with MBARI's *miniROV* using a Mini Zeus camera by Insight Pacific, fitted with a Sony FCB-H11 module and 5.1–51 mm 10 x zoom lens. *Doc Ricketts* ROV video was recorded with an Ikegama high-definition camera fitted with a HA10Xt.2 Fujinon lens. Both ROV's were equipped with two parallel laser beams, which were used to measure the width of the seafloor in the field of view. White balancing of the camera was done on each dive as the seafloor was approached. While transiting, ROV pilots sought to maintain the vehicle at a constant altitude off the seafloor (1–4 m). ROV altitude and speed over the bottom varied based on the terrain, water column currents, and ship handling conditions.

ROV positions were measured using Ultra Short Base Line (USBL) systems with respect to a global positioning system (GPS) antenna on the ships. Instrumentation on the ROVs (situated 1–4 m above the seafloor) recorded pressure (i.e., depth; Valeport "Ultra P″), salinity (conductivity) and temperature (Valeport "Mini CT"). Dissolved oxygen from the ROV *Doc Ricketts* was taken at 1–4 m above the seafloor (Seabird SBE model 43). While the *miniROV* also transected at 1–4 m above the seafloor, its dissolved oxygen sensor was located on a clump weight connected by a 30 m long umbilical, resulting in some uncertainty in the dissolved oxygen concentration on the seafloor. Oxygen concentrations <0.5 ml l $^{-1}$ were considered to be in the OMZ (Levin, 2003).

2.2. Video annotation

To document and enumerate demersal and benthic megafauna, surficial geological habitats, biological detritus and anthropogenic debris from video, MBARI's Video Annotation and Reference System (VARS) was used at sea during cruises and onshore for post-cruise work (Schlining and Jacobsen Stout, 2006). All areas observed during the cruises were characterized in "observational" mode (semi-quantitative). Specific linear transects were annotated in a strictly "quantitative" mode at sites within the region (Fig. 1). Taxonomic identifications of megafauna were made to the lowest practical taxonomic level for animals readily visible in video (~1 cm in size or larger). Video transects using an ROV may be imperfect for documenting highly mobile fishes but are generally comparable amongst similar studies. Most taxa annotated in this project are documented in a dynamic web-based database called The Deep-Sea Guide (Jacobsen Stout et al., 2022). Species and taxa identifications are presumptive, based on morphotypes, and present-day knowledge of MBARI's benthic megafaunal experts. Taxa names were checked for validity against the World Register for Marine Species (January 2022, WoRMS, http://www.marinespecies.org).

The ROV camera was adjusted to maintain a 1 or 2 m-wide field of view during all quantitative transects. The width of the field of view was determined using the parallel laser beams in the video (14.5 cm apart for *miniROV*, 29 cm apart for *Doc Ricketts*). We measured the distance of travel using QGIS (v. 3.12.0-Bucureşti) to establish an equal total area for each transect. Quantitative video transects were annotated by documenting each megafaunal animal. To avoid bias in counts of the number of megafauna due to field of view distortion due to the oblique camera view (Wakefield and Genin, 1987), animals in the upper third of the image were not counted. Only those organisms passing through the midline swath of ROV video were counted (Appendix 4).

2.3. Surficial geologic habitat characterization

Surficial geologic habitats were identified from video using substratum, rugosity, and vertical slope designations (Table 1). Each observation was first assessed for the primary habitat category based on substratum appearance (following categorizations mud, coarse sand, cobble, boulder, or bedrock) that constituted at least 50% of the field of view (Table 1). Additional observations are made as habitat changes. To provide consistency and comparability, categorizations followed Coastal and Marine Ecological Classification Standard (CMECS) protocols (Marine and Coastal Spatial Data Subcommittee, Federal Geographic Data Committee 2012). A second substratum constituting at least an additional 20% of the field of view was also noted. Mud and coarse sand were grouped into a soft substratum group. Cobble, boulder and bedrock were grouped into a mixed/hard group. To more fully understand differences in biological communities, refine biotopes and to groundtruth MBES data, modifiers were employed (depression, dropstone, eroded (scouring), folded (deformed/bent), hummocky (small regular mounds in the sediment), mud veneer, outcrop, slabs).

Table 1
Surficial habitat categories used for the documentation and analysis within the study area. Each of 7200 observations were assigned primary substratum, secondary substratum, rugosity, and slope indicators. Modifiers were added to annotations to further define habitats and assist with mapping efforts. The top set of descriptors (frequently used) are referenced in other tables and figures in this study.

Primary substratum (>50%)	Secondary substratum (>20%)	Overall Rugosity	Slope (degrees)	Modifiers
mud, coarse sand, pebble*, cobble, boulder, bedrock	mud, coarse sand, pebble*, cobble, boulder, bedrock	flat, rugose	0–5, 5–30 30–60, 60–90	Frequently used: folded, hummocky, mud veneer, outcrop, and slabs Occasionally used: depression, dropstone, and eroded

Grainsize of substratum categories: mud: 90% median is < 0.0625, coarse sand: ≥ 90% median is 0.0625–0.125 mm, pebble: 4–62 mm, cobble: 64–255, boulder: 256–4096 mm bedrock: continuous formations of bedrock that cover 50% or more of the area. *only observed when brought up from depth.

General terms for rugosity of "flat" and "rugose" were used to describe the seafloor. To enhance comparison of biological communities in multivariate analyses, primary habitat and rugosity were ranked in order of increasing rugosity and the highest surface area: mud, muddy coarse sand, hummocky mud, cobble, boulder, bedrock slab, and bedrock outcrop. Slope was visually estimated as a vertical angle of 0–5, 5–30, 30–60, or 60–90°.

2.4. Megafaunal community characterization

Quantitative video transects were stratified by depth and substratum. ROV sites were selected during the planning phase, and based on mapping products to identify species at stratified depth classes; shallow (Zone 1, 300–500 m), shallow (Zone 2, 501–700 m), mid-deep (Zone 3, 701–900 m), and deep (Zone 4, >900 m; Table 2). High priority was given to collecting transects in soft substratum outside pockmark fields, soft substratum within pockmark fields, and hard or mixed substratum (mixed/hard) areas within each depth category based on MBES system data (Cochrane et al., 2022). When possible, two to three widely distanced (>7 km) locations were surveyed for site-level replication. Within each site (Fig. 1), transects were replicated as many times as possible with a goal of three and a minimum distance of 1 km between transects. The targeted area for each transect was >200 m^2.

This design (Table 2) ensured adequate video sampling to further map habitats (Cochrane et al., 2022) and define distinct benthic species groupings. Discrepancies between backscatter results and actual substrata sometimes yielded an incomplete replication of all stratified comparisons. Within the shallower strata (Zone 1, 300–500 m) mixed/hard substratum was present only at Site Y in the southern region of study area, where no pockmarks are present. At the mid-shallow (Zone 2, 501–700 m) pockmarks occur only at Site G in the north of the study area. Weather issues prevented the collection of additional soft substratum data for Site H.

2.5. Pockmark field biological community characterization

To determine if unique biological communities exist within individual pockmarks compared with the non-pockmark areas outside them, we sampled sites within two geographically separated pockmark fields (Fig. 1, Sites R and B3).

We compared six quantitative video transects at each of the two Sites, R (940 m depth) and B3 (870 m depth. The twelve ROV transects were 200 m^2 each. We traversed a total of six individual pockmarks and an equal distance of the immediate non-pockmark surrounding area. Results from inside and outside the three pockmarks at each of the two sites were combined for analysis since the linear transects were contiguous.

Pockmark macrofaunal samples were collected using 6.9 cm diameter push cores, which were inserted into the seafloor using the manipulator arm of ROV *Doc Ricketts*. Three push cores were taken inside and three outside each of three individual pockmarks at Site R equaling 18 samples. Collections were replicated inside and outside of three pockmarks at Site G collecting another 18 samples for a total of 36 samples. Onboard, the top five cm of sediment was sieved, and macrofauna were preserved with 95% EtOH. Organisms large enough to be retained on 300 μm sieve were sorted from sediments and identified by taxonomic experts through ABA Consultants, Santa Cruz, California.

2.6. Data analysis

Relationships between the mean physical variables for each transect were tested against one another to determine their degree of correlation using Pearson Product Moment Correlation. Highly correlated variables ($r > 0.60$) were noted.

For analysis, hard substratum was combined with five substrata categories that were a mix of hard and soft called 'mixed/hard'.

For quantitative video transects, counts of all animals and debris were totaled by transect and divided by the transect area to calculate the density of each. We conducted 91 quantitative linear transects at 13 region-wide sites (Fig. 1, Table 2). The *Doc Ricketts* ROV surveyed 14 transects at three sites and the *miniROV* surveyed 77 transects at 10 sites over 11 dives. To examine biological community composition, species richness and the densities for each transect were used. We conducted two-way analysis of variance (ANOVA) and Tukey HSD post hoc tests to examine differences in the mean density and species richness within each depth and substratum category. Regional diversity was further examined by calculating the effective number of species (Hill number analysis), which includes the exponential of Shannon's entropy index and the inverse of Simpson's concentration index, using PRIMER-E v.7 (Chao et al., 2009, 2014; Clarke and Gorley, 2015). To evaluate differences in density and species richness inside vs. outside pockmarks, we used paired, 2-tailed t-tests on video transects and macrofaunal samples.

For multi-variate analysis, square-root and fourth-root transformed data were tested. The 4th-root transform was conducted to minimize the effect of highly abundant mobile, and possibly transitory organisms such as ophiuroids (brittle stars). Groupings were determined by hierarchical cluster analysis (group average) and non-metric multidimensional scaling (nMDS) analysis, based on a Bray Curtis similarity matrix of species diversity and density, using each individual transect. The 4th-root transformed data produced an nMDS plot with less stress (goodness of fit; 0.16 vs. 0.17 for the square-root transformed data). This stress level indicates a potentially useful representation of the data (Clarke and Gorley, 2015).

To elucidate megafaunal communities that more completely explained our findings beyond just depth and substratum, we created SIMPROF groups using PRIMER-E v.7. SIMPROF creates biological community groups of in the absence of structure (e.g. depth, substratum). We used the SIMPROF groupings resulting in >60% similarity, followed by a similarity profile global test for significance. Primer-E v.7 SIMPROF groups were plotted in 2-dimensions using the original nMDS ordination positions for transects by assigning a centroid position that is the average position of all the transects within each SIMPROF group. To explain the differences among the groups, we applied the mean values for environmental factors from the group transects, forming multi-factor biotopes. Segmented bubble plots overlaid each group to show the relative weight of each environmental variable (Purcell et al., 2014). Individual species contributions within each group were calculated using SIMPER analyses. These groups served as the basis of our multi-factor biotopes and thus, SIMPROF groupings are hereafter referred to as biotopes. For this study, biotopes are defined as a distinctive megafaunal community composition established by species richness, abundance, dominant species (top 60% of abundance), trophic level composition, mobility composition, found in a specific physical environment (depth, temperature, salinity, oxygen, substrate type, slope, and rugosity) based on quantitative data. At the biotope level we also indicate the data status (baseline vs. subsequent survey), and observed disturbance (anthropogenic or ephemeral biodetritus).

We conducted Distance Based Redundancy Analysis (dbRDA, Primer-E v.7) using the Bray-Curtis resemblance matrix for biotope groups and a Euclidean Distance resemblance matrix on normalized environmental data for depth, oxygen, sediment, rugosity, slope and temperature. Primer's Relate function was used to calculate a Spearman Rank Correlation to look for overall similarities in the matrices; step-wise Distance-based multivariate multiple regression (DistLM) marginal tests were used to assess probabilities.

3. Results

During the three cruises on which 40 ROV dives were conducted, 46.8 km of the seafloor was traversed at an estimated average 4 m observational field of view. From 185 h of observational and quantitative transects at 25 major sites (Fig. 1), nearly 120,000 annotations were

Table 2
Stratified depth and substratum survey implementation for quantitative transects analyzed from sites in the study area. Survey effort to collect video from multiple (replicate) transects across four depth zones and three major substratum categories (soft, mixed/hard, and pockmark fields). Depth Zone 1 was 300–500 m, Zone 2 was 501–700 m, Zone 3 was 701–900m, and Zone 4 was >900 m. Note that no pockmark fields occurred between 300 and 500 m depth and were limited at 501–700 m.

Depth (m)	Substratum	Site	Depth min. (m)	Depth max. (m)	Transect replic.	Dive #	Transect	Width (m)	Length (m)	Area m2
300–500	soft	U	410	413	1	M140	U-A	2	100	200
300–500	soft	U	413	416	2	M140	U–B	2	100	200
300–500	soft	U	417	420	3	M140	U–C	2	100	200
300–500	soft	U	423	426	4	M140	U-D	2	100	200
300–500	soft	U	426	427	5	M140	U-E	2	100	200
300–500	soft	U	427	430	6	M140	U–F	2	100	200
300–500	soft	Y	386	386	7	M138	Y2-A	2	100	200
300–500	soft	Y	386	388	8	M138	Y2–B	2	100	200
300–500	mixed/hard	Y	371	373	1	M138	Y1-A	2	100	200
300–500	mixed/hard	Y	371	374	2	M138	Y1–B	2	100	200
300–500	mixed/hard	Y	374	378	3	M138	Y1–C	2	100	200
300–500	mixed/hard	Y	378	388	4	M138	Y3-A	2	100	200
300–500	mixed/hard	Y	381	391	5	M138	Y3–B	2	100	200
300–500	mixed/hard	Y	378	392	6	M138	Y3–C	2	100	200
300–500	mixed/hard	Y	383	384	7	M138	Y4-A	2	100	200
300–500	mixed/hard	Y	381	384	8	M138	Y4–B	2	100	200
300–500	mixed/hard	Y	381	382	9	M138	Y4–C	2	100	200
300–500	pockmark field	none in region	–	–	–	na	–	–	–	–
501–700	soft	H	634	637	1	M139	H4-A	2	100	200
501–700	soft	H	627	633	2	M139	H4–B	2	100	200
501–700	soft	H	624	630	3	M139	H4–C	2	100	200
501–700	soft	H	672	686	4	M139	H6-A	2	100	200
501–700	soft	H	688	702	5	M139	H6–B	2	100	200
501–700	soft	H	696	703	6	M139	H3-A	2	100	200
501–700	soft	H	683	695	7	M139	H3–B	2	100	200
501–700	soft	H	700	714	8	M139	H3-D	2	100	200
501–700	mixed/hard	H	606	610	1	M139	H5-A	2	100	200
501–700	mixed/hard	H	608	611	2	M139	H5–B	2	100	200
501–700	mixed/hard	H	611	619	3	M139	H5–C	2	100	200
501–700	mixed/hard	H	606	608	4	M140	H1-A	0.84	200	168
501–700	mixed/hard	K	678	704	5	D1212	K-E	1	200	200
501–700	mixed/hard	K	671	678	6	D1211	K–F	1	90	90
501–700	mixed/hard	H	667	682	7	D1211	H3–C	2	94	188
501–700	mixed/hard	K	703	712	8	D1211	K-G	1	192	192
501–700	mixed/hard	K	710	720	9	D1211	K–H	1	148	148
501–700	pockmark field	G	691	695	1	D1210	G-A	1	200	200
501–700	pockmark field	G	690	697	2	D1210	G-B	1	200	200
501–700	pockmark field	G	691	692	3	D1210	G-C	1	200	200
701–900	soft	K	719	728	1	D1212	K-A	1	200	200
701–900	soft	K	726	729	2	D1212	K–B	1.75	114	200
701–900	soft	K	729	731	3	D1212	K–C	1.75	92	160
701–900	soft	B1	768	769	4	M142	B1-A	2	100	200
701–900	soft	B1	770	771	5	M142	B1–B	2	100	200
701–900	soft	B1	771	772	6	M142	B1–C	2	100	200
701–900	soft	H	745	759	7	M139	H7-A	2	100	200
701–900	soft	H	770	776	8	M139	H7–B	2	100	200
701–900	soft	H	779	796	9	M139	H7–C	2	100	200
701–900	mixed/hard	H	775	796	1	M139	H2-A	2	100	200
701–900	mixed/hard	H	739	759	2	M139	H2–B	2	100	200
701–900	mixed/hard	H	720	737	3	M139	H2–C	2	100	200
701–900	mixed/hard	H	859	868	4	M139	H8-A	2	100	200
701–900	mixed/hard	H	859	863	5	M139	H8–B	2	100	200
701–900	mixed/hard	H	865	883	6	M139	H8–C	2	87	174
701–900	mixed/hard	K	720	730	7	D1212	K-D	1	200	200
701–900	mixed/hard	H	771	758	8	M139	H2-D	2	100	200
701–900	mixed/hard	H	860	898	9	D1208	H10-A	1	200	200
701–900	pockmark field	B3	868	868	1	M143	B3-A	2	100	200
701–900	pockmark field	B3	868	871	2	M143	B3–B	2	100	200
701–900	pockmark field	B3	871	874	3	M143	B3–C	2	100	200
701–900	pockmark field	B3	869	869	4	M143	B3-D	2	100	200
701–900	pockmark field	B3	871	876	5	M143	B3-E	2	100	200
701–900	pockmark field	B3	868	873	6	M143	B3–F	2	100	200
701–900	pockmark field	T	870	873	7	M147	T-A	2	100	200
701–900	pockmark field	T	872	875	8	M147	T-B	2	100	200
701–900	pockmark field	T	877	879	9	M147	T-C	2	100	200
>900	soft	J	918	919	1	M137	J1-A	1	100	100
>900	soft	J	916	918	2	M137	J1-B	1	100	100
>900	soft	J	915	916	3	M137	J1-C	1	100	100
>900	soft	S	1172	1175	4	M145	S-A	2	100	200
>900	soft	S	1173	1176	5	M145	S–B	2	100	200
>900	soft	S	1165	1173	6	M145	S–C	2	100	200
>900	soft	H	1011	1041	7	D1209	H9-A	1	200	200

(continued on next page)

Table 2 (*continued*)

Depth (m)	Substratum	Site	Depth min. (m)	Depth max. (m)	Transect replic.	Dive #	Transect	Width (m)	Length (m)	Area m2
>900	soft	H	904	908	8	D1209	H9–B	1	200	200
>900	soft	H	903	1011	9	D1209	H9–C	1	200	200
>900	mixed/hard	J	904	906	1	M137	J2-A	1	100	100
>900	mixed/hard	J	906	908	2	M137	J2-B	1	100	100
>900	mixed/hard	J	909	917	3	M137	J2-C	1	100	100
>900	mixed/hard	S	1118	1130	4	M145	S-D	2	100	200
>900	mixed/hard	S	1105	1116	5	M145	S-E	2	100	200
>900	mixed/hard	S	1103	1106	6	M145	S–F	2	100	200
>900	mixed/hard	S	1100	1113	7	M145	S-G	2	100	200
>900	mixed/hard	S	1114	1121	8	M145	S–H	2	100	200
>900	mixed/hard	S	1109	1113	9	M145	S–I	2	100	200
>900	pockmark field	R	936	938	1	M141	R-A	2	100	200
>900	pockmark field	R	939	940	2	M141	R–B	2	100	200
>900	pockmark field	R	940	943	3	M141	R–C	2	100	200
>900	pockmark field	A	1111	1114	4	M144	A-A	1.33	150	200
>900	pockmark field	A	1114	1118	5	M144	A-B	1.33	150	200
>900	pockmark field	A	1120	1122	6	M144	A-C	1.33	150	200
>900	pockmark field	V	1014	1014	7	M146	V-A	2	100	200
>900	pockmark field	V	1014	1014	8	M146	V–B	2	100	200
>900	pockmark field	V	1014	1014	9	M146	V–C	2	100	200

created. Results are given here for the four main components of investigation, abiotic factors, surficial geological classifications, megafaunal and macrofaunal sampling from pockmark features, and culminating in the establishment of multi-factored biotopes.

3.1. Physical factors (depth, temperature, salinity, oxygen)

Depth on dives within the survey area ranged from 379 to 1173 m, oxygen from 0.25 to 0.81 ml l^{-1}, temperature from 3.6 to 7.0 °C, and salinity from 34.1 to 34.6 PSU (Fig. 2). The results of Pearson Correlation tests revealed that depth and salinity were positively correlated ($r = 0.872$, $p < 0.001$) and depth and temperature were negatively correlated ($r = -0.965$, $p < 0.001$). Data reflect a well-developed OMZ (e.g., O_2 concentrations <0.5 ml l^{-1}) that extends between 550 and 1150 m (Fig. 2).

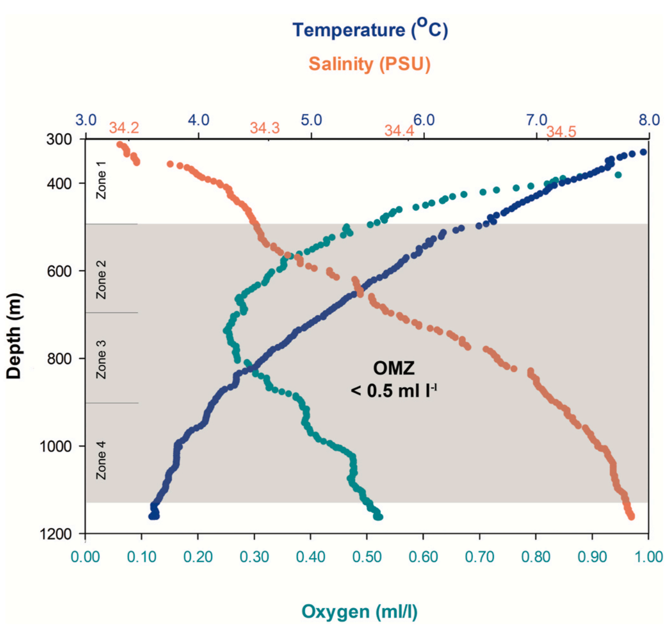

Fig. 2. Oxygen, temperature, and salinity for a water column profile from the deepest dive conducted within the study region (M145). A well-formed Oxygen Minimum Zone (OMZ) was evident between 500 and 1150 m water depth (y-axis) on this dive, with lowest oxygen levels at around 775 m. Zones 1–4 shown to the right of the y-axis indicate the depth categories used in the study design. Dive M145 was at site S in the northern part of the study area.

3.2. Surficial geological habitat characterization

For all ROV footage, more than 7600 observations regarding the surficial geological habitat character were made. The primary habitat in areas surveyed was soft substratum (80%, Fig. 3 A–C, Table 3). Hummocky mud (Fig. 3A, Table 3) occurred in 18% of the region and was present at all depth zones, all oxygen levels and all temperatures. Greenish-black mud draped coarse sand containing glauconite (Fig. 3C) covered 8.2% of the surveyed area. These sands occurred on flat plains between adjacent higher hard bottom areas on Santa Lucia Bank.

Areas estimated to be 100% hard substratum (solid bedrock or outcrop, Fig. 3F) were rare at 3.2% of the surveyed area. Mixed/hard substratum constituted a total of 19.8% of the surveyed region (Table 3). These included areas with varying amounts of cobble, biologically eroded boulders, or broken slabs of bedrock interspersed with mud covering the seafloor (Fig. 3D and E). Bedrock slab was the largest mixed/hard substratum category, representing 8.2% of the area surveyed. In some areas bedrock slabs were ~ 2–5 cm thick, while others were >30 cm thick. Pebble-sized rocks were only observed when they were brought to the seafloor surface in push cores.

The majority of the seabed within the study area was only mildly sloped and non-rugose (78% 0–5° slope, 71% flat or mildly rugose, Table 4). Rugose (hard substratum-dominated) areas were generally on 5–30° slopes and were observed in the southern portion of the region and at Site S in the north (Fig. 1, Table 4). Very steep slopes (60–90°) occurred at Sites K and S and were 100% bedrock representing 3.2% of the area surveyed (rock outcrops, Table 4). Occasional patches of bacterial mat were observed, most under 15 cm in diameter, and commonly observed to be associated with decomposing organic material. A few larger mats were clearly covering decomposing kelp. We saw no evidence of the megafaunal animal assemblages that are commonly associated with chemosynthetic biological communities (Sibuet and Olu, 1998) near the observed mats or elsewhere on these dives. All observations of bacterial mats occurred within the OMZ (Fig. 2).

3.3. Megafaunal community summary

Over 101,000 megafaunal organisms from among at least 228 presumptive taxa were observed in observational and quantitative video (Appendix A). Echinoderms (sea cucumbers, seastars, brittle stars, urchins, and crinoids) were the most abundant phylum-level group and comprised 46 different taxa (Fig. 4). Vertebrate chordates (bony fishes and elasmobranchs) were also abundant and represented the most speciose group (54 taxa). The most abundant benthic organisms were mobile (71.8%: sessile = 28.2%, Appendix A). Sessile animals were

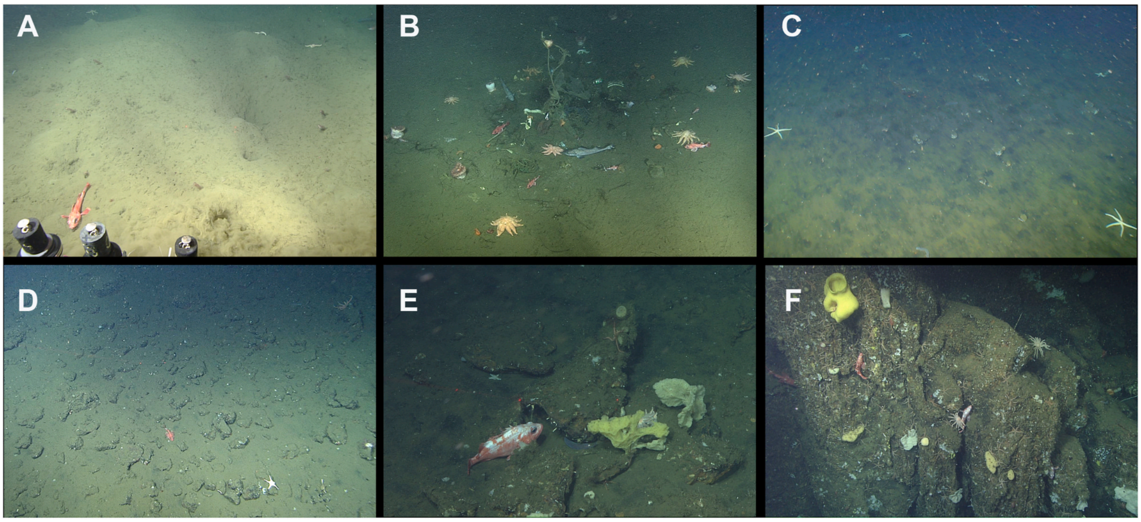

Fig. 3. Seafloor habitats observed within the study region. A–C are soft substratum: A. hummocky mud (small, frequent mounds, 687 m depth) B. biological detritus and marine litter (935 m) and C. Greenish-black mud draped coarse sand (766 m). D and E are a mix of soft and hard substrata: D. cobble (575 m) and E. bedrock slabs (477 m). F. is the only type of completely hard substratum observed, referred to as bedrock outcrop (447 m).

associated with hard substratum, but present in high numbers in soft substrate as well in the form of sea pens and anemones. Evaluation of trophic levels for megafauna revealed 35% predator/scavengers, 34% surface deposit feeders, and 30% suspension/filter feeders. Few subsurface deposit feeders and mixed-feeding animals were observed.

Cnidarians (anemones, corals, sea pens) were consistently observed in the region, and represented by 45 taxa (Appendix A). Small paragorgids (likely *Paragorgia stephencairnsi* or *P. yutlinux* (n = 119) and *Swiftia* spp. (n = 729) were present on rocky slopes. *Alternapathes* (n = 13) and *Parastenella* (n = 11) were sparse. *Isidella tentaculum* were rare and relatively small in size (<1 m height) when encountered (n = 5).

We noted no unexpected depth ranges for any of the species observed. Rockfish in the genus *Sebastolobus* were present over the entire depth range, with other *Sebastes* spp. occurring only <500 m. Sablefish (*Anoplopoma fimbria*), and the flatfish species *Embassichthys bathybius* and *Microstomus pacificus* occurred at all depths. Eelpouts in the genus *Lycodes* were replaced by *Lycenchelys croatalinus* on the benthos at depths >600 m. *Lycodapus fierasfer,* Macrourids and Liparids occurred frequently >600 m as well. Cerianthid anemones, sea anemones, sea pens and the urchin *Strongylocentrotus fragilis* were found at all depths, while octocorals were generally found deeper than 600 m. The holothurian *Psolus squamatus* occurred over most of the entire depth range, but *Apostichopus leukothele* was replaced by *Pannychia* spp. > 600 m. Sea stars in the presumptive genus *Myxoderma* were abundant from shallow to deep as were Ophiuroidea spp.

Nearly 5000 dead and dying pyrosome tunicates were observed on the seafloor. Other pelagic debris present in some of the same areas included dead salps. A layer of phytodetritus accumulation on the seafloor was apparent at the most southerly location we visited (Site J, Fig. 1). Shallow-water plant material accumulated in areas consisting of kelp fronds, holdfasts and eel grass. The empty shells (tests) of burrowing irregular urchins (Spatangoida) were seen in areas with hummocky mud between the depths of 412–1005 m.

3.4. *Megafaunal community associations with depth and substrata: quantitative video transects*

There were 173 taxa observed on transects (Appendix A). Overall species richness ranged from 0.04 to 0.275 m^{-2} (8–55 taxa), and densities from 0.11 to 12.9 m^{-2} (Table 5).

Replication of transects at multiple region-wide sites was not always possible for each of the four depth zones and three substratum zones analyzed (Table 2), resulting in pseudoreplication for some transects. This may have resulted in limited detection of the variation in species and abundances at the depth zone 300–500 m with mixed/hard substratum and the 501–700 m soft substratum and pockmark field transects. This effect was mitigated by separating each transect at the same general site by 1–5 km, which ensured the independence of transects. Species accumulation curves, evaluated for each of the four depth and three substratum categories, demonstrated that for most depth vs. substratum categories, species richness was nearing an asymptote, indicating sufficient sampling (Appendix B). A notable exception was from 501 to 700 m depth within the pockmark field where we were only able to conduct three transects.

3.4.1. *Statistical analyses*

Depth vs. Substratum. The result of the 2-way ANOVA demonstrated that both density and species richness were significant for the depth vs. substratum interaction (each $p < 0.001$, Table 5), indicating that density and species richness varied differently among depths and substratum types.

For pockmark fields, density declined strongly with depth, while in soft sediments the decline with depth was milder; density was highest at 301–500 m (Table 5, d x s factor Table 6). Mixed/hard substratum supported high densities until depth reached >900 m, then dropped markedly. Pockmark fields also declined strongly in species richness with depth, while soft substratum increased in richness above 300–500 m and peaked at 501–700 m (Table 5, d x s factor Table 6). Species richness in mixed/hard substratum increased with depth and was highest at 701–900 m depth.

Depth. ANOVA results were significant for density amongst depth categories ($F(3,91) = 6.6$, $p < 0.001$, Table 5). A Tukey HSD post-hoc test revealed significant pairwise differences in the mean density of organisms between 300 and 500 m vs. > 900 m ($p = 0.003$), and 501–700 vs. >900 m ($p < 0.001$, Table 6). There was no significant difference in species richness for depth categories (($F(3,91) = 1.5$, $p = 0.23$, range = 17–27 taxa). Two additional indices (Hill numbers) exponential of Shannon's entropy index and inverse of Simpson's index are shown in Table 5 and show similar patterns of diversity.

Substratum. The density of megafauna was significantly different amongst our substratum groups ($F(2,91) = 8.9$, $p < 0.001$, Table 5). Highest species richness was observed in mixed/hard substratum habitats (3.7 m^{-2} ± 2.9) and was lowest in soft substratum and pockmark fields (indistinguishable from each other; 1.6 m^{-2} each ± 1.8, 1.9). The

Table 3
Summary of ROV dives conducted in the region and surficial geological habitat observations made (all transects, both quantitative and observational). Distance reflects the total linear path the ROV traveled during each dive. Benthic position at dive start is shown as latitude and longitude, as well as depth. Surficial geological habitat observations are placed into Soft or Mixed/Hard Substratum categories and each substratum category is further divided into sub-categories with values indicating the estimated number of km present for that dive. Boulder and Bedrock with folded and bedded modifiers were rare and totaled <1% of substrate, <0.3 km, dives is summed at the bottom with the percentage of each habitat type.

Dive #	Distance (km)	Starting lat	Starting long	Starting depth (m)	Mud	Mud hummocky	Mud coarse sand	Mud cobble	Mud veneer	Total soft substrate	Cobble	Bedded rock	Folded rock	Bedrock slabs	Boulder	Bedrock	Total mixed/ hard substrate
Doc Ricketts 1120	0.6	35.515316	−121.6309	935.9	0.0	0.6	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1121	0.2	35.488967	−121.4988	833.4	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1122	0.9	35.378077	−121.5310	979.4	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1123	1.1	35.371926	−121.5119	955.4	1.1	0.0	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1124	0.7	35.433014	−121.5765	1057.6	0.1	0.6	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1125	0.5	35.390891	−121.5207	940.7	0.0	0.5	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1126	1.0	35.516426	−121.6381	951.6	0.0	1.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1127	0.8	35.475342	−121.4805	861.8	0.0	0.8	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1128	1.5	35.007678	−121.4995	816.9	0.1	0.0	0.3	0.0	0.0	0.4	1.1	0.0	0.0	0.0	0.0	0.0	1.1
Doc Ricketts 1129	0.7	34.964066	−121.3566	484.7	0.0	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.3	0.0	0.0	0.3
Doc Ricketts 1130	0.9	35.738558	−121.7811	993.2	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1131	0.7	35.647315	−121.9245	1126	0.7	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cruise 1	9.6				2.0	5.5	0.6	0.0	0.0	8.1	1.1	0.0	0.0	0.4	0.0	0.0	1.4
miniROV 0137	1.5	35.518024	−121.6320	935.7	0.9	0.4	0.0	0.0	0.0	1.4	0.2	0.0	0.0	0.0	0.0	0.0	0.2
miniROV 0138	2.8	35.518884	−121.6320	932.6	0.2	0.0	0.0	0.0	0.9	1.1	0.6	0.0	0.0	0.8	0.0	0.3	1.7
miniROV 0139	5.6	35.47774	−121.4815	820.1	1.5	0.2	3.6	0.0	0.0	5.3	0.3	0.0	0.0	0.0	0.0	0.0	0.3
miniROV 0140	0.9	35.474844	−121.4712	843.8	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
miniROV 0141	2.0	35.007693	−121.4564	483.4	0.0	2.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
miniROV 0142	1.5	35.210177	−121.4069	750.1	0.0	1.5	0.0	0.0	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0

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Table 3 (*continued*)

Dive #	Distance (km)	Starting lat	Starting long	Starting depth (m)	Mud	Mud hummocky	Mud coarse sand	Mud cobble	Mud veneer	Total soft substrate	Cobble	Bedded rock	Folded rock	Bedrock slabs	Boulder	Bedrock	Total mixed/ hard substrate
miniROV 0143	1.2	35.041874	−121.5600	983.2	1.2	0.0	0.0	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
miniROV 0144	0.9	35.07973	−121.5796	1038.9	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
miniROV 0145	2.1	35.236125	−121.3465	691.5	0.0	0.7	0.0	0.0	0.0	0.7	0.6	0.0	0.0	0.2	0.0	0.5	1.3
miniROV 0146	0.6	35.197616	−121.4012	712.9	0.0	0.6	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
miniROV 0147	0.9	35.196256	−121.4024	716.9	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
miniROV 0148	0.8	34.951577	−121.3925	460.4	0.0	0.8	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cruise 2	20.9				3.9	9.0	3.6	0.0	0.9	17.4	1.7	0.0	0.0	0.9	0.0	0.8	3.5
Doc Ricketts 1202	0.1	35.022069	−121.3955	435.8	0.0	0.1	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1203	0.6	35.187578	−121.4057	717.1	0.0	0.6	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1204	0.4	35.563363	−121.7178	942.1	0.0	0.4	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1205	0.9	35.730541	−121.7864	986.3	0.0	0.9	0.0	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1206	1.2	34.574317	−121.2534	918.8	0.4	0.0	0.2	0.0	0.0	0.6	0.0	0.0	0.0	0.3	0.2	0.1	0.6
Doc Ricketts 1207	0.9	34.894941	−121.0585	377.7	0.0	0.0	0.6	0.0	0.3	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1208	0.8	35.053649	−121.5330	893.7	0.0	0.0	0.0	0.0	0.3	0.3	0.5	0.0	0.0	0.0	0.0	0.0	0.5
Doc Ricketts 1209	1.1	35.549266	−121.3248	411.3	1.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1210	1.1	35.515875	−121.6249	933.6	0.0	1.1	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1211	1.6	35.601641	−121.5772	768.5	0.6	0.0	0.7	0.0	0.0	1.3	0.0	0.0	0.0	0.3	0.0	0.0	0.3
Doc Ricketts 1212	1.3	35.600959	−121.6619	868	0.0	0.0	0.7	0.0	0.0	0.7	0.1	0.0	0.0	0.2	0.0	0.4	0.6
Doc Ricketts 1213	1.6	35.756055	−121.8679	1109.8	0.1	0.0	0.4	0.0	0.0	0.5	0.0	0.0	0.0	1.1	0.0	0.0	1.1
Doc Ricketts 1214	1.1	35.642089	−121.9327	1170.8	0.2	0.0	0.8	0.0	0.0	1.0	0.0	0.0	0.0	0.1	0.0	0.0	0.1

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Table 3 (*continued*)

Dive #	Distance (km)	Starting lat	Starting long	Starting depth (m)	Mud	Mud hummocky	Mud coarse sand	Mud cobble	Mud veneer	Total soft substrate	Cobble	Bedded rock	Folded rock	Bedrock slabs	Boulder	Bedrock	Total mixed/hard substrate
Doc Ricketts 1215	2.2	35.609611	−121.8420	1014.2	0.4	0.0	0.6	0.0	0.0	1.0	0.3	0.0	0.0	0.6	0.0	0.2	1.2
Doc Ricketts 1216	0.8	35.666917	−121.6890	870	0.8	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Doc Ricketts 1217	0.6	35.745405	−121.7889	1004.3	0.6	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cruise 3	16.3				4.2	3.2	4.0	0.0	0.6	12.0	0.9	0.0	0.0	2.5	0.2	0.7	4.4
Total (km)	46.8				10.0	17.7	8.2	0.1	1.5	37.5	3.7	0.0	0.0	3.8	0.2	1.5	9.3
Percent of total					21.4	37.9	17.5	0.2	3.1	80.1	7.8	0.0	0.1	8.2	0.5	3.2	19.8

Table 4
Summary of slope and rugosity observations for dives (both quantitative transects and observational video). Distance reflects the total linear path the ROV traveled during each dive. Values indicate the estimated distance (km) for each slope and rugosity category. Summed at the bottom are the total distance and percent of all dives binned into each slope and rugosity category.

Dive #	Distance (km)	Slope (degrees)				Rugosity	
		0–5	5–30	30–60	60–90	flat	rugose
Doc Ricketts 1120	0.6	0.6	0.0	0.0	0.0	0.6	0.0
Doc Ricketts 1121	0.2	0.2	0.0	0.0	0.0	0.2	0.0
Doc Ricketts 1122	0.9	0.9	0.0	0.0	0.0	0.9	0.0
Doc Ricketts 1123	1.1	1.1	0.0	0.0	0.0	1.1	0.0
Doc Ricketts 1124	0.7	0.7	0.0	0.0	0.0	0.7	0.0
Doc Ricketts 1125	0.5	0.5	0.0	0.0	0.0	0.5	0.0
Doc Ricketts 1126	1.0	1.0	0.0	0.0	0.0	1.0	0.0
Doc Ricketts 1127	0.8	0.8	0.0	0.0	0.0	0.8	0.0
Doc Ricketts 1128	1.5	0.1	0.2	1.2	0.0	0.4	1.1
Doc Ricketts 1129	0.7	0.3	0.4	0.0	0.0	0.3	0.4
Doc Ricketts 1130	0.9	0.9	0.0	0.0	0.0	0.9	0.0
Doc Ricketts 1131	0.7	0.7	0.0	0.0	0.0	0.7	0.0
Doc Ricketts 1202	0.1	0.1	0.0	0.0	0.0	0.1	0.0
Doc Ricketts 1203	0.6	0.6	0.0	0.0	0.0	0.6	0.0
Doc Ricketts 1204	0.4	0.4	0.0	0.0	0.0	0.4	0.0
Doc Ricketts 1205	0.9	0.9	0.0	0.0	0.0	0.9	0.0
Doc Ricketts 1206	1.2	0.2	0.8	0.2	0.0	0.2	1.0
Doc Ricketts 1207	0.9	0.6	0.2	0.1	0.0	0.5	0.4
Doc Ricketts 1208	0.8	0.3	0.5	0.0	0.0	0.3	0.5
Doc Ricketts 1209	1.1	1.1	0.0	0.0	0.0	1.1	0.0
Doc Ricketts 1210	1.1	1.1	0.0	0.0	0.0	1.1	0.0
Doc Ricketts 1211	1.6	0.8	0.7	0.0	0.0	1.0	0.5
Doc Ricketts 1212	1.3	0.7	0.1	0.5	0.0	0.7	0.6
Doc Ricketts 1213	1.6	1.6	0.0	0.0	0.0	0.5	1.1
Doc Ricketts 1214	1.1	1.0	0.1	0.0	0.0	1.0	0.1
Doc Ricketts 1215	2.2	0.6	0.7	0.8	0.1	0.6	1.5
Doc Ricketts 1216	0.8	0.8	0.0	0.0	0.0	0.8	0.0
Doc Ricketts 1217	0.6	0.6	0.0	0.0	0.0	0.6	0.0
Mini ROV 0137	1.5	1.5	0.0	0.0	0.0	0.2	1.4
Mini ROV 0138	2.8	1.7	1.1	0.0	0.0	0.9	1.9
Mini ROV 0139	5.6	4.1	1.5	0.0	0.0	3.3	2.3
Mini ROV 0140	0.9	0.9	0.0	0.0	0.0	0.9	0.0
Mini ROV 0141	2.0	2.0	0.0	0.0	0.0	2.0	0.0
Mini ROV 0142	1.5	1.5	0.0	0.0	0.0	1.5	0.0

(*continued on next page*)

Table 4 (*continued*)

Dive #	Distance (km)	Slope (degrees)				Rugosity	
		0–5	5–30	30–60	60–90	flat	rugose
Mini ROV 0143	1.2	1.2	0.0	0.0	0.0	1.2	0.0
Mini ROV 0144	0.9	0.9	0.0	0.0	0.0	0.9	0.0
Mini ROV 0145	2.1	0.7	0.4	0.6	0.4	1.1	1.0
Mini ROV 0146	0.6	0.6	0.0	0.0	0.0	0.6	0.0
Mini ROV 0147	0.9	0.9	0.0	0.0	0.0	0.9	0.0
Mini ROV 0148	0.8	0.8	0.0	0.0	0.0	0.8	0.0
Total km	**46.8**	**36.5**	**6.4**	**3.4**	**0.5**	**33.0**	**13.8**
Percent of total		**77.9**	**13.7**	**7.3**	**1.0**	**70.5**	**29.5**

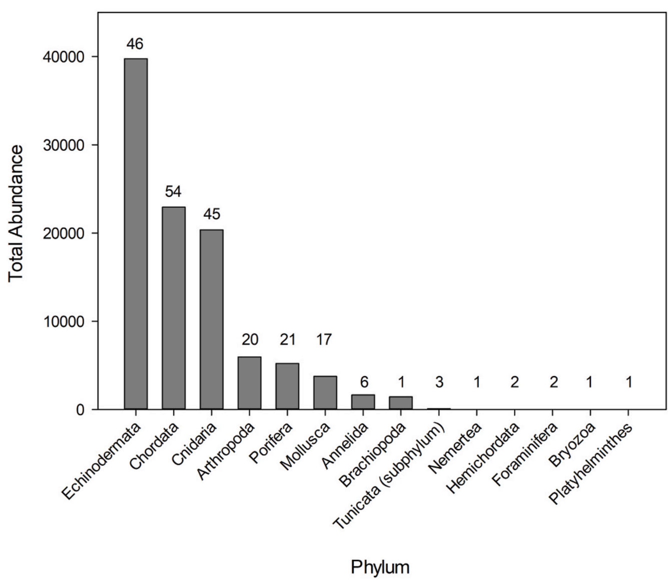

Fig. 4. The total abundance of megafaunal observations from quantitative and observational dives by phylum. The number of taxa represented by each group is listed above each bar.

Table 5
Mean megafaunal diversity and density (m-2, ± = std. dev.) results by depth and substratum for 91 quantitative transects. Results of ANOVA tests (α = 0.05) show that density was sig. different for depth and substratum. Species richness was sig. for substratum, but not for depth. Both density and species richness were sig. for the interaction depth x substrate. Rows in bold are totals for each category. n = the number of transects, S = species richness, expH' = exponential of Shannon's entropy index, 1/γ = inverse of Simpson's conventration index.

Transect Type	n	S	expH′	1/γ	density
300–500 m	17	21.5 ± 9.8	4.3 ± 2.6	1.0 ± 1	3.6 ± 2.2
mixed/hard	9	28.8 ± 5.6	6.4 ± 1.8	1.0 ± 0.1	5.1 ± 1.5
soft	8	13.3 ± 6.5	2.0 ± 0.56	1.2 ± 1.7	1.8 ± 1.2
501–700 m	20	27.1 ± 8.8	8.6 ± 3.8	1.6 ± 1.4	3.5 ± 3.4
mixed/hard	9	34.2 ± 7.5	10.8 ± 4.3	1.3 ± 0.7	4.1 ± 3.3
pockmark field	3	24.3 ± 4.2	6.0 ± 0.6	1.0 ± 0.2	5.2 ± 2.6
soft	8	20.1 ± 3.8	7.1 ± 2.5	2.3 ± 2.3	2.4 ± 3.6
701–900 m	27	24.1 ± 13.3	8.6 ± 5.0	5.5 ± 9.9	2.3 ± 2.6
mixed/hard	9	40.8 ± 8.1	14.3 ± 4.2	1.1 ± 0.2	4.5 ± 3.8
pockmark field	9	14.8 ± 2.8	5.3 ± 1.1	6.7 ± 8.7	1.3 ± 0.3
soft	9	16.7 ± 5.6	6.1 ± 1.9	9.2 ± 15.3	1.2 ± 0.5
>900 m	27	20.9 ± 10	8.8 ± 5.1	11.8 ± 23.0	1.0 ± 0.4
mixed/hard	9	33.3 ± 5.1	15.0 ± 2.2	17.5 ± 31.8	1.1 ± 0.2
pockmark field	9	13.6 ± 2.7	5.6 ± 1.5	11.2 ± 13.2	0.7 ± 0.4
soft	9	15.7 ± 5	5.9 ± 3.6	4.2 ± 5.4	1.0 ± 0.4
mixed/hard	36	34.3 ± 7.7	4.8 ± 15.8	11.6 ± 4.7	3.7 ± 2.9
pockmark field	21	15.6 ± 4.6	6.0 ± 8.3	5.5 ± 1.2	1.6 ± 1.8
soft	34	16.4 ± 5.6	4.5 ± 8.7	5.3 ± 3.0	1.6 ± 1.9
2-Way ANOVA					
Parameter/Factor	SS	df	MS	F	*p*
Density (m-2)					
Depth	110	3	36.6	6.6	<0.001
Substratum	99.2	2	49.6	8.9	<0.001
Depth x substratum	243.1	10	24.3	5.6	<0.001
Error	348.1	80	4.3		
Species richness (m-2)					
Depth	520	3	173	1.5	0.227
Substratum	7176	2	3588	88.6	<0.001
Depth x substratum	8299	10	829	27.2	<0.001
Error	2439	80	30.4		

Tukey HSD post-hoc test revealed significant pairwise differences between mixed vs. pockmark ($p = 0.003$) and mixed vs. soft substrata ($p = 0.001$, Table 6). Species richness was significantly different by substratum. Mixed/hard substratum was highest at 34.3 ± 7.7. Comparable means were observed for soft substratum (16.4 m^{-2} ± 5.6) and pockmark fields (15.6 m^{-2} ± 4.6) (($F(2,91) = 88.6$, $p < 0.001$). The Tukey HSD post-hoc test revealed significant pairwise differences between mixed vs. pockmark ($p < 0.001$) and mixed vs. soft substrata ($p < 0.001$). Additional diversity indices (Hill numbers) exponential of Shannon's entropy index and Shannon's Diversity are shown in Table 5.

The similarity of biological communities can be visualized and further analyzed by using ordination methods. A plot showing the nMDS data (Fig. 5) illustrates the relationships of individual transects (each data point) for the four depth categories and three substratum types. The relative similarity of the species composition and abundances observed on each transect form identifiable groups. The closer the transects on the group plots are located, the more similar the biological communities.

Overall, transects within the depth vs. substratum categories were less than 40% similar; the ellipses reveal numerous non-depth and substratum related clusters, even at this low similarity percentage (Fig. 5). Depth ranges are only generally clustered together. Mixed/hard substratum transects generally cluster together, supporting the finding that densities and species richness for mixed/hard substratum was significantly different from them both. There is some, but not complete, clustering of soft and pockmark field substratum transects. While the mean densities and species richness for soft and pockmark field were not significantly different, nMDS analysis shows that there was community separation. The individual species in each group were somewhat different (500–700 m, 52 total species, 55.8% overlap between soft and pockmark field megafauna; 700–900 m, 49 species with 61.2% overlap; >900 m, 49 species, 53.1% overlap).

3.4.2. *Multi-factored biotopes*

The original depth and substratum categories describe the study area

Table 6
Results of Tukey HSD post hoc tests. Levels for the given parameters and factors were signifcantly different (p). Density and species richness per m2. d x s = depth x substratum.

Parameter	Factor	Level	Level	*p*
Density	depth	300–500	>900	<0.001
	depth	500–700	>900	<0.001
	substratum	mixed/hard	pockmark field	0.003
	substratum	mixed/hard	soft	0.001
	d x s	mixed/hard 300–500	mixed/hard >900	0.005
	d x s	mixed/hard 300–500	pockmark field 700–900	0.008
	d x s	mixed/hard 300–500	pockmark field >900	0.001
	d x s	mixed/hard 300–500	soft 700–900	0.006
	d x s	mixed/hard 300–500	soft >900	0.004
	d x s	mixed/hard 500–700	pockmark field >900	0.030
	d x s	mixed/hard 700–900	mixed/hard >900	0.036
	d x s	mixed/hard 700–900	pockmark field >900	0.010
	d x s	mixed/hard 700–900	soft 700–900	0.042
	d x s	mixed/hard 700–900	soft >900	0.026
Species richness	substratum	mixed/hard	pockmark field	<0.001
	substratum	mixed/hard	soft	<0.001
	d x s	mixed/hard 300–500	mixed/hard 700–900	0.001
	d x s	mixed/hard 300–500	pockmark field 700–900	<0.001
	d x s	mixed/hard 300–500	pockmark field >900	<0.001
	d x s	mixed/hard 300–500	soft 300–500	<0.001
	d x s	mixed/hard 300–500	soft 700–900	0.001
	d x s	mixed/hard 300–500	soft >900	<0.001
	d x s	mixed/hard 500–700	pockmark field 700–900	<0.001
	d x s	mixed/hard 500–700	pockmark field >900	<0.001
	d x s	mixed/hard 500–700	soft 300–500	<0.001
	d x s	mixed/hard 500–700	soft 500–700	<0.001
	d x s	mixed/hard 500–700	soft 700–900	<0.001
	d x s	mixed/hard 500–700	soft >900	<0.001
	d x s	mixed/hard 700–900	pockmark field 500–700	0.001
	d x s	mixed/hard 700–900	pockmark field 700–900	<0.001
	d x s	mixed/hard 700–900	pockmark field >900	<0.001
	d x s	mixed/hard 700–900	soft 300–500	<0.001
	d x s	mixed/hard 700–900	soft 500–700	<0.001
	d x s	mixed/hard 700–900	soft 700–900	<0.001
	d x s	mixed/hard 700–900	soft >900	<0.001
	d x s	mixed/hard >900	pockmark field 700–900	<0.001
	d x s	mixed/hard >900	pockmark field >900	<0.001
	d x s	mixed/hard >900	soft 300–500	<0.001
	d x s	mixed/hard >900	soft 500–700	<0.001
	d x s	mixed/hard >900	soft 700–900	<0.001
	d x s	mixed/hard >900	soft >900	<0.001

in sufficient detail to show general trends, but there is not enough of a signal to fully define the habitats present. The a priori depth and substratum groups clustered at < 40% indicating low similarity in the broad design, therefore we moved beyond our initial hypothesis and further analysis was undertaken in an effort to explain additional environmental conditions that better define communities and biotopes.

We used SIMPROF biotic data to cluster sites (>60% similarity) without regard to a priori group structure; in this analysis, depth and substratum categories were ignored and biological community structure alone formed groupings. The SIMPROF null hypothesis of an absence of structure was rejected (sample statistic = 0.1 (p = 0.001), π = 7.23), and eighteen SIMPROF groups were formed where three or more transects combined in similarity (Table 7, Appendix C). These groups reflect 77% of megafaunal transects in the analysis. We used these groups to define biotopes by describing the environmental conditions that were present when highly similar megafaunal assemblages occurred. SIMPER analysis provided the contribution of each species to biotope groupings (Table 7, Fig. 6, Appendix C).

Sixty-eight percent of individual transects (n = 62 of 91) and 72% of biotopes (n = 13 of 18) were located within the OMZ. We presumed transects with no oxygen measurements were in the OMZ because their depths were fully within the low oxygen zone (Fig. 2). Biotopes 2, 3, 4, 5, 6, 10, 11, 12, 13, 15, 16, 17 and 18 (Fig. 2, Table 7) were all located in low oxygen conditions where we observed 117 taxa. Mean diversity at low oxygen levels was variable and ranged from 15.7 to 45.7 taxa (Table 7). Highest diversities within the OMZ were observed on 5–30° slopes with 100% bedrock and bedrock slabs, and lowest in mud-laden areas. Mean densities were also variable and ranged from 0.6 to 6.7 m^{-2}. Highest density within the OMZ occurred on 5–30° slopes with bedrock and bedrock slabs, and at the highest temperatures. Low densities occurred in mud and muddy coarse sand habitats.

The most dissimilar biotopes were 1, 7, 8, 14 and 16 (Fig. 6) and are described here. See Table 7 and Appendix C for further summary and details of all 18 biotopes. Correlation of biological communities and the six environmental variables was significant (ρ = 0.789, p = 0.01). dbRDA results reiterated that depth and temperature were strongly negatively correlated (Fig. 7). Rugosity, slope and sediment type were mostly strongly correlated with biological communities based on the distance-based multivariate multiple regression (p = rugosity 0.001, slope 0.001, sediment 0.009, temperature 0.01, depth 0.013, and oxygen 0.036).

Biotope 1. Communities were 61% similar to each other and found on hummocky soft mud on flat terrain at Site U (Fig. 1). This community was located at shallow depths (421 m ± 6.8), and at relatively high oxygen concentration and temperatures. This biotope exhibits a low mean number of taxa (10.5 ± 1.7) and relatively low megafaunal abundance (1.1 m^{-2} ± 0.8). The community was heavily dominated by the seastar *Myxoderma platycanthum*, a mobile surface deposit feeder and secondarily by the flatfish *Microstomus pacificus*. Baseline data, observed disturbance (pyrosoma detritus).

Biotope 7. This taxa assemblage was 80% similar. Substratum consisted of cobble-sized rock on a 5–30° slope. This highly rugose, high-surface area habitat (Site Y, Fig. 1) at shallow depth ($\overline{X}$ = 379 m ± 4.8) with relatively high oxygen levels and temperatures supported a large number of taxa ($\overline{X}$ = 33 ± 1.8) and a high mean abundance of 5.0 m^{-2} ± 0.2. Mobile ophiacanthid brittle stars were in high abundance at

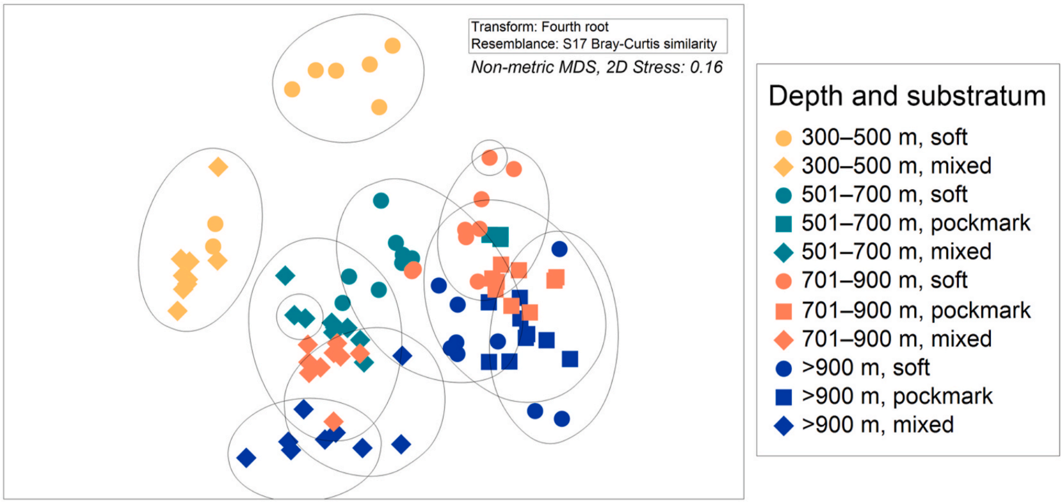

Fig. 5. Non-metric multidimensional scaling (nMDS) ordination with symbols highlighting depth and substratum categories. Based on a Bray-Curtis species and density similarity matrix on 4th-root transformed data. Individual transects are plotted as symbols. The closer in space symbols are located, the more similar the biological community is based on the species and densities present. Ellipses indicate clustering at the 40% similarity level, which is generally considered low. Depth ranges and substratum categories are only generally clustered together.

these sites as was the urchin *Stronglycentrotus fragilis*. Seventy-five percent of organisms were mobile and 69% were surface deposit feeders. Baseline data, observed disturbance (pyrosoma detritus).

Biotope 8. Exhibited 69% community similarity. The surficial habitat consisted of mud with 10% bedrock slab on 30–60° slopes. All transects associated with this biotope were at Site S (Fig. 1) at a mean water depth of 1111 m ± 6.0). Mean oxygen levels were just above the level used to define the OMZ (0.5 ml^{-1}), and temperatures were low. This area supported high diversity ($\bar{X}$ = 35 taxa ±6.6; crustaceans, brittle stars, sponges, seastars, sea cucumbers, etc.), but low density ($\bar{X}$ = 1.1 m^{-2} ± 0.03). The community was comprised mostly of mobile predators/scavengers, mobile surface deposit feeders, along with sessile suspension/filter feeders. Baseline data, observed disturbance (pyrosoma detritus).

Biotope 14. Exhibited 63% community similarity. These transects were located on flat muddy bottom with no bedrock slab, also at Site S. Located at slightly deeper depth, ($\bar{X}$ = 1173 m ± 2.6), they also exhibited higher mean oxygen concentration (0.52 ml^{-1}) and low temperatures. Low abundance and low diversity ($\bar{X}$ = 10.7 taxa ±2.1, 0.5 m^{-2} ± 0.02) was observed. The functionally mobile "tumbleweed" anemone *Liponema brevicorne*, mobile predators *Neptunea-Buccinum* complex snails and *Sebastolobus* rockfish dominated there. Baseline data, observed disturbance (pyrosoma detritus).

Biotope 16. Exhibited 64% community similarity. Transects were all located on flat mud plains with greenish-black mud draped coarse sand containing glauconite at Site K (Fig. 1), with a mean of 727 m (±2.6) depth. Oxygen concentrations for these transects was not measured, however the water depth puts them well within the OMZ (Fig. 2). Mid-range temperatures were recorded. Low abundance and low diversity ($\bar{X}$ = 15.7 taxa ±3.0, 1.1 m^{-2} ± 0.05) was observed. Nearly all organisms were mobile predators and scavengers and were represented by two species of shrimps and the snake eel-pout *Lycenchelys croatalinus*. The sea cucumber *Pannychia* sp. 1, a mobile surface deposit feeder, was present as well. Baseline data, observed disturbance (pyrosoma detritus, trash).

3.5. *Pockmark field biological community structure*

Megafauna. Thirty-three taxa in and around pockmarks were observed on the 18 transects from Sites B3 and R (Fig. 1; Table 8). There were no significant differences in either density nor species richness of megafauna at either of the two sites. Both areas were characterized by small cerianthid anemones, sea pens, seastars, rockfish and eelpout fish. No recurring taxa were found exclusively inside or outside pockmarks. Rockfish were specifically assessed, and we found that at Site R (Fig. 1) they were present in equal numbers inside and outside pockmarks. At Site B3, there were more rockfish inside pockmarks, but not significantly so. There was generally more pyrosome detritus inside pockmarks as well, but also not significantly so. A total of 16 drift kelp and eel grass plus six items of marine litter were observed in these transects; they were roughly evenly distributed inside and outside pockmarks.

Macrofauna. A total of 29 taxa were found in sediment samples taken with push cores (Table 9). These included crustacean species of amphipods, cumaceans, ostracods, tanaids, and isopods, bivalve molluscs, and polychaete worms. Crustaceans comprised 55% of abundance. The mean density of macrofaunal organisms present inside pockmarks (n = 3), vs. outside pockmarks (n = 3) was not significantly different for any of the three individual pockmarks tested (Table 8). As well, species richness did not significantly (Table 8). While there were no statistically significant differences in the diversity and density of macrofaunal organisms present inside vs. outside pockmarks, there was high variation for three species (two amphipods and a bivalve) at specific pockmarks, indicating faunal patchiness.

4. Discussion

The State of California is actively engaged with the BOEM in planning for the possible siting of offshore floating wind projects within outer continental shelf regions. BOEM has made a call for interest in two regions offshore central California at 400–1200 m depths for developing areas for floating wind technology. These data will be used to evaluate potential direct, indirect and cumulative impacts to the specific marine environment studied here. Should an offshore floating windfarm project be conducted in the region, these data provide a detailed basis for future Before-After-Control-Impact (BACI) designs for monitoring and detection of environmental change. The observational ground-truthing of mapping data also inform regional predictive mapping in an effort to characterize the physical benthic habitat in areas not sampled (Cochrane et al., 2022). At the same time, NOAA is conducting an environmental review in this area for the proposed designation of Chumash Heritage National Marine Sanctuary.

Biotopes, as a method to evaluate other marine environments (e.g. Nagelkerken et al., 2000; Olenin and Daunys, 2004), and for some deep water studies (e.g. Buhl-Mortensen et al., 2020; Dimitrakopoulos and

Table 7
Summary of biotopes derived from SIMPROF groups based on Bray-Curtis similarity matrix of megafauna species and abundances from quantitative transects. Results of these 18 groups represent 77% of the quantitative transects where more than 3 transects made up a group. Similarity % within each group ranged from 61 to 80%. #spp. = number of species m-2 SF = suspension/filter feeders pred = predators/scavengers SDF = surface deposit feeders SSDF = subsurface deposit feeders Mixed = mixed feeding type.

Biotope	Transects	Substrate	Mean #spp.	Total spp. range	Density (m-2)	Slope (deg)	Rugosity	Mean Depth (m)	O2 (ml l-1)	Temp (C)	Salinty (PSU)	Mobility (m-2)		Trophic (m-2)				
												Mobile	Sessile	SF	Pred	SDF	SSDF	Mixed
1	6	mud	10.5	8–12	1.1	0–5	hummocky	421	0.80	7.08	34.27	99.0	1.0	1.4	8.5	90.1	0.0	0.0
2	9	mud	16.0	10–17	1.2	0–5	hummocky	872	0.31	4.38	34.49	51.0	49.0	52.2	45.2	2.6	0.0	0.1
3	3	mud	14.3	12–16	1.0	0–5	hummocky	939	0.36	4.16	34.52	28.5	71.5	71.6	27.4	1.0	0.0	0.0
4	5	muddy coarse sand + sparse cobble	21.8	19–28	1.3	0–5	mildy rugose	721	0.27	5.04	34.43	69.8	30.2	33.7	14.0	52.3	0.0	0.0
5	3	muddy coarse sand	17.3	14–20	0.6	0–5	flat	631	0.26	5.37	34.40	89.6	10.4	14.3	25.5	60.2	0.0	0.0
6	3	mud	18.3	17–19	2.6	0–5	flat	917	0.42	4.01	34.53	13.4	86.6	86.6	12.1	1.3	0.0	0.0
7	5	cobble (large)	33.0	31–34	5.0	5–30	rugose	379	0.81	7.23	34.28	75.5	24.5	24.2	6.5	69.2	0.0	0.0
8	3	mud, some bedrock slabs	35.0	28–40	1.1	30–60	rugose	1111	0.50	3.63	34.56	71.7	28.3	27.7	51.6	20.6	0.0	0.0
9	3	mud with cobble	37.0	35–38	1.0	5–30	mildy rugose	1114	0.51	3.59	34.57	70.2	29.8	30.5	40.6	28.9	0.0	0.0
10	3	bedrock	41.0	33–48	6.7	5–30	rugose	697	OMZ	5.06	34.33	77.8	22.2	23.0	42.3	34.7	0.0	0.0
11	3	cobble	35.0	33–36	4.6	0–5	rugose	611	0.27	5.44	34.39	72.3	27.7	27.2	13.6	59.2	0.0	0.0
12	3	bedrock slabs	45.7	39–55	4.4	5–30	rugose	866	0.32	4.43	34.49	30.4	69.6	67.2	21.0	11.7	0.0	0.1
13	3	bedrock slabs	43.7	42–46	4.4	5–30	rugose	753	0.28	4.76	34.45	52.3	47.7	48.6	17.0	34.4	0.0	0.0
14	3	mud	10.7	8–12	0.5	0–5	flat	1173	0.52	3.59	34.57	97.8	2.2	60.2	31.9	7.9	0.0	0.0
15	3	mud	25.0	21–29	5.2	0–5	hummocky	693	OMZ	5.00	34.33	30.7	69.3	69.9	26.6	3.4	0.1	0.0
16	3	muddy coarse sand	15.7	12–18	1.1	0–5	flat	727	OMZ	4.86	34.36	96.5	3.5	4.2	86.2	9.6	0.0	0.0
17	6	mud	14.0	9–18	0.5	0–5	hummocky	1066	0.49	3.72	34.56	39.7	60.3	64.3	32.2	3.3	0.0	0.1
18	3	mud	16.7	15–17	1.6	0–5	hummocky	770	0.26	4.62	34.46	51.9	48.1	57.3	25.4	17.1	0.0	0.1

Three biotopes with no measured O2 levels are presumed to be at OMZ levels based on depth.

Troumbis, 2008) have been previously employed. The term biotope is used to describe a habitat and the collection of animals living within it, many times at a gross level (e.g. mangroves vs. coral reef). In practice, the biological and physical factors incorporated into a biotope description varies widely. In the past, not all deep-sea ecological investigations were capable of sampling what are now standard environmental variables, but with the advent of ROV's, landers and other benthic vehicles, most are now able to determine geographic location, water depth, temperature, and salinity. Advances in instrumentation and the recognition of changing oxygen levels in our oceans suggests that adding this factor into datasets is of import in monitoring natural change and anthropogenic disturbance. Standardized surficial geological terms, enhanced biological community indicators (dominant organisms, tracking of admixture changes, trophic and mobility composition) and documentation of direct visual indicators of biological or geological disturbance also provide a means for detailed monitoring of changes and meaningful comparison to other deep sea areas. These types of detailed investigations provide data for larger scale whole-community modeling.

Previous approaches to elucidate species associations with environmental factors on the US West Coast revealed distinct macrofaunal and megafaunal communities associated with sediment and depth changes. South of this study area, investigation of major patterns in macrofaunal benthic communities determined important differences in depth, sediment, temperature, and oxygen (Lissner, 1989; Hyland et al., 1994). Several studies sought to classify benthic sedimentary habitats across the shelf and upper slope in the Pacific Northwest based on the macrofaunal organisms living in and on the sediment (Henkel and Politano, 2017; Henkel and Nelson, 2018; Henkle and Gilbane, 2020). Henkle and Gilbane (2020) applied a cluster analysis approach to seafloor video and compared biological similarity groups with available physical data near rocky features at three sites offshore Oregon and Washington (Hemery et al., 2018). As an alternative approach, modeling has also been applied along the US West Coast to map broad scale seafloor habitat suitability and suitability of occurrences (Poti et al., 2020). These models cannot directly predict distributions of communities or provide direct, spatial information about taxonomic richness, but are instead used to infer patterns in predicted habitat suitability across taxa and contribute to marine planning and assessments of potential impacts of activities on biota. The benefit of this type of approach is the ability to integrate many physical factors, such as current direction, water column nutrient levels, and other broad area indicators into a model. For occurrence models, the relative importance of each environmental predictor to model fitting is also presented and may provide useful hypotheses for future studies aimed more at inference about the ecological drivers and mechanisms behind the spatial distributions of macrofauna in the study area. The output modeled maps have corresponding coefficient of variation of model predictions and therefore provide a measure of the variability, or uncertainty, associated with the model predictions for each taxon. These modeling approaches to date are applied to a single species or taxonomic group and cannot integrate species communities and similarity relationships.

4.1. *Ecological importance*

These ROV observations provide documentation of the surficial habitats and megafauna that characterize the seafloor off central California in and around areas important for energy and conservation planning. This characterization of the seafloor also is important from an ecological perspective to understand how the biological communities interact with their physical environment. The density of organisms in all substrata decreased as water depth increased, although the density of taxa decreased at different rates. Rugose, hard substrate supported the highest densities. Species richness decreased with depth for both soft substrata categories, but mixed/hard areas maintained high richness at all depths and supported more than twice the number of megafaunal taxa. This is a common pattern found on continental slopes (Rex, 1981;

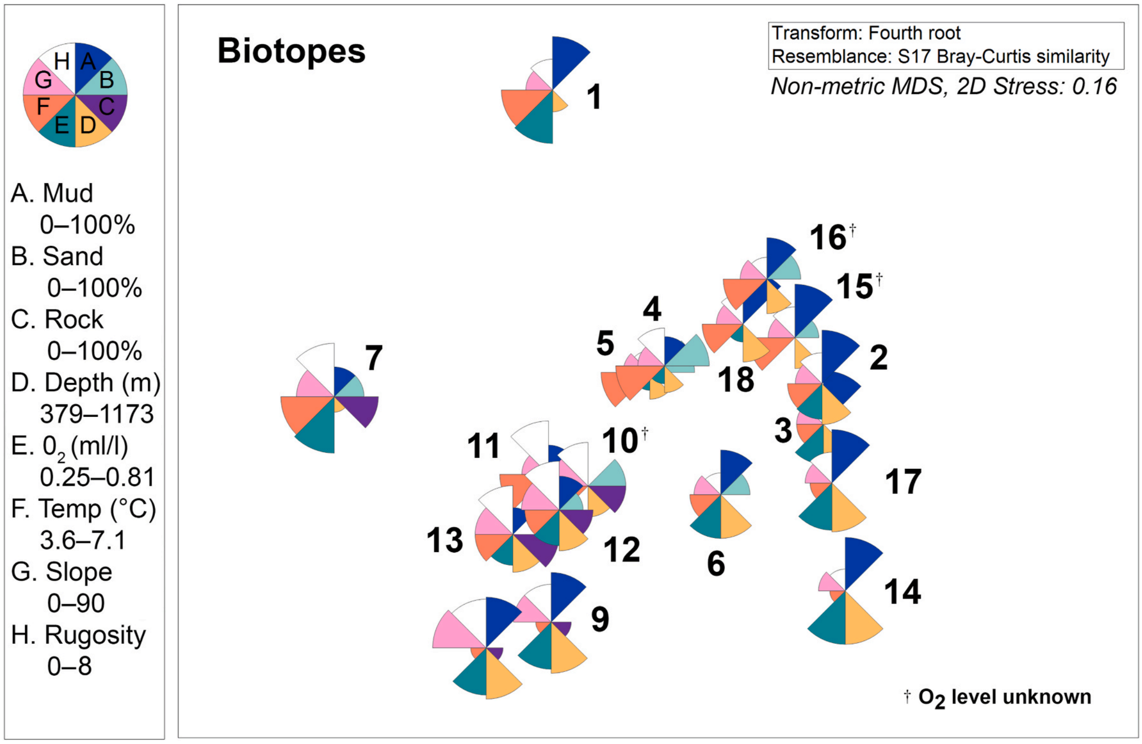

Fig. 6. Segmented bubble plot demarking 18 biotopes. Plots are positioned in the non-metric multidimensional scaling (nMDS) ordination defining statistically significant SIMPROF biological community clusters with similarity >60%. Segments of each bubble plot are labeled A-H on the left of the figure and represent the abiotic factors of the biotope. The length of each segment shows the relative differences in abiotic/environmental factors among biotopes. For example, biotope 1 muddy, with high temperature and oxygen. Data are presented in Table 7 and Appendix C.

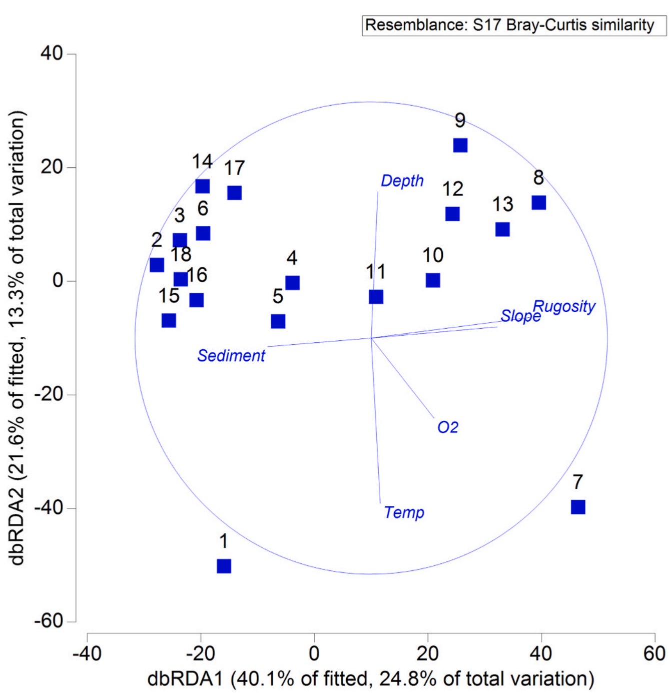

Fig. 7. Distance-based redundancy analysis (dbRDA) shows correlations for biotic assemblages (biotopes) and six environmental parameters. Symbols represent biotopes. Depth and temperature were strongly negatively correlated. Slope, rugosity and sediment type were mostly strongly correlated with biological communities.

Table 8
Results of t-tests for video transect (megafauna) and pushcore (macrofauna) sampling to compare the effect of inside vs. outside pockmarks. While 6 transects were conducted at each site (3 inside and 3 outside), results at each site were pooled for analysis since transects were contiguous. No significant differences were seen between the two treatments. ± = std. dev. n = the number of pockmarks for megafauna and pushcores for macrofauna.

Megafauna	n	mean inside	mean outside	*p*
Density m-2				
Site R	3	209 ± 73	311 ± 138	0.343
Site B3	3	205 ± 76	248 ± 105	0.600
Species richness m-2				
Site R	3	15.7 ± 2.1	14.3 ± 3.5	0.602
Site B3	3	14.0 ± 1.0	12.7 ± 1.2	0.205
Macrofauna	**n**	**mean inside**	**mean outside**	***p***
Density 221 cm-3				
Pockmark A	3	5.7 ± 1.5	11.3 ± 3.5	0.14
Pockmark B	3	3.0 ± 1.7	7.7 ± 1.5	0.12
Pockmark C	3	2.3 ± 2.1	1.7 ± 1.5	0.18
Species richness 221 cm-3				

Ramirez-Llodra et al., 2010). The observed densities for fishes, megafaunal invertebrates, drift kelp and eel grass are similar compared with the available information for the wider region to the north and south and at similar depths, (Vetter and Dayton, 1999; Yoklavich et al., 2000; Love and Yoklavich, 2006; Lindholm and DeVogelaere, 2009; Hallenbeck et al., 2012; Huff et al., 2013; Shester et al., 2017; Whitmire et al., 2017; Jacobsen Stout et al., 2022). Very high abundances of brittle stars and sea urchins were present in areas. These animals are known to form

Table 9
List of macrofaunal (infaunal) organisms identified from sediment samples by major taxonomic group.

Polychaeta	Ophelina acuminata
Polychaeta	Orbiniidae
Polychaeta	Paraonidae
Polychaeta	Dorvilleidae
Polychaeta	Subadyte sp.
Polychaeta	Spiochaetopterus costarum
Cmplx Polychaeta	Prionospio sp.
Polychaeta	Flabelligeridae
Polychaeta	Aricidea (Allia) antennata
Amphipoda	Ampelisca unsocalae
Amphipoda	Byblis barbarensis
Amphipoda	Bathymedon sp. Amphipoda
Monoculodes latissimanus Amphipoda	Nicippe tumida
Amphipoda	Harpiniopsis epistomata
Amphipoda	Hippomedon sp.
Cumacea	Lampropidae sp. F
Cumacea	Eudorella arctica
Cumacea	Eudorella sp.
Cumacea	Leucon bishopi
Cumacea	Leucon magnadentata
Isopoda	Eurycope californiensis
Isopoda	Munnopsurus sp. A Tanaidacea
Carpoapseudes caraspinosus Ostracoda	Bathyleberis sp.
Bivalvia	Nuculana juv.
Bivalvia	Yoldiella nana
Bivalvia	Adontorhina lynnae
Bivalvia	Neilonella mexicana

feeding and spawning aggregations and have been previously observed along the California coast (Lauzon-Guay and Scheibling, 2007; Stöhr et al., 2012; Jacobsen Stout et al., 2022). Only one rare species was encountered for this region (the bony fish *Eretmichthys pinnatus*), and no organisms appeared to be undescribed species (Burton and Lundsten, 2008; Burton et al., 2017; Burton and Lea, 2019; Jacobsen Stout et al., 2022).

Some globally occurring pockmark features have been associated with methane venting and evidence of chemosynthetic biological communities (Liu et al., 2019). Here, our findings did not reveal any known chemosynthetic associated species, which is consistent with subsequent geophysical findings that confirm that these pockmarks are not venting gas, but rather are formed by intermittent non-channelized turbidity flows (Walton et al., 2021; Lundsten et al., 2022). Our detailed examination of individual pockmarks and the areas just outside them also did not reveal significant biological community differences for megafaunal or macrofaunal community compositions. While inactive pockmarks in the Portuguese margin did find biological community differences in macrofaunal and microbial communities when compared to the surrounding seafloor (Rodrigues et al., 2019). It should be noted that macrofaunal sampling in this study was limited; a larger sample size could have potentially yielded different results.

Oxygen minimum zones are worldwide features resulting in gradients in biological activity and vary with latitude globally. More experimental research is needed to understand the effects of low oxygen, as the prevalence of low oxygen is expected to expand with ocean warming and acidification (Breitburg et al., 2018; Sampaio et al., 2021). Hypoxic environments can lead to lower species diversity and density for megafauna and macrofauna since many organisms are sensitive to, or cannot adapt to, low O_2 conditions (Gooday et al., 2009; Levin et al., 2009; Breitburg et al., 2018); adaptions for low oxygen levels can also lead to increased endemism (Gooday et al., 2010). Inhabiting these zones ephemerally or permanently may offer reduced competition and a refuge from predators (Gilly et al., 2013; Breitburg et al., 2018; Kuhnz et al., 2019; Gallo et al., 2020). The current upper and lower OMZ boundaries in the study region were comparable to other central coastal California areas at similar depths (Gilly et al., 2013). About 70% of quantitative data from this study were in the OMZ, thus this dataset provides baseline information on low dissolved oxygen concentration megafauna within the region (Fig. 2). A paucity of species may have been anticipated within the local OMZ, yet 117 of the total observed 173 species (68%) were observed there. The highest diversity in the region was at 772 m depth on hard substratum. OMZ boundary edge effects have been proposed as an explanation for unexpected high diversity (Gooday et al., 2009), however the highest diversity, along with the highest densities in this study were in the core of the OMZ. In the context of this study, the presence of hard substratum was a stronger predictor of species richness and density than oxygen levels. In a recent study of oxygen levels at Northeast Pacific seamounts, Ross et al. (2020) estimate that these waters have lost 15% of dissolved oxygen over the past 60 years and that the OMZ may deepen by 3 m per year in the future. This suggests that the current 'baseline' faunal assemblages found in this study may reflect an already altered ecosystem.

Deep-sea corals are known to provide important biogenic habitat for a wide variety of fishes and invertebrates in terms of shelter, habitat heterogeneity, carbon and nutrient cycling (Winship et al., 2020). Interestingly, no large (>1 m height) or abundant hard corals were observed at the specific areas we visited. Several hypotheses could explain the low abundance and small size (and perhaps age) of the these hard corals among depths and substratum types: 1) oxygen levels, 2) depth, 3) temperature, 4) carbon and nutrient flux, and 5) substratum type. Few data are available on the localized current regimes and carbon flow to the seafloor at these locations, which can bring nutrients to sessile suspension feeding animals, and may dictate coral distributions (Huff et al., 2013). While there is insufficient data to reject some of these hypotheses currently, we suspect substratum, and possibly nutrient availability are likely to play a large role. Hard substratum as deep as 1100 m was explored in this study, yet only a few hard corals were seen, and they were small (~0.5 m height, first author observations). In contrast, two nearby topographic highs (Davidson Seamount and Sur Ridge) both support more corals. Davidson Seamount is a hard substratum region to the northwest that supports large stands of corals including dense stands of the bubblegum coral, *Paragorgia arborea*, which were not observed in this study. *P. arborea* found on Davidson Seamount occur in deeper, more oxygen rich, cooler temperature water (1241–3040 m depth, $\overline{X} = 1291$ (±75), dissolved oxygen 0.85 ml l^{-1} ± 0.16 and temperature of 2.7 ± 0.22) (Jacobsen Stout et al., 2022). Sur Ridge supports *P. arborea* in locally high densities (826–1290 m depth, $\overline{X} = 1091$ (±154), dissolved oxygen 0.53 ml l^{-1} ± 0.16 and temperature of 3.64 ± 0.44) (Jacobsen Stout et al., 2022). *Isidella tentaculum* occurs at Sur Ridge as well from 747 to 1303 m depth with the largest and densest stands at a mean depth of 1107 m ± 0.147 (dissolved oxygen 0.55 ml l^{-1} ± 0.15 and temperature of 3.53 ± 0.33) (Jacobsen Stout et al., 2022). The exposed rocks on all three banks differ. Basalt is exposed on Davidson Seamount (Clague et al., 2009), Mesozoic age rocks of the Franciscan Formation are thought to be exposed on Sur Ridge (Greene et al., 1998) and Miocene aged rocks of the Monterey Formation occur on Santa Lucia Bank (McCulloch, 1987; Nicholson et al., 1992). The decreased competence of the strata found in the study area (tabular hard substratum) may provide less favorable surfaces for attachment (first author personal observation, Jacobsen Stout et al., 2022). Large sessile organisms probably fail to live long in the study area due to the relatively friable substratum and they are doomed to fall over when it finally erodes around them. In a succeeding cruise to Santa Lucia Bank in 2020, *E/V Nautilus* explored an area at 1000 m depth and found some larger corals on a very steep scarp (Raineault et al., 2021). These new data points may provide insight and the impetus for study of these hypotheses.

Fresh biological detritus in the form of abundant dead and dying pyrosomes, and to a much lesser extent salps, present during the later portion of the study period. However, no pyrosomes were observed on the seafloor during the R/V *Western Flyer* cruise in February 2019, and only a dozen observations were made in the water column, indicating that their high abundance was ephemeral. Offshore central California, dead and dying pyrosomes were first seen by MBARI in increased numbers at a recurrently-sampled site (Station M, 4000 m, southwest of the current study area) in the fall of 2012 (Kuhnz et al., 2020). They were rarely observed anywhere offshore central California prior to 2012 (Jacobsen Stout et al., 2022). In June 2015, pyrosomes were present on the deep seafloor at Station M reaching nearly 100% bottom coverage. There was another apparent "bloom" in March 2017. By 2019, MBARI was again observing them in very high densities in numerous areas along the coast of central California, including in this study, and to depths as shallow as 400 m. At least 30 different taxa feed on these midwater tunicates; they are eaten by anemones, snails, sea stars, crinoids, sea cucumbers, urchins and crabs (Jacobsen Stout et al., 2022). This large flux of carbon to the seafloor will likely alter biological community composition for an unknown period. The impact of this bloom may have an effect on the abundance and distribution of megafauna observed in future investigations of the region.

5. Conclusions

Defining multi-factored biotopes was an effective method for defining high levels of community similarity and the abiotic factors that defined them. Although 80% of the study area was soft substratum, we observed differences in biological communities where as few as one measured environmental factor varied. Pockmarks did not support unique megafauna or macrofauna and were similar in biodiversity and density to the communities just outside them. In this study offshore Morro Bay, California, distinct groupings of biological communities in association with substrata are important for making marine planning decisions and designing future impact assessments. Potential impact studies conducted in the future should be evaluated in light of the observed high, and likely ephemeral carbon flux to the seafloor. Changes in the dissolved oxygen levels over time may alter megafaunal assemblages as well.

Author statement

L. Kuhnz: Conceptualization; Data curation; Formal analysis; Investigation; Methodology; Writing - review & editing. L. Gilbane: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Writing - review & editing. G. Cochrane: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Writing - review & editing. C. Paull: Conceptualization; Data curation; Formal analysis; Funding acquisition; Investigation; Methodology; Project administration; Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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