



Using deep-sea images to examine ecosystem services associated with methane seeps

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ABSTRACT

Deep-sea images are routinely collected during at-sea expeditions and represent a repository of under-utilized knowledge. We leveraged dive videos collected by the remotely-operated vehicle *Hercules* (deployed from E/V *Nautilus*, operated by the Ocean Exploration Trust), and adapted biological trait analysis, to develop an approach that characterizes ecosystem services. Specifically, fisheries and climate-regulating services related to carbon are assessed for three southern California methane seeps: Point Dume (~725 m), Palos Verdes (~506 m), and Del Mar (~1023 m). Our results enable qualitative intra-site comparisons that suggest seep activity influences ecosystem services differentially among sites, and site-to-site comparisons that suggest the Del Mar site provides the highest relative contributions to fisheries and carbon services. This study represents a first step towards ecosystem services characterization and quantification using deep-sea images. The results presented herein are foundational, and continued development should help guide research and management priorities by identifying potential sources of ecosystem services.

1. Introduction

The deep sea (here defined as greater than 200 m water depth) hosts diverse habitats with a myriad of ecological processes that enable ecosystem services (Armstrong et al., 2012; Thurber et al., 2014). Ecosystem services can be categorized as provisioning, regulating, cultural, and supporting services. Provisioning services in the deep sea include fisheries landings for food (Clark et al., 2016) and genetic resources for industrial and pharmaceutical uses (Blasiak et al., 2018). Regulating services refers to processes such as carbon cycling (Cartapanis et al., 2016; Sweetman et al., 2019), and other elemental and biogeochemical cycles that are integral to global environmental health (Blöthe et al., 2015; Huang et al., 2019). Additionally, deep-sea habitats provide cultural services, or non-material benefits, including education and outreach opportunities (Hoeberechts et al., 2015) as well as aesthetic value and art inspiration (Simonson, 2019). Supporting services are those that enable these other categories of services, i.e., ecological functions and physical processes. From an ecosystem services perspective, human well-being is increased by the existence and health of ecosystem structures and ecological functions (Millennium Ecosystem Assessment, 2005; Haines-Young and Potschin-Young, 2018), providing

a tangible argument for more holistic environmental management and protection (Le et al., 2017).

Ecosystem services can be difficult to quantify, especially in marine environments such as deep continental shelf habitats (among others) where interactions and boundaries can be dynamic and loosely-coupled (Barbier et al., 2011). However, technological developments have greatly aided deep-sea scientific research (e.g., Corinaldesi 2015; Aguzzi et al., 2019). Advances in deep-sea imaging (visual data in the form of pictures and videos) provide useful information on physical and biological characteristics of underwater habitats (Macreadie et al., 2018). Imagery can be collected via cameras mounted on underwater observatories (De Leo et al., 2018), drop cameras (Clayton and Dennison, 2017), landers (Lavaley et al., 2017; Gallo et al., 2020), autonomous underwater vehicles (Mejía-Mercado et al., 2019), remotely-operated vehicles (ROVs; Myhre et al., 2018), and human-occupied vehicles (Gallo et al., 2015). Deep-sea expeditions routinely collect imagery for scientific (e.g., National Deep Submergence Facility, Ocean Networks Canada), outreach (e.g., NOAA Office of Ocean Exploration and Research, Ocean Exploration Trust, Schmidt Ocean Institute), and industry (e.g., Gates et al., 2017; Simon-Lledó et al., 2019) purposes. As a result, there is a wealth of imagery that continues to grow over time as

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interest in deep-sea exploration and resources expands.

Imagery has been instrumental to advancing our understanding of deep-sea habitats and enabling our ability to properly protect them. For example, Amon et al. (2016) used visual data to characterize the diversity and abundance of megafauna in a polymetallic nodule claim within the Clarion-Clipperton Fracture Zone, providing important baseline information for assessing impacts from potential seabed mining. Another scientific application of deep-sea imagery is evaluating vulnerable marine ecosystems such as sponge gardens that enhance local biodiversity and impact biogeochemical cycling (Maldonado et al., 2015; Santín et al., 2018). Additionally, images and videos provide an opportunity to visualize organisms *in situ*, which can be important for behavioral observations (Katija et al., 2017), for observing taxa that avoid sampling equipment (Ayma et al., 2016), and for minimizing disturbances associated with nets, dredges, grabs, or other means of sample collection.

With the magnitude of deep-sea imagery being collected, there is opportunity to leverage existing data to characterize, and ideally quantify, ecosystem services. Visual data are often not analyzed or only partially analyzed for specific, funded applications, such as physical and biological descriptions. However, deep-sea imagery represents a repository of knowledge about the diversity and abundance of organisms in a given locale, and how they interact with their environment and the other individuals at that locale. This can help illuminate what ecosystem services exist as well as the processes that enable them (i.e., functions). Despite these advantages, application of deep-sea imagery to characterizing ecosystem services has been limited. To date, investigators have used ROV imagery to characterize the southern California Del Mar methane seep and its megafaunal community (Grupe et al., 2015), observing elevated densities of commercially valuable *Sebastolobus* spp. (thornyheads) at the seep relative to background areas. Other deep-sea studies that utilize imagery often discuss implications for ecosystem services, but do not explicitly aim to characterize these. For example, Chauvet et al. (2019) use deep-sea imagery from the Ocean Networks Canada cabled seafloor observatory to describe interannual densities and size distributions of commercially-fished *Chionoecetes tanneri* (tanner crabs). Tanner crab population dynamics and how they relate to environmental conditions, such as surface blooms that have the potential to influence tanner crab migration patterns, can inform the management of fisheries services. These studies illustrate the utility of image-based assessments, and there is likely an abundance of video and still-frame imagery available from international sea-going expeditions, spanning decades, that could be available for further examination and study, e.g., collected by the academic, government, or philanthropic sectors.

In the summer of 2015, Ocean Exploration Trust (OET) completed an expedition to explore methane seeps and other deep-sea habitats along the southern California continental margin (Levin et al., 2016a). Methane seeps are found in every ocean from shallow to deep water (Judd, 2003) and are still being discovered today (Seabrook et al., 2018; Sen et al., 2019; Vedenin et al., 2020). At these sites, geological processes lead to seepage of methane and sulfur-rich fluids from the seabed (Sibuet and Olu, 1998), which fuel chemoautotrophic microbial communities (Martens et al., 1994; Boetius et al., 2000; Orphan et al., 2002) that act as the base of a food web for distinct biological communities in an otherwise food-limited environment (Levin, 2005; Åström et al., 2018). Many “background” species can also be found at methane seeps (Levin et al., 2016b), aggregating around authigenic carbonates (Treude et al., 2011), snail egg towers (Levin and Dayton, 2009), or other structures that increase habitat heterogeneity. An additional layer of complexity exists along the northeastern Pacific continental margin in the form of an oxygen minimum zone (OMZ), which is a midwater feature of naturally-occurring lower dissolved oxygen concentrations ($<22 \mu\text{mol/kg}$, $<0.5 \text{ ml/l}$). The OMZ can intersect benthic environments to shape local biological communities (Sellanes et al., 2010; Gallo and Levin, 2016; Neira et al., 2013), and resulting ecosystem services,

such as fish catch (Keller et al., 2015). OMZs can also contribute to regulating services through their influence on nitrogen and sulfur cycling (Gilly et al., 2013).

The objective of this paper is to develop a methodology and analyze the resulting data to characterize deep-sea ecosystem services at and around methane seeps within the southern California OMZ using deep-sea images. We adapt biological trait analysis to target ecosystem services and focus specifically on fisheries and climate-regulating services related to carbon (hereafter referred to as “carbon services”). Trait-based approaches help capture organism contributions to ecosystem services by focusing on function rather than taxonomy (e.g., Rees et al., 2012). Commercially-fished species have previously been found at southern California methane seeps (Grupe et al., 2015) and continental margins have been estimated to sequester significant amounts of marine carbon (Muller-Karger et al., 2005). These services are likely mediated, in part, by megafauna. We discuss visual indicators of microbially-driven services, where relevant, but they are likely to be more amenable to other methods. We use examples from three southern California upper slope methane seeps (from north to south): Point Dume (724.5 m), Palos Verdes (505.6 m), and Del Mar (1023.4 m). For two of these sites (Point Dume and Palos Verdes), we provide the first detailed characterization of megafauna. Key questions addressed are: (1) Which megafaunal taxa are present at a given site? (2) What functional traits or behaviors do the community exhibit? (3) How might these traits promote ecosystem services? And (4) How can deep-sea exploration and observing be conducted in a way that facilitates quantification of ecosystem services? We examine the hypothesis that methane seeps, with elevated local (chemosynthetic) primary production, provide more fisheries and carbon services than adjacent non-seep areas by testing for differences among active seep sites, transition areas, and non-seep background areas. Additionally, we investigate how these services relate to depth, dissolved oxygen concentrations, and temperature. We also hypothesize that fisheries and carbon services increase with megafaunal diversity, which has been shown to increase ecological function, such as benthic fluxes of nutrients (Belley and Snelgrove, 2016), that can contribute to ecosystem services.

2. Methods

2.1. Study sites

The southern California continental margin is an active, narrow, steep slope, and is home to an expanding OMZ that sits between

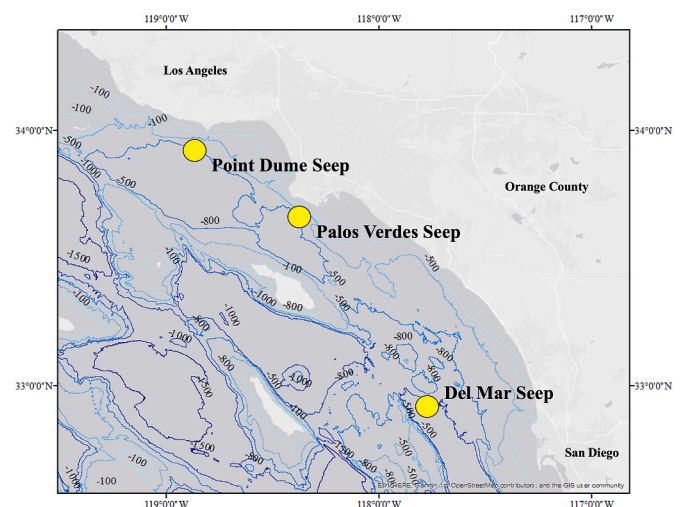


Fig. 1. Locations of the three methane seep study sites in southern California: Point Dume seep, Palos Verdes seep, and Del Mar seep. Bathymetry data from the NOAA National Centers for Environmental Information.

approximately 450–1100 m (Helly and Levin, 2004; Stramma et al., 2010; Bograd et al., 2015). Our three study sites (Fig. 1) were chosen because they showed preliminary signs of both fisheries services (i.e., presence of commercial species) and carbon services (i.e., bacterial mats that are consistent with carbon fixation/net primary production). They also included both “active seep” areas (characterized by visual indicators of seepage such as bacterial mats, clam beds, or bubbling) as well as “background” areas (no visual indicators of seepage). These three sites are used to demonstrate an ecosystem services-based approach to analyzing deep-sea imagery collected by an ROV. The Point Dume (mean depth 725 m) and Palos Verdes (mean depth 506 m) seeps were newly discovered during the expedition NA066 (Levin et al., 2016a). The Point Dume seep lies along a submarine river channel within the core of the OMZ, peppered with carbonate chimneys that have visually evident fluid flow (Levin et al., 2016a). Palos Verdes seep is less than 5 km from shore and characterized by large carbonate rocks covered by megafaunal aggregations (Levin et al., 2016a). Del Mar seep (mean depth 1023 m) lies within a network of strike-slip faults at the lower boundary of the OMZ (Maloney et al., 2015). It was discovered by graduate students at Scripps Institution of Oceanography in 2015 (Maloney et al., 2015) and has since been visited several times.

2.2. ROV dives

Exploration dives were conducted by ROVs *Hercules* and *Argus* aboard the *EV Nautilus* in July and August 2015 as part of the OET southern California borderlands expedition NA066. High-definition video (1080i) was taken continuously during each dive with a maximum ROV speed of 1 knot. Dives ranged between 4 and 18 h duration. The ROV recorded location, depth, temperature, conductivity, sound velocity, and oxygen concentrations. Because OET is focused on ocean exploration and telecommunication, we were not able to extract quantitative data from the dive videos due to changes in ROV altitude, camera zoom, and non-visible laser references (see Section 4.3.). However, the qualitative descriptions based on presence-absence and frequency of occurrence of individuals and species are remarkably useful, especially in deep-sea systems that are rarely visualized and costly to study. Metadata from each dive are summarized in Table 1.

2.3. Video analysis

Videos from each dive were segmented into 5-min clips that were each treated as a “sample” and annotated by hand in Microsoft Excel™ (the full protocol can be found in Appendix A). Information regarding the ROV, surrounding environment (including seep activity), and megafauna encountered (morphotype, location, behavior) was also collected (Table 2; Fig. 2). Seep activity is separated into three categories: active seep sites with visual indicators of active seepage (e.g., dense bacterial mats and clam beds, bubbling), transition areas with visual indicators of sparse or prior seepage (e.g., patchy bacterial mats with less than 50% cover, dead clam beds with broken shells, carbonates without signs of seepage), and non-seep background areas generally associated with soft sediment habitats (Appendix A). For each organism, the microhabitat they were observed either on or above was also noted (e.g., soft sediment, carbonate, bacterial mat, clam bed). For the first

Table 2

Observation type, observation options, and percentage of time the remotely-operated vehicle (ROV) spent doing the activity, at seepage activities or sea-floor microhabitats throughout each dive (accounting for 100% of its time). Observation options are mutually exclusive within each category.

Observation Type	Observation Options	Point Dume (%)	Palos Verdes (%)	Del Mar (%)
ROV activity	Stationary: Inactive	17.5	16.7	17.2
	Stationary: Pan/Focus	8.6	19.4	29.6
	Stationary: Sampling	11.6	12.5	19.1
	Mobile: Search	58.8	43.0	17.9
Seep activity	Mobile: Transect	3.5	8.4	16.2
	Active Site	37.2	24.9	59.5
	Transition	24.5	1.4	0
	Off-site	37.0	66.2	40.5
	Water column	1.3	7.5	0
Microhabitat	Soft sediment (background)	53.1	76.6	57.2
	Carbonate	0	6.5	16.4
	Bacterial mat: full	5.7	0	17.3
	Bacterial mat: patchy	41.2	4.2	0
	Clam bed: full	0	0	7.2
	Clam bed: scattered	0	12.7	1.9

minute of each video, animals were counted. For the remaining 4 min, a list of morphotypes was generated. Here, we use the expression ‘morphotype’ to represent all our taxon identifications because they are solely based upon morphology without genetic verification. Each morphotype was identified to the lowest possible taxonomic level (note that, in some cases, our visual data were sufficient to putatively ally a morphotype to a species, though in many cases this was impractical).

2.4. Trait analysis

Observable traits that support fisheries or carbon services were chosen (Table 3), and each morphotype was assigned a modality for selected traits based on a literature review (Appendix B). Fisheries ‘ecosystem services’ traits are related to whether the species is commercially-valuable and whether a commercially-valuable species interacts with it as predator or prey. Carbon traits are related to carbon cycling. For example, feeding mode can contribute to carbon fixation, i.e., primary production by autotrophic organisms is a direct carbon dioxide removal pathway. Carbon transport, which can play a significant role in the food-limited deep ocean (Shen et al., 2020), can be attributed to biological traits such as mobility and whether the organism is a diel vertical migrator. Body size and calcification can contribute to carbon storage, i.e., as biomass. If an organism was not identified to species level or if there was no existing information on the species (e.g., what it eats), then characteristics from its higher-level taxonomic group or a closely related species were used to assign trait modalities.

2.5. Ecosystem service scores

An “ecosystem services score” reflects the relative contribution of a taxa, site, or habitat to a given ecosystem service, i.e., fisheries scores for

Table 1

Remotely-operated vehicle *Hercules* dive location and environmental data from Ocean Exploration Trust expedition NA066 off of the southern California borderlands.

Dive #	Date (2015)	Site	Latitude (°N)	Longitude (°W)	Mean Water Depth (m)	Mean Temperature (°C)	Mean Dissolved Oxygen Concentration (µm/kg)	Hours of dive analyzed
H1456	9 August	Point Dume	33.943	118.841	724.5	5.55	2.76	16.6
H1452	4–5 August	Palos Verdes	33.684	118.366	505.6	7.29	20.24	20.8
H1444	27–28 July	West Del Mar	32.903	117.782	1023.4	4.12	15.54	7.1

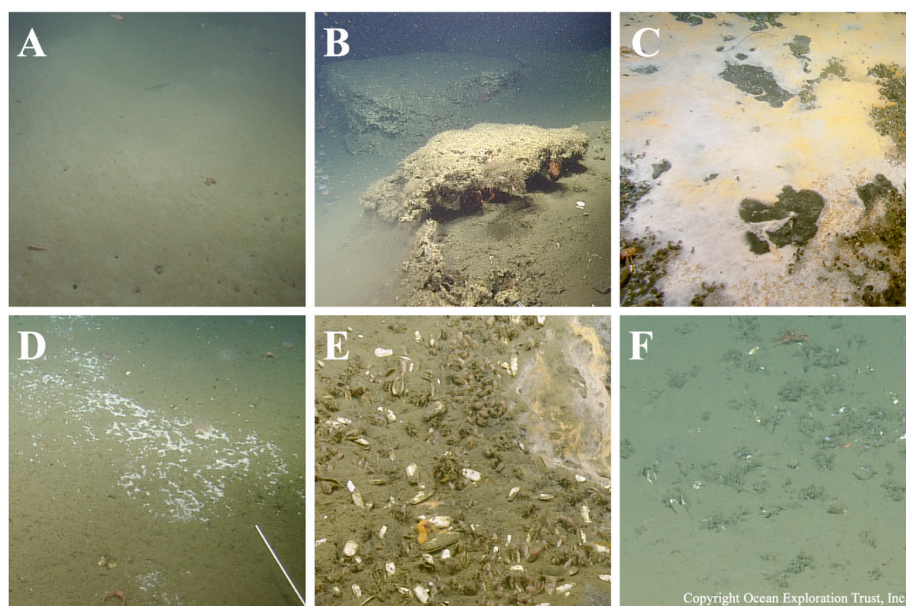


Fig. 2. Examples of seafloor microhabitats observed during the dives: (A) soft sediment (background), (B) carbonate mounds near Palos Verdes seep, (C) full bacterial mat near Point Dume seep, (D) patchy bacterial mat near Del Mar seep, (E) full clam bed near Point Dume seep, and (F) scattered clam bed near Del Mar seep.

Table 3

Traits and their modalities that contribute to fisheries and climate-regulating services related to carbon. Higher points indicate modalities that contribute more to the respective ecosystem service.

Ecosystem service	Trait	Modality (Points)	Reference
Fisheries – characteristic	Commercially valuable	Yes (1) No (0)	Koslow et al. (2000)
Fisheries – trophic support	Predator	Active (2)	Yang and Somero (1993);
	Prey	Passive (1)	Jacobson and Vetter, 1996; Dufault et al. (2009); Hattori et al. (2009)
		No (0)	
		Yes (1)	
		No (0)	
Carbon – fixation and cycling	Feeding mode	Autotrophic (5)	Doering et al. (1986); Reinthaler et al. (2010);
		Predator (4)	Wilmers et al. (2012);
		Filter feeder (3)	Atwood et al. (2015)
		Deposit feeder (2)	
		Scavenger (1)	
Carbon – transport	Mobility	High (3)	
		Medium (2)	
		Low (1)	
		None (0)	
Carbon – transport	Bioturbation	High (3)	Vardaro et al. (2009);
		Medium (2)	Martinetto et al. (2016);
		Low (1)	Hou et al. (2017); Gogina et al. (2020)
		None (0)	
Carbon – transport	Diel vertical migration	Yes (1)	Hidaka et al. (2001);
		No (0)	Hudson, 2012; Klevjer et al. (2016)
Carbon – storage	Calcification	Yes (1)	
		No (0)	
Carbon – storage	Body size	>10 cm (3)	
		3–10 cm (2)	
		<3 cm (1)	

fisheries services or carbon scores for carbon services. For each trait modality, we used fuzzy coding (Chevenet et al., 1994) to assign points that capture the extent to which the modality contributes to each service (Table 3). For example, a commercially-valuable species contributes one point (and otherwise zero) to the fisheries score of its morphotype. Based

on trait analysis, each morphotype was assigned a fisheries and carbon score, which is the sum of trait modality points. The maximum fisheries score a morphotype could have was four and the minimum score was zero. For carbon services, the maximum score was sixteen and the minimum score was two. Then, each video (both within the 1-min subset and the whole 5-min clip) was assigned a fisheries and carbon score, which is the sum of morphotype scores for each morphotype for which at least one individual occurred. These ecosystem services scores were standardized by the number of morphotypes found in each video clip. We were not able to calculate faunal densities from the videos due to unknown and variable camera field-of-view (see Section 4.3), so we use presence-absence data.

2.6. Statistical analysis

All statistical analyses were done in R (version 3.5.2.; R Core Team 2018), using the base package unless otherwise noted. Data were tested for normality using a Shapiro-Wilk test (Thode, 2002 as cited by Ghasemi and Zahediasl, 2012). Because data did not meet normality conditions, non-parametric tests were used. An ANOSIM (package ‘vegan’; Oksanen et al., 2022) was used to test for differences among the biological communities at each site. The Kruskal-Wallis test-by-ranks was used to test for significant differences in ecosystem services scores among sites, seep activity, and microhabitats (Ostertagová et al., 2014), and a *post hoc* Dunn test with a Bonferroni correction (package ‘dunn.test’; Dinno, 2017) was used to identify which groups were different. Correlations among ecosystem services scores and environmental variables were tested using Spearman’s rank coefficient (Zar, 2005). We also used linear mixed models (package ‘lme4’; Bates et al., 2015) that were compared using Akaike’s information criterion (AIC) weights (package ‘AICcmodavg’; Mazerolle, 2020) to explore which environmental parameters may be useful explanatory variables for ecosystem services scores. Within the models, site and habitat were defined as random effects while either depth, temperature, or oxygen concentration were fixed. All ecosystem services score analyses were done for the first-minute subset, as well as for the whole video clip, in efforts to decrease temporal dependence among samples. We tested whether the first minute of each 5-min video was representative of the whole video with a chi-squared test.

3. Results

We present here results from this methodology, including initial biological characterizations of several seep ecosystems. These characterizations are critical in the deep ocean, where there have been fewer opportunities for visualization in comparison to coastal and shallow-water systems. Approximately 20,000 individuals from 100 morphotypes were identified in 44.5 h of video. The morphotypes grouped into seven functional groups based largely upon feeding attributes: scavengers (approximately 290 individuals), benthic filter feeders & microcarnivores (3570 individuals), benthic deposit feeders & bacterivores (3590 individuals), demersal predators (9240 individuals), pelagic predators (180 individuals), gelatinous plankton (3080 individuals), and symbiont-bearing taxa (generally unable to count individuals, e.g., colonial species such as foliicolinids, species that burrow in the sediment such as bivalves) (Table 4; Fig. 3). Demersal predators had the most morphotypes with 37, most of which were fish species (Fig. 4A, Fig. 4B). Both pelagic predators and symbiont-bearing taxa had only three morphotypes observed.

The most frequently occurring morphotypes (occurrence defined here as at least one individual of the morphotype was present and does not necessarily reflect how many individuals were present at a given time; Fig. 4C) among all sites were *Poralia rufescens* (jellyfish; 12.5%), *Sebastolobus altivelis* (shortspine thornyhead; 9.4%), *Voragonema pedunculata* (hydrozoan; 7.8%), *Liponema anemones* (6.9%), and *Nezumia liolepis* (smooth grenadier; 5.8%) (Appendix C). There was a significant difference among the biological communities at our sites ($R = 0.356$, $p < 0.01$). Among sites, Palos Verdes had the highest total number of morphotypes (79), followed by Del Mar (38), and lastly Point Dume (31). Palos Verdes also had the highest number of morphotypes unique to the site (47) whereas Del Mar and Point Dume had fifteen and six unique morphotypes, respectively. The first-minute subset was not representative of the whole clip relative to fisheries ($X^2 = 47.16$, $df = 1$, $p < 0.01$) and carbon scores ($X^2 = 80.40$, $df = 1$, $p < 0.01$), so results discussed are for the whole 5-min clip (scores for the 1-min subset are still shown in Table 5).

3.1. Point Dume (~698–757 m)

The Point Dume dive (#H1456) spent approximately 37% of the time at the active seep site, 25% in transition areas, and 37% in background areas (Table 2). This site had the lowest overlying oxygen concentrations with a mean of $2.76 \mu\text{m O}_2/\text{kg}$ (Table 1). During this dive, the most frequently occurring morphotypes were *Poralia rufescens* (18.5%), *Liponema anemones* (14.6%), galatheid crabs (11.7%), *Sebastolobus altivelis* (8.2%), and *Nezumia liolepis* (8.0%) (Appendix C). These five

Table 4
Functional groups used, morphotypes included in them, and average fisheries and carbon score assigned to the morphotypes in the functional group.

Functional Group	Morphotypes included	Average fisheries score	Average carbon score
Scavengers	Hagfish, shrimp, amphipods	2.00	10.53
Benthic filter feeders & microcarnivores	Sea anemones, sea pens, corals, sponges	1.63	5.71
Benthic deposit feeders & bacterivores	Sea cucumbers, urchins, snails, brittle stars	1.32	8.05
Demersal predators	Demersal and benthic fish, crabs, sea stars	3.09	11.40
Pelagic predators	Midwater fish, squid, chaetognaths	2.91	10.85
Gelatinous plankton	Jellies, ctenophores, siphonophores	1.01	7.26
Symbiont-bearing taxa	Vesicomyid clams, lucinid clams, foliicolinids	0.93	10.60

morphotypes comprised over half of the megafauna occurrences during this dive. Other morphotypes were relatively rare; 22.5% of morphotypes only occurred once. Number of morphotypes was significantly negatively correlated with water depth ($\rho = -0.27$, $p < 0.01$), which ranged from 698 m to 755 m, and positively correlated with oxygen ($\rho = 0.21$, $p < 0.01$), ranging from $2.23 \mu\text{m}/\text{kg}$ to $4.55 \mu\text{m}/\text{kg}$. Depth and oxygen negatively covaried with each other ($\rho = -0.18$, $p = 0.01$). There were no significant correlations ($p > 0.05$) between the number of functional groups in a video with depth, oxygen, or temperature.

Background areas had significantly higher fisheries scores than both active and transition areas by 20% and 16.5%, respectively ($X^2 = 41.00$, $df = 2$, $p < 0.01$; Table 5; Fig. 5C). Soft sediment substrates, which are associated with background areas, also had significantly higher fisheries scores than bacterial mats by 16.3% ($X^2 = 41.62$, $df = 1$, $p < 0.01$). With respect to carbon, the same pattern was observed among seep activity: background areas had significantly higher carbon scores than active and transition areas by 17.4% and 17.6%, respectively ($X^2 = 50.74$, $df = 2$, $p < 0.01$; Table 5; Fig. 5D). Oxygen negatively covaried with depth ($\rho = -0.18$, $p = 0.01$). Fisheries ($\rho = 0.27$, $p < 0.01$) and carbon scores ($\rho = 0.38$, $p < 0.01$) were also significantly positively correlated with depth. Fisheries scores were significantly positively correlated with temperature at this site ($\rho = 0.17$, $p = 0.02$).

3.2. Palos Verdes (~278–799 m)

During the Palos Verdes dive (#H1452), the ROV spent approximately 25% of its time at the active seep site, 1% in transition areas, and 66% in background areas (Table 2). The most frequently occurring morphotypes were *Poralia rufescens* (10.8%), *Sebastolobus altivelis* (8.9%), *Voragonema pedunculata* (6.4%), *Nezumia liolepis* (5.4%), and a diversity of midwater fish (4.6%) (Appendix C). Midwater fish were grouped together because they were difficult to identify through these dive videos and seemed to function in similar ways relative to fisheries (through trophic interactions (Young et al., 2015; Choy et al., 2016)) and carbon services (through their transport and storage of large amounts of biomass (Davison et al., 2013; Trueman et al., 2014; Davison et al., 2015)). The percentage of singletons, i.e., morphotypes that were observed exactly once, was 13.9%, which was the lowest of all sites. Oxygen ($\rho = -0.97$, $p < 0.01$) and temperature ($\rho = -0.96$, $p < 0.01$) significantly covaried with depth. Number of morphotypes was significantly positively correlated with depth ($\rho = 0.60$, $p < 0.01$) between 278 m and 799 m, and negatively correlated with oxygen ($\rho = -0.59$, $p < 0.01$), which ranged between $2.12 \mu\text{m}/\text{kg}$ to $54.76 \mu\text{m}/\text{kg}$, and temperature ($\rho = -0.58$, $p < 0.01$), ranging from 5.35°C to 9.48°C . The number of functional groups exhibited the same patterns with depth, oxygen, and temperature.

Palos Verdes transition areas, which included carbonate mounds, provided significantly higher fisheries scores than both active and background areas by 12.3% and 6.3%, respectively ($X^2 = 8.29$, $df = 2$, $p = 0.02$; Table 5; Fig. 5C). There were no significant differences in fisheries or carbon scores among the seepage microhabitats. Neither fisheries nor carbon scores were significantly correlated with depth, oxygen, or temperature at this site.

3.3. Del Mar (~987–1030 m)

The Del Mar dive (#H1444) spent approximately 60% of the time at the active seep site and 40% in background areas (transition areas were not evident during this dive; Table 2). At the Del Mar seep, the most frequently occurring morphotypes were *Voragonema pedunculata* (30.0%), *Sebastolobus altivelis* (15.5%), *Eusergestes similis* (shrimp; 6.7%), a diversity of midwater fish (4.5%), *Anoplopoma fimbria* (sablefish; 4.4%) and lithodid crabs (4.4%) (Appendix C). Neither the number of morphotypes nor functional groups were significantly correlated with depth, temperature, or oxygen.

There were no significant differences in fisheries nor carbon scores

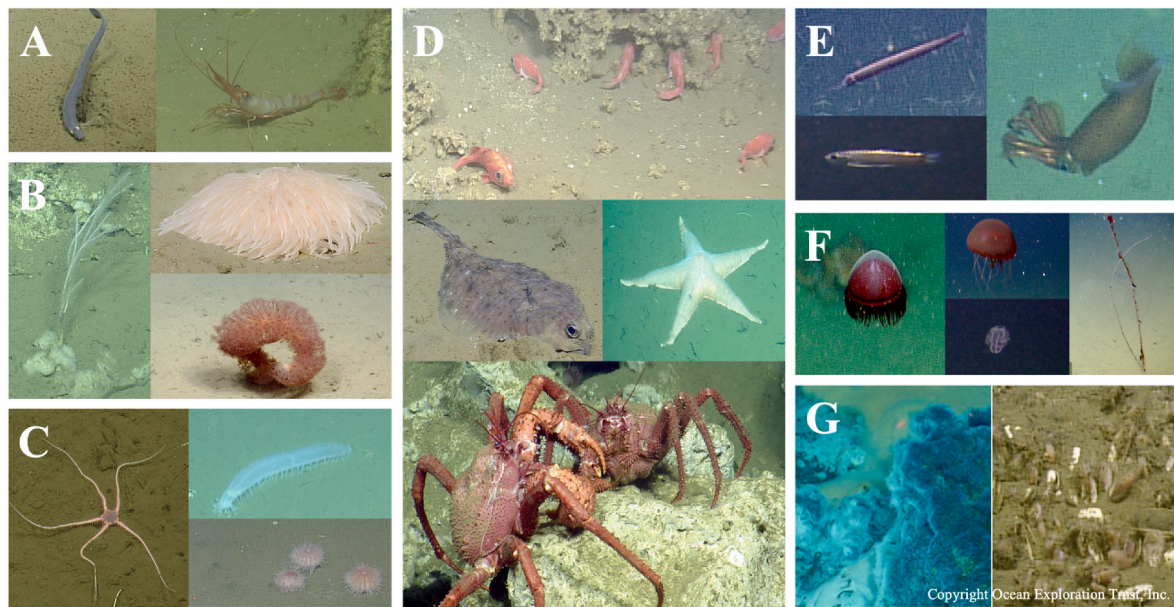


Fig. 3. Example morphotypes of each functional group: (A) scavengers – *Eptatretus* spp., shrimp (e.g., Sergestid sp); (B) benthic filter feeders & microcarnivores – *Cladorhizidae*, *Liponema* sea anemones, sea pen; (C) benthic deposit feeders – brittle star (e.g., *Asteronyx* sp.), sea cucumber, *Strongylocentrotus fragilis*; (D) demersal predators – groundfish (*Sebastes* spp., *Microstomus pacificus*), *Hippasteri* sp., Lithodid sp.; (E) pelagic predators – midwater fish, *Gonatus* sp.; (F) gelatinous plankton – jellies (e.g., *Voronema pedunculata*, *Poralia rufescens*), ctenophores, siphonophores; and (G) symbiont-bearing taxa – Folliculinidae, vesicomyid clams.

among areas with different seep activity or microhabitats at Del Mar seep. However, fisheries scores were significantly negatively correlated with oxygen ($\rho = -0.40$, $p < 0.01$) between 14.85 $\mu\text{m/kg}$ to 15.56 $\mu\text{m/kg}$.

3.4. Across all three sites

Overall, fisheries and carbon scores were significantly positively correlated with each other ($\rho = 0.86$, $p < 0.01$). The number of morphotypes was also positively correlated with fisheries ($\rho = 0.19$, $p < 0.01$) and carbon scores ($\rho = 0.18$, $p < 0.01$). However, neither fisheries nor carbon scores were correlated with the number of functional groups present nor the number of morphotypes present within any one functional group. For fisheries scores, the null linear mixed model (site and habitat as random effects with no fixed effects) performed the best, carrying 34% of the cumulative model weight (evidence ratio = 1.56). For carbon scores, the best performing model (site and habitat as random effects with depth as a fixed effect) carried 25% of the cumulative model weight (evidence ratio = 1.21).

With respect to fisheries, Del Mar had significantly higher scores than Palos Verdes by 12% ($X^2 = 8.83$, $df = 2$, $p = 0.01$; Fig. 5A). Active seeps had significantly lower fisheries scores than background areas by 6% ($X^2 = 14.02$, $df = 3$, $p = 0.01$). Del Mar also had significantly higher carbon scores than both Point Dume and Palos Verdes by 13.4% and 14%, respectively ($X^2 = 15.03$, $df = 2$, $p < 0.01$; Fig. 5B). Across all three sites, there were no significant differences in carbon scores among microhabitats (i.e., soft sediment, bacterial mat, clam bed, carbonate).

Among active seeps, Del Mar had significantly higher fisheries ($X^2 = 7.13$, $df = 2$, $p = 0.03$; Fig. 5C) and carbon scores ($X^2 = 12.35$, $df = 2$, $p < 0.01$; Fig. 5D) than Point Dume by 15% and 20%, respectively. Palos Verdes transitions areas had higher fisheries scores than Point Dume transition areas by 8% ($X^2 = 4.02$, $df = 1$, $p = 0.04$; Fig. 5C), but significantly lower fisheries scores than Point Dume and Del Mar among background areas by 14.8% and 17.5%, respectively ($X^2 = 27.83$, $df = 2$, $p < 0.01$; Fig. 5C). This was also the case for carbon scores ($X^2 = 33.46$, $df = 2$, $p < 0.01$; Fig. 5D).

4. Discussion

4.1. Describing the biological community

Image and statistical analyses presented herein and elsewhere (Dunlop et al., 2015; Amon et al., 2016; Cooper et al., 2019; Smith et al., 2019) underscore the value of using video for both quantitative and qualitative data. Specifically, our results suggest that the number of megafaunal morphotypes increases with oxygenation among sites: The Palos Verdes dive had the highest number of morphotypes as well as the highest mean overlying oxygen concentration of 20.24 $\mu\text{m/kg}$ (Table 1). Morphotypes represent diversity, but do not always capture richness nor evenness so these indices are not necessarily correlated. Oxygen has been shown to influence biodiversity of invertebrates and fish on Pacific continental margins with a strong threshold effect as diversity can begin decreasing at approximately 22 $\mu\text{m/kg}$ (Sperling et al., 2016; Gallo et al., 2020). Whereas this elevated oxygen could be an artefact of the larger distance and wider depth range (~278–799 m) covered by the dive. Nevertheless, the number of morphotypes observed in each video during the Palos Verdes dive was negatively correlated with oxygen, with the highest number of morphotypes (>20) found in videos with oxygen levels ranging from 2.18 to 2.26 $\mu\text{m/kg}$. Number of morphotypes was also positively correlated with depth. Because oxygen and depth covaried, it is not possible to separate their effects on number of morphotypes during the Palos Verdes dive. However, as described in previous studies, hypoxic conditions can exert selective pressure that increases specialization of taxa for increased diversity (Rogers, 2000). Gallo and Levin (2016), for example, found diverse assemblages of fish in the Pacific, Atlantic, and Indian Oceans with physiological, morphological, and behavioral adaptations for life in OMZs. Additionally, increased biodiversity with water depth, with maxima from 1500 to 3000 m, has been documented in many taxa globally (Rex, 1981), such as demersal fish in the northeast Atlantic (Mindel et al., 2016) and cnidarians, echinoderms, and gastropods in the Caribbean (Hernández-Ávila et al., 2018).

In contrast to Palos Verdes, the entire Point Dume dive occurred within the core of the California OMZ with mean oxygen levels of 2.76 $\mu\text{m/kg}$ (sea surface oxygen concentrations are upwards of 250 $\mu\text{m/kg}$).

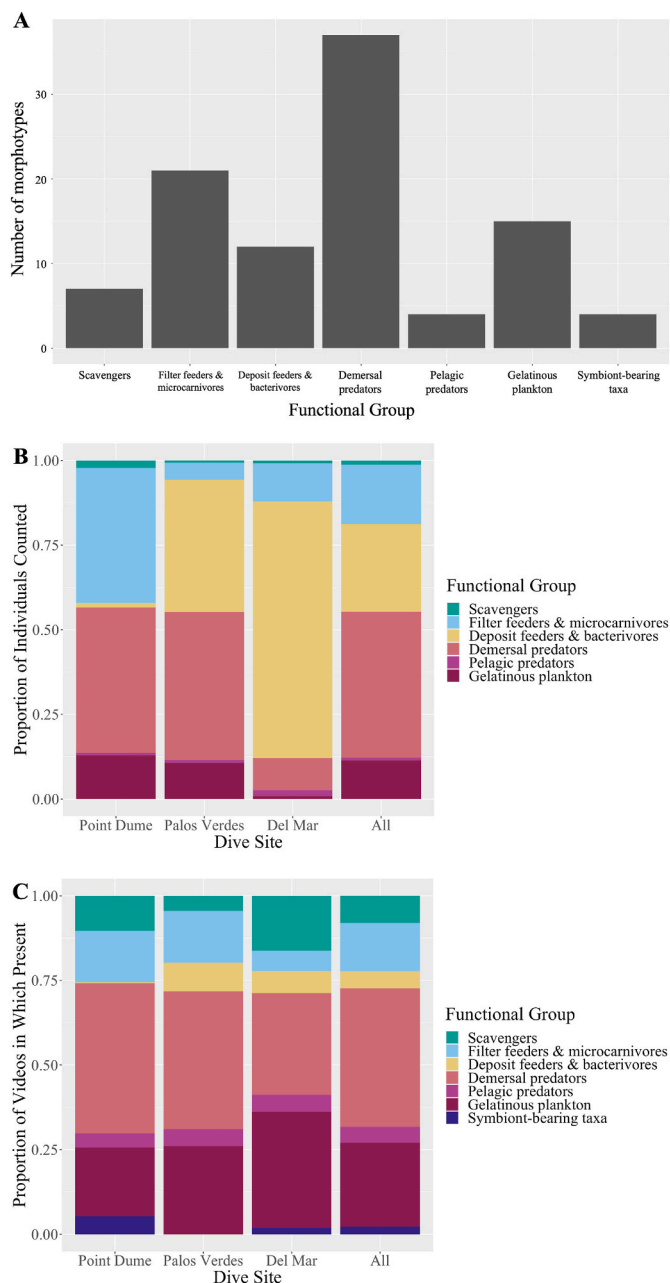


Fig. 4. (A) The number of morphotypes included in each functional group, (B) the proportion of individuals counted in each functional group across all videos, and (C) the proportion of videos in which each functional group had at least one individual occur at three methane seeps off southern California within the 1-min subset.

During this ROV dive, the number of morphotypes was significantly positively correlated with oxygen and negatively with depth. Because the Point Dume seep field resides in suboxic water, further decreases in dissolved oxygen may surpass physiological tolerances of some taxa (Seibel, 2011; Wishner et al., 2018). This could result in the loss of available habitat and shifting faunal distribution due to deoxygenation associated with climate change (see Cheung et al., 2009; Deutsch et al., 2015). As oxygen deoxygenation continues to expand and intensify the OMZ (Bograd et al., 2008; Stramma and Schmidtke, 2019), animals that cannot tolerate low oxygen conditions will lose available habitat, while those that are more tolerant will distribute accordingly (Netburn and Anthony Koslow, 2015). The decrease in number of morphotypes with depth observed at Point Dume may be driven by the significant negative

Table 5

Mean and standard deviation of ecosystem services scores, standardized by the number of morphotypes, for each site. Transition areas were not delimited for Del Mar. Among sites (horizontal rows excluding the Overall column), scores with different superscripts (a, b) denote a significant difference ($p < 0.05$). Among seep activity within a site (shaded vertical columns), scores with different superscripts (x, y) denote a significant difference ($p < 0.05$). For example, Palos Verdes and Del Mar fisheries scores are significantly different from each other, but neither are significantly different from Point Dume fisheries scores; and there were no significant differences in carbon scores among seep activity within the Palos Verdes site.

Service	Point Dume	Palos Verdes	Del Mar	Overall
Fisheries score	2.71 ± 0.86 ^{ab}	2.61 ± 0.82 ^a	3.09 ± 1.38 ^b	2.72 ± 0.95
Fisheries score – 1-min	2.22 ± 0.59	2.42 ± 0.77	2.30 ± 1.30	2.32 ± 0.79
Fisheries score – active	2.38 ± 0.78 ^{a,x}	2.35 ± 0.76 ^{ab,x}	2.98 ± 1.45 ^b	2.58 ± 1.09 ^x
Fisheries score – transition	2.52 ± 0.45 ^{a,x}	2.84 ± 0.66 ^{b,y}	NA	2.52 ± 0.45 ^{xy}
Fisheries score – background	3.18 ± 0.97 ^{a,y}	2.59 ± 0.86 ^{b,x}	3.29 ± 1.23 ^a	2.82 ± 0.98 ^y
Carbon score	11.69 ± 3.09 ^a	11.59 ± 3.20 ^a	13.96 ± 5.47 ^b	11.99 ± 3.69
Carbon score – 1-min	9.47 ± 1.71	10.53 ± 2.30	10.56 ± 3.51	10.08 ± 2.33
Carbon score – active	10.61 ± 2.67 ^{a,x}	11.63 ± 2.66 ^{ab}	14.03 ± 5.93 ^b	11.94 ± 4.34
Carbon score – transition	10.58 ± 1.54 ^x	11.75 ± 2.55	NA	10.58 ± 1.54
Carbon score – background	13.57 ± 3.42 ^{a,y}	11.53 ± 3.45 ^b	13.84 ± 4.68 ^a	12.34 ± 3.73

correlation between oxygen and depth. Notably, the correlation between number of morphotypes and depth here are opposite to that observed during the Palos Verdes dive, emphasizing the role of dissolved oxygen in the observed ecological patterns and the extent of ecosystem services.

4.2. Traits that support fisheries and carbon services

All three sites showed evidence of bacterial mats (Fig. 6), likely indicative of microbial sulfide oxidation resulting from methane oxidation coupled with sulfate reduction in the sediment (Hoehler et al., 1994). Sulfide oxidation by microbes can lower the concentration of sulfide in the overlying water (Lavik et al., 2009), which could facilitate occurrence of morphotypes that are sulfide intolerant and contribute to ecosystem services. Biotic and abiotic sulfide oxidation, however, also consume oxygen, and active seep areas consume two orders of magnitude more oxygen than non-seep areas (Boetius and Wenzhöfer, 2013). However, seep influence on sediment macrofauna communities, on which megafauna could be feeding, seems to be limited (Levin et al., 2000; Demopoulos et al., 2018). Only 25% of morphotypes occurred resting directly on or hovering above the bacterial mat, most frequently *Liponema* anemones (13.4%), *Poralia rufescens* (11.6%), and galatheid crabs (10.2%). One morphotype of polychaete was found exclusively on bacterial mats with two occurrences (possibly dorvilleid worms that are often found at seeps offshore the western U.S.; Levin et al., 2003; Levin, 2005). Our results suggest that the active seep areas of Point Dume have lower fisheries and carbon scores than transition and background areas (Table 5). Intense methane seepage and sulfidic conditions may act synergistically with exceptionally low oxygen to reduce the occurrence of functional traits that generate ecosystem services. The limited utility of our linear mixed model results may provide additional evidence of these context-dependent, synergistic effects of the environment on ecosystem services scores. While our study focused on ecosystem services mediated by megafauna, it should be noted that the bacterial mats at Point Dume were visually the most expansive of the three sites. The

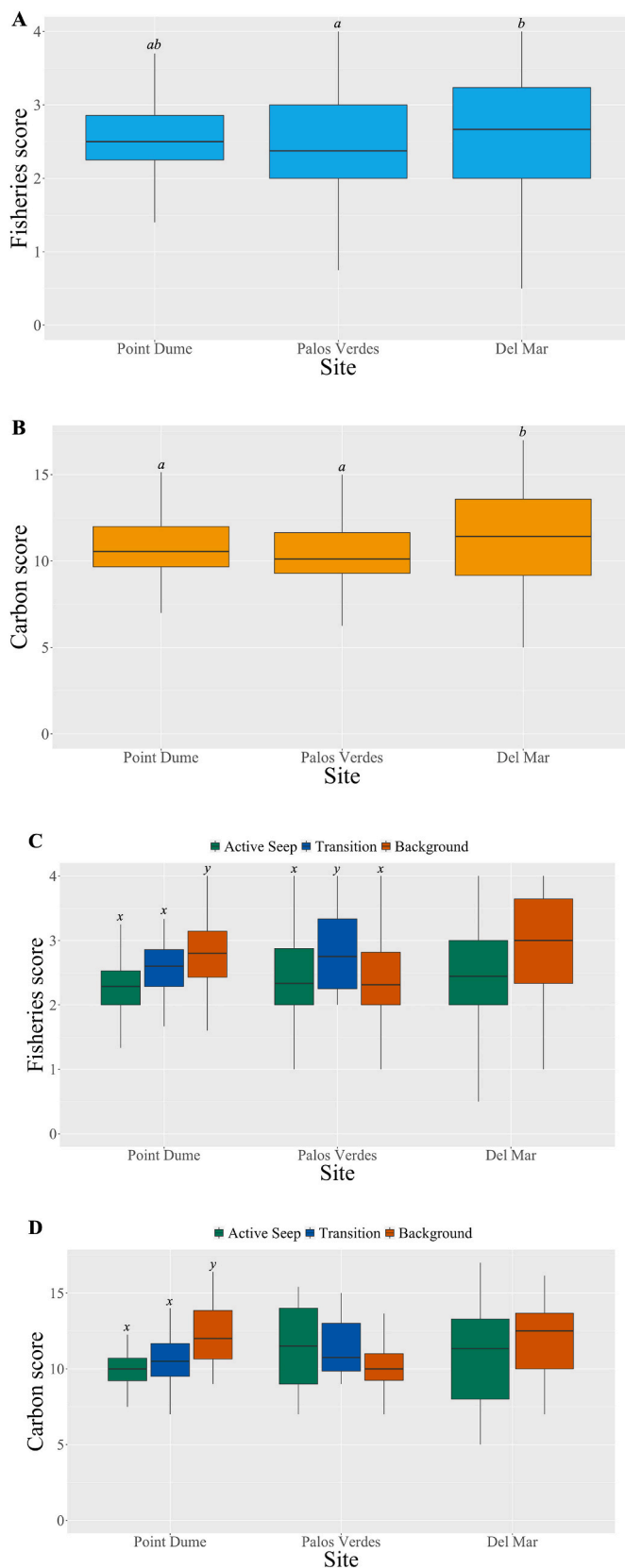


Fig. 5. Quartiles of ecosystem services scores for (A) fisheries among sites; (B) carbon among sites; (C) fisheries among seep activity for each site; and (D) carbon among seep activity for each site. Significant differences ($p < 0.05$) are denoted among sites with a, b (A–B) and among seep activity within sites with x, y (C–D); additional comparisons are discussed in Section 3.4.

bacterial mats represent elevated levels of local primary chemosynthetic production, which likely comprises a significant process in the carbon cycle (Rothschild and Mancinelli, 1990).

Continental margins contribute disproportionately to global carbon and nutrient cycling (Elrod et al., 2004; Little et al., 2016); although they comprise approximately 20% of global ocean surface area (Jahnke, 2010), continental margins have been estimated to sequester more than 40% of carbon in the ocean (Muller-Karger et al., 2005). Additionally, the coupling of anaerobic oxidation of methane and sulfate reduction by seep microbes serves as a carbon sink by creating elevated concentrations of bicarbonate as a byproduct that can precipitate into carbonate rocks (Naehr et al., 2007; Marlow et al., 2014), which were observed throughout the dive sites and represent an additional carbon service although not one mediated by megafauna. We did not find significant correlations between oxygen, which ranged from 2.01 to 4.73 $\mu\text{m/kg}$, and ecosystem services scores at Point Dume. However, scores were significantly correlated with water depth which negatively covaried with oxygen. Unfortunately, separating these effects is not possible with the extant data. In the case of Del Mar seep, Grupe et al. (2015) found higher densities of commercially-valuable species at the active seep than in adjacent, background areas. Our results here contrast because we found no significant differences in ecosystem services scores among the active seep and background area during the Del Mar dive. This suggests that the Del Mar area, in general, may contribute more to fisheries and carbon services than our other study sites.

Palos Verdes transition areas provided significantly higher fisheries services than active and background areas (Table 5). As mentioned before, this is likely driven by the large aggregations of fish found on carbonate rocks in transition areas (Fig. 6). Southern California has four commercial deep-sea fisheries: shortspine thornyhead (*Sebastolobus altivelis*), longspine thornyhead (*Sebastolobus alascanus*), sablefish (*Anoplopoma fimbria*), and Dover sole (*Microstomus pacificus*) (Keller et al., 2015). Several of these species have previously been found on resting on and/or hovering above methane seeps (Grupe et al., 2015), but it is unclear how the methane seeps are utilized. Hypotheses include feeding in localized, high-productivity areas (Seabrook et al., 2019); breeding and laying eggs (Treude et al., 2011); avoiding predators (Tobler et al., 2016); or removing parasites (Tobler et al., 2007). These species also interact with seep environments through bioturbation (Yahel et al., 2008) and transporting chemosynthetic production to adjacent environments (Seabrook et al., 2019). While the utility of these ecosystem services scores could be improved with faunal densities, they provide preliminary insight about what types of microhabitats and which environmental variables may be important to specific services at specific sites. For example, methane seeps have been recognized as essential fish habitat (Pacific Fishery Management Council, 2019), which are all habitats necessary for fish feeding, growth, and reproduction.

One drawback to using deep-sea imagery for trait-based ecosystem services assessment is that it does not capture processes that happen below the sediment surface or on microscopic scales. The traits in Table 3 are not exhaustive of characteristics that can contribute to fisheries or carbon services, but they were ascertainable from our dive videos. While deep-sea imagery may not be able to confirm regulating services, like metabolomics or metatranscriptomics could (e.g., Dong et al., 2019; Lan et al., 2019), it does provide insight on animal behavior that can support ecosystem services. For example, midwater fish (e.g., myctophids, bristlemouths, barbeled dragonfish) would often be seen near the seafloor and sometimes swimming into it (Fig. 6). This could potentially represent an important benthic-pelagic interaction that contributes to carbon export.

4.3. Recommendations for future studies of ecosystem services based on images

There are several limitations of the video data used in this study that

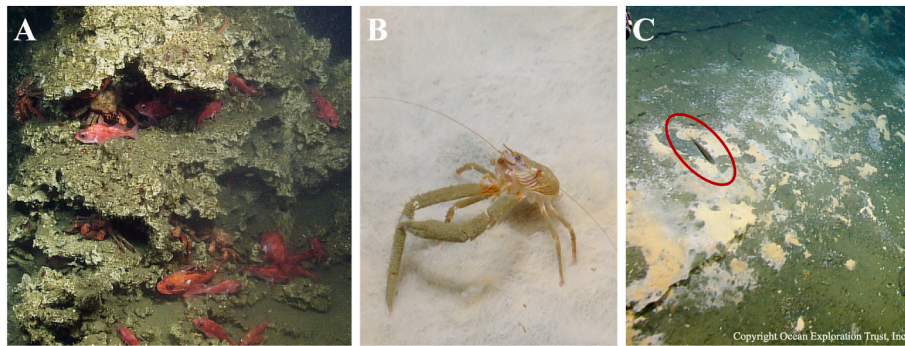


Fig. 6. Examples of microhabitats and traits that support ecosystem services: (A) commercially-valuable *Sebastes* and *Sebastolobus* spp. aggregating on carbonate rocks, (B) Galatheid crab feeding on bacterial mat or associated invertebrates, and (C) midwater fish observed at an active seep.

can be addressed in future studies. First, because of the aforementioned changes in attitude and altitude of the ROV, we were unable to calculate spatial area covered by the ROV, and therefore could not conduct quantitative video transects to determine faunal densities. Ideally, science submersibles would have a standalone imaging system with fixed focal length cameras and orientation to better allow for quantitative image analysis, a technique that has been used in previous studies (e.g., Podowski et al., 2010). In order to achieve this, standards regarding how to collect pictures and videos from deep-sea sampling instruments could be useful (e.g., Levin et al., 2019). The resulting data from transects with consistent ROV altitude, camera zoom, speed, and a laser for scale can then be used to calculate faunal densities and other diversity metrics (e.g., Amon et al., 2016; Simon-Lledó et al., 2019). A quantitative transect would also allow for comparison among locations and time periods (e.g., Rosen and Lauermann, 2016).

Additionally, faunal identification from video can be difficult, even for experts. We use morphotypes and functional groups as a first-order estimation of the species present. As imaging technology continues to advance, the resolution of pictures and videos becomes increasingly helpful for post-analysis (Dumke et al., 2018), such as the creation of three-dimensional reconstructions (e.g., Bodenmann et al., 2017). Imagery should be analyzed consistently, which may mean cross-referencing protocols and morphotype atlases if more than one person is conducting the analysis. Human bias is inherent to current image analysis but can be minimized with extensive training (Matabos et al., 2017). As more deep-sea imagery is analyzed and libraries are produced, there are possibilities to incorporate machine learning algorithms in collaboration with computer science and programming (Qin et al., 2015).

The high cost of deep-sea ROV operations can be prohibitive, so there is some responsibility to be as cost-effective as possible. Starting with bathymetry maps and information from other sonar systems (e.g., multibeam, split-beam) not only facilitate safety for the ship and science crews, but also help identify specific dive targets to ensure effective use of ship time (Raineault et al., 2012). Environmental parameters should be measured in association with imagery to help establish baselines in addition to explaining differences and diversity in biological communities (Levin, 2005). For example, porewater chemistry is a fundamental parameter that influences the sediment community (Gieskes et al., 2011), which can contribute to fisheries services (i.e., as prey of commercial species) and carbon services (i.e., as bioturbators).

One inherent limitation of an image-based approach is that visual indicators are required. Processes that happen on microscopic scales and below the sediment surface are not captured with images unless there is some indicator visible on camera, e.g., bacterial mats. As more deep-ocean data and knowledge are collected about both physical and ecological processes, more can be inferred from visual indicators and this approach can be refined. For example, known prey of commercially-valuable species were all given the same points but, as we learn more

about trophic support and food web dynamics, prey can be assigned points differentially based upon the proportion of diet they comprise.

4.4. Environmental management implications

The approach developed in this study can support environmental decision-making, such as in the designation of spatial protections, consideration of ecosystem service tradeoffs, and understanding the context-dependent roles of methane seeps. This analysis can identify areas of potentially high ecosystem services provision, such as the Del Mar seep that had relatively high fisheries and carbon scores, which may be important for designating essential fish habitat or marine-protected areas (Lindegren et al., 2018). Even qualitative data have significant value for management of data-poor, deep-sea habitats. They can help establish new species (Ford et al., 2020), vulnerable marine ecosystems and significant adverse impacts (Baco et al., 2020), methane sources (e.g., Point Dume seeps with active bubbling) and sinks (e.g., non-active Palos Verdes seeps with authigenic carbonates), or methane hydrates that are of potential interest to the energy industry. As the climate system continues to be perturbed by human activity, carbon services are of utmost importance, especially those associated with deep-ocean habitats that act as long-term storage of carbon (Hilmi et al., 2021). Qualitative data can also be used to identify areas of interest for follow-on projects and studies; functional and ecosystem services data are needed to justify to grants programs why an area may be important and the support is necessary.

An ecosystem-services approach can investigate tradeoffs that may need to be considered during the environmental decision-making process (Boulton et al., 2016). For example, if methane seeps provide differential ecosystem services, one prioritization metric for spatial protections could be weighted ecosystem services scores (e.g., Werner et al., 2014). An ecosystem-services approach can also help facilitate payment for environmental damages by considering the processes that lead to the service, such as nursery grounds, that are often overlooked and by tying them to human well-being. Lastly, results from this approach advance our understanding of ecosystem services associated with methane seeps. They highlight the context-dependent role of methane seeps in providing fisheries and carbon services along an oxygen gradient: while the combination of seepage and low oxygen seemed to suppress ecosystem services scores at Point Dume, which is situated in the core of the OMZ, at the Palos Verdes and Del Mar seeps, situated at the OMZ boundaries, the ecosystem services seemed to benefit from at least some seep activity.

5. Conclusions

In addition to describing biological communities, deep-sea imagery can be amenable to characterizing ecosystem services. Our first hypothesis that methane seeps provide more services than adjacent non-

seep areas was not supported by our results. Seep activity seems to influence ecosystem services differentially among sites, which emphasizes the context-dependence of environmental factors. Our second hypothesis that services increased with diversity was supported by our results. This study highlights how existing dive videos, of which there are thousands that span decades of time, along with existing analysis tools can be leveraged to generate useful information on ecosystem services such as fisheries and climate-regulating services related to carbon. We further recognize that standardized sampling would increase the capacity for quantification and comparison of ecosystem services across space and time, but also recognize the challenges in developing a universally acceptable standard (even if such a standard were to be adopted, consistent implementation can be difficult considering technological and logistical impediments). A service-based approach links ecosystem structures and ecological processes to human well-being, which can provide recommendations for environmental decision-making. This is increasingly important at methane seeps, which occur on continental margins that continue to be impacted by fishing, oil and gas extraction, waste disposal, climate change (Armstrong et al., 2019), and other human activities.

Author statement

Jennifer T. Le: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Visualization, Project administration. Peter R. Girguis: Investigation, Resources, Writing – Review & Editing, Supervision, Funding Acquisition. Lisa A. Levin: Conceptualization, Methodology, Investigation, Resources, Writing – Reviewing & Editing, Supervision, Funding Acquisition.

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

Raw video data are available upon request to Ocean Exploration Trust. Processed data/code are available upon request to the corresponding author.

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Appendices.

Appendix A. Protocol used to analyze remotely-operated vehicle (ROV) dive videos in this study

ROV:

1. Tag the video with an “activity” (what the ROV is doing) – indicate start and end times
 - a. Stationary: Inactive
 - b. Stationary: Pan/Focus (camera movement)
 - c. Stationary: Sampling [Sampling type (push core, slurp, grab, Niskin)]
 - d. Mobile: Search (exploratory)
 - e. Mobile: Transect (directed movement)
2. Tag the video with a “habitat” as they appear in the video – indicate start and end times
 - a. Active Site (seep, whale fall, canyon)
 - b. Transition (some signs of activity, e.g., carbonate rocks but no bacterial mats)
 - c. Off-site: Moving Towards
 - d. Off-site: Moving Away
 - e. Water Column (more than 3m off the bottom)
3. Tag the video with dominant “substrate” as they appear in the video – indicate start and end times
 - a. Soft Sediment
 - b. Carbonate (only really at seeps)
 - c. Bacterial Mat: Full (more than 50% cover)
 - d. Bacterial Mat: Patchy
 - e. Clam Bed: Full (more than 50% cover)
 - f. Clam Bed: Scattered
 - g. Mixed (more than one substrate visible other than sediment) – specify substrates in “notes” section
 - h. Make note of lebenspuren: lots of pits and burrows, ampharetids, etc.

FAUNA:

4. Please check and update the fauna identification document regularly. Count individuals as they cross into the lower 2/3 of the screen.
5. Note the position of each individual.
 - a. On Bottom (on top of the sediment, rock): On Top, Buried, Inside
 - b. On Benthic Organism (on top of another organism that is attached to the bottom) – note what the benthic organism is
 - c. Demersal (within one body length of the benthos)
 - d. Water Column (more than one body length from the benthos)
6. Record what substrate each individual is on or hovering over (“location”), i.e., if a jelly is in the water column but hovering over bacterial mat, then tag this with bacterial mat. Use the same characterizations as Step 3.
7. Determine what each individual is doing.
 - a. Stationary
 - b. Mobile: Swimming (active), Drifting (inactive)
 - c. Ventilating, Breathing
 - d. Feeding
 - e. Start a new line for any individual(s) that are doing different things, e.g., 5 anemones on the sediment, 2 anemones on stalked sponges
8. For high “density” areas (more than 25% of the frame), estimate the percent coverage of the organism, start time, and end time.
9. Also note any terrestrial plants, trash, etc. in the videos.
10. Miscellaneous: Make any notes about interesting observations, i.e., there were lots of/no particulates in the water, transition zone between brittle stars and holothurians, continuation of sampling from the previous video, etc.

Appendix B. Trait-based points assigned to individual morphotypes found within this study and their morphotype fisheries and carbon scores

Taxa	Common name	Commercial	Predator of target	Prey of target	Feeding mode	Mobility	Bioturbation	Diel vertical migration	Calcification	Body size	Fisheries Score	Carbon Score	References
Amphipod	Amphipod	0	0	1	1	1	2	1	1	1	1	7	
<i>Actinaria</i> sp 01	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell (1977)
<i>Actiniidae</i> sp 01	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell (1977)
<i>Actiniidae</i> sp 02	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell (1977)
<i>Actiniidae</i> sp 03	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell (1977)
<i>Bolocera</i> sp	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell (1977)
<i>Liponema</i> sp	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell (1977)
<i>Asteronyx</i> sp	Brittlestar	0	1	1	4	1	3	0	0	3	2	11	Pearson and Gage (1984); Fujita and Ohta, 1988
<i>Brisingidae</i>	Brittlestar	0	1	1	3	1	3	0	0	3	2	10	Pearson and Gage (1984); Fujita and Ohta, 1988
<i>Ophiurida</i> sp 01	Brittlestar	0	1	1	4	1	3	0	0	1	2	9	Pearson and Gage (1984); Fujita and Ohta, 1988
<i>Spinophiura jolliveti</i>	Brittlestar	0	1	1	4	1	3	0	0	1	2	9	Pearson and Gage (1984); Fujita and Ohta, 1988
<i>Cataetx rubirostris</i>	Brotula	0	2	0	4	3	3	0	0	3	2	13	
<i>Cladorhizidae</i>	Carnivorous sponge	0	1	1	3	0	0	0	0	2	2	5	Vacelet & Dupont (2004)
<i>Scyliorhinidae</i>	Catshark	0	2	1	4	3	1	0	0	3	3	11	
<i>Chaetognath</i>	Chaetognath	0	0	1	4	2	0	1	0	1	1	8	Alvarez-Cadena (1993)
<i>Lucinidae</i>	Clam	0	0	1	5	1	3	0	1	1	1	11	Peek et al., 1998
<i>Vesicomyidae</i>	Clam	0	0	1	5	1	3	0	1	1	1	11	Peek et al., 1998
<i>Zoanthid</i>	Coral	0	0	1	3	0	0	0	1	1	1	5	
<i>Galatheid</i> sp	Crab	0	1	1	2	1	3	0	1	2	2	9	Cartes (1993)
<i>Lithodidae</i> sp	Crab	0	1	1	2	1	3	0	1	3	2	10	Cartes (1993)
<i>Lithodidae</i> sp 02	Crab	0	1	1	2	1	3	0	1	3	2	10	Cartes (1993)
<i>Paguroidea</i>	Crab	0	1	1	2	1	3	0	1	2	2	9	Cartes (1993)
<i>Bolinopsis</i> sp	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Mills (1995)
<i>Ctenophora</i> spp 01	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Mills (1995)
<i>Ctenophora</i> spp 02	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Mills (1995)
<i>Ctenophore</i> 03	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Mills (1995)
<i>Lampocteis cruentiventer</i>	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Mills (1995)
<i>Ophidiidae</i> sp	Cusk eel	0	2	1	4	3	3	0	0	3	3	13	

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Taxa	Common name	Commercial	Predator of target	Prey of target	Feeding mode	Mobility	Bioturbation	Diel vertical migration	Calcification	Body size	Fisheries Score	Carbon Score	References
<i>Embassichthys bathybius</i>	Deep sea sole	0	2	1	4	3	3	0	0	3	3	13	Pearson and Gage (1984); Fujita and Ohta, 1988
<i>Microstomas pacificus</i>	Dover sole	1	2	1	4	3	3	0	0	3	4	13	
<i>Dromalia alexandri</i>	Dromalia	0	0	1	3	2	1	0	0	2	1	8	
Zoarcid	Eelpout	0	2	1	4	3	3	0	0	3	3	13	Hissmann, 2005
<i>Folliculinidae</i>	Folliculinid	0	0	0	5	0	0	0	0	1	0	6	
Foram01	Foram	0	0	0	2	0	2	0	1	1	0	6	Pasulka et al. (2017)
Foraminifera	Foram	0	0	0	2	0	2	0	1	1	0	6	
<i>Coryphaenoides acrolepis</i>	Grenadier	0	2	1	4	3	3	0	0	3	3	13	
<i>Nezumia liolepis</i>	Grenadier	0	2	1	4	3	3	0	0	3	3	13	
<i>Eptatretus</i> spp	Hagfish	0	1	1	1	3	3	0	0	3	2	10	
<i>Merluccius productus</i>	Hake	1	2	1	4	3	3	0	0	3	4	13	
<i>Aeginura</i>	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Larson et al., 1991
<i>Atolla</i> spp	Jelly	0	0	1	3	2	0	0	0	2	1	7	
Jelly03	Jelly	0	0	1	3	2	0	0	0	2	1	7	
<i>Poralia refescens</i>	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Larson et al., 1991
Scyphozoa spp 01	Jelly	0	0	1	3	2	0	0	0	2	1	7	
Scyphozoa spp 02	Jelly	0	0	1	3	2	0	0	0	2	1	7	
<i>Voragonema pedunculata</i>	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel et al., 1982; Larson et al., 1991
<i>Ophiodon elongatus</i>	Lingcod	0	2	1	4	3	3	0	0	3	3	13	
Midwater fish	Midwater fish	0	2	1	4	3	1	1	0	2	3	11	
<i>Heteropolypus</i> sp	Mushroom coral	0	0	1	3	0	0	0	1	2	1	6	
Octopus	Octopus	0	2	1	4	2	3	0	0	2	3	11	
Pteropod	Pteropod	0	0	1	3	2	0	1	0	1	1	7	
<i>Bathyraja spinosissima</i>	Ray	0	2	1	4	3	3	0	0	3	3	13	Angel & Pugh (2000)
<i>Rajidae</i> spp	Ray	0	2	1	4	3	3	0	0	3	3	13	
<i>Glyptocephalus zachirus</i>	Rex sole	1	2	1	4	3	3	0	0	3	4	13	
<i>Sebastes</i> spp	Rockfish	1	2	1	4	3	3	0	0	3	4	13	
<i>Anoplopoma fimbria</i>	Sablefish	1	2	1	4	3	3	0	0	3	4	13	
Holothuroidea	Sea cucumber	0	0	1	2	1	3	0	0	2	1	8	
White Sea Cucumber	Sea cucumber	0	0	1	2	1	3	0	0	2	1	8	Miller et al. (2000)
<i>Funiculina</i> sp	Sea pen	0	0	1	3	0	0	0	0	3	1	6	
<i>Pennatulacea</i> sp 01	Sea pen	0	0	1	3	0	0	0	0	3	1	6	
<i>Sessiliflorae</i> sp	Sea pen	0	0	1	3	0	0	0	0	3	1	6	Best (1988)
<i>Asteroidea</i> sp 01	Seastar	0	1	1	4	1	3	0	0	2	2	10	
<i>Hippasteria</i> sp 01	Seastar	0	1	1	4	1	3	0	0	2	2	10	
<i>Eusergestes similis</i>	Shrimp	0	1	1	4	3	1	1	1	1	2	11	Lauerman (1998)
<i>Pandalopsis</i> sp	Shrimp	0	1	1	4	2	1	1	1	1	2	10	
<i>Peracarid</i> sp 01	Shrimp	0	1	1	4	3	1	1	1	1	2	11	
<i>Petalidium suspiciosum</i>	Shrimp	0	1	1	4	2	1	1	1	1	2	10	Cartes (1993)
<i>Sergestidae</i> sp	Shrimp	0	1	1	4	1	1	1	1	1	2	9	
Siphonophore	Siphonophore	0	0	1	3	2	0	1	0	3	1	9	
<i>Lyopsetta exilis</i>	Slender sole	1	2	1	4	3	3	0	0	2	4	12	

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Taxa	Common name	Commercial	Predator of target	Prey of target	Feeding mode	Mobility	Bioturbation	Diel vertical migration	Calcification	Body size	Fisheries Score	Carbon Score	References
<i>Alepocephalus tenebrosus</i>	Slickhead	0	2	1	4	3	1	0	0	3	3	11	
Gastropod sp 01	Slug	0	0	1	2	1	3	0	0	1	1	7	
<i>Alia</i> snail	Snail	0	0	1	2	1	2	0	1	1	1	7	
<i>Buccinidae</i> sp 01	Snail	0	0	1	2	1	2	0	1	1	1	7	
Gastropod sp 02	Snail	0	0	1	2	1	2	0	1	1	1	7	
Provanna	Snail	0	0	1	2	1	2	0	1	1	1	7	
<i>Liparidae</i>	Snailfish	0	2	1	4	3	3	0	0	2	3	12	
<i>Nemichthyidae</i>	Snipe eel	0	2	1	4	3	1	0	0	3	3	11	
Encrusting Sponge	Sponge	0	0	1	3	0	0	0	0	3	1	6	
Porifera sp 01	Sponge	0	0	1	3	0	0	0	0	3	1	6	
Porifera sp 02	Sponge	0	0	1	3	0	0	0	0	3	1	6	
Porifera sp 03	Sponge	0	0	1	3	0	0	0	0	3	1	6	
Sponge	Sponge	0	0	1	3	0	0	0	0	3	1	6	
Gonatus sp	Squid	0	0	1	4	3	1	0	0	2	1	10	
Rockfish/Thornyhead	Thornyhead	1	2	1	4	3	3	0	0	3	4	13	
<i>Sebastolobus alascanus</i>	Thornyhead	1	2	1	4	3	3	0	0	3	4	13	
<i>Sebastolobus altivelis</i>	Thornyhead	1	2	1	4	3	3	0	0	2	4	12	
Tunicate01	Tunicate	0	0	1	3	2	0	0	0	3	1	8	
<i>Umbellula</i> sp	Umbellula	0	0	1	3	0	0	0	0	3	1	6	
<i>Strongylocentrotus fragilis</i>	Urchin	0	1	1	2	1	3	0	1	2	2	9	
<i>Netastomatidae</i>	Witchface eel	0	2	1	4	3	1	0	0	3	3	11	Merrett and Saldanha, 1985
Flatworm01	Worm	0	0	1	2	1	2	0	0	1	1	6	
Flatworm02	Worm	0	0	1	2	1	2	0	0	1	1	6	
Polychaete01	Worm	0	0	1	2	1	2	0	0	1	1	6	
Polychaete01	Worm	0	0	1	2	1	2	0	0	1	1	6	
Polychaete02	Worm	0	0	1	2	1	2	0	0	1	1	6	
Polychaete03	Worm	0	0	1	2	1	2	0	0	1	1	6	
Polychaete04	Worm	0	0	1	2	1	2	0	0	1	1	6	
<i>Polynoidae</i>	Worm	0	0	1	4	1	2	0	0	1	1	8	Chevaldonné et al., 1998
Serpulid	Worm	0	0	1	2	1	0	0	0	1	1	4	Bornhold & Milliman (1973)
<i>Siboglinidae</i>	Worm	0	0	1	2	1	2	0	0	1	1	6	Hilário et al., 2011

Appendix C. Frequency of occurrence of each morphotype, presented as a percentage of total morphotype occurrences, for each dive as well as among all dives

Morphotype	Point Dume	Palos Verdes	Del Mar	All dives
<i>Alepocephalus tenebrosus</i>	0	0	2	0.3
<i>Anoplopoma fimbria</i>	0	3.6	4.4	2.3
<i>Bathyrhaja spinosissima</i>	0	0	0.4	0
<i>Cataetys rubirostris</i>	0	0	0	0
<i>Cladorhizidae</i>	0	0	0.4	0
<i>Coryphaenoides acrolepis</i>	0.2	0	0	0.1
<i>Embassichthys bathybius</i>	0	0.1	0	0
<i>Eptatretus</i> spp	2.6	0.8	4.2	1.9
<i>Glyptocephalus zachirus</i>	0	0.2	0.9	0.2
<i>Liparidae</i>	0	0.1	0	0
<i>Lyopsetta exilis</i>	0	0.1	0	0.1
<i>Merluccius productus</i>	0	0.5	0	0.3
<i>Microstomus pacificus</i>	4.6	4	0.7	3.8
Midwater fish	3.7	4.6	4.5	4.2
<i>Nemichthyidae</i>	0	0.8	0	0.4
<i>Netastomatidae</i>	0	1.2	0	0.6
<i>Nezumia liolepis</i>	8	5.4	0.2	5.8
<i>Ophiodon elongatus</i>	0	0	0	0
<i>Rajidae</i> spp	0	0	0	0
<i>Scyliorhinidae</i>	5.2	1.4	0	2.7
<i>Sebastes</i> spp	0	0.5	0	0.2
<i>Sebastolobus alascanus</i>	0.2	0	0	0.1
<i>Sebastolobus altivelis</i>	8.2	8.9	15.5	9.4
Zoarcid	2.4	0.1	0	1
Holothuroidea	0.1	3.6	0.9	1.9
White Sea Cucumber	0	0.1	0	0

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(continued)	Point Dume	Palos Verdes	Del Mar	All dives
<i>Strongylocentrotus fragilis</i>	0	3.9	0	1.9
Ophidiidae spp	0	0	0	0
Ophiurida spp 01	0.3	2.8	0	1.5
Asteroidea sp 01	0.1	4.1	0	2
Asteronyx spp	0	0.8	0	0.4
Brisingiidae	0	0.4	0	0.2
<i>Hippasteria</i> spp. 01	0	0.2	0	0.1
<i>Gonatus</i> sp	0	0.1	0	0
Octopus	0	0.6	0	0.3
Pteropod	0	0.1	0.5	0.1
<i>Eusergestes similis</i>	6.4	2.9	6.7	4.7
Galatheid spp	11.7	0.4	0	4.7
Lithodidae spp	0	0.7	4.4	0.9
Lithodidae spp 02	0	2.1	0	1
<i>Pandalopsis</i> spp	0.1	0	2.4	0.3
Peracarid spp 01	0.1	0	0	0
Sergestidae spp	0.1	0.5	2.7	0.6
Chaetognath	0	0	0	0
Amphipod	0	0	0.2	0
Lucinidae	4.6	0	0	1.8
Vesicomyidae	0	0	0.2	0
<i>Alia permodesta</i>	0.2	0	0	0.1
Buccinidae sp 01	0	0	0.9	0.1
Gastropod sp 01	0	0.1	0	0
Gastropod sp 02	0.1	0	0	0
Paguroidea	0	0	0.4	0
<i>Provanna</i>	0	0	3.1	0.4
<i>Heteropolypus</i> sp	0	0.7	0	0.3
Zoanthid	0	0.1	0	0
<i>Umbellula</i> spp	0	1.6	0	0.8
Actinaria spp 01	0	0.3	0	0.2
Actiniidae spp 01	0	0.2	3.8	0.6
Actiniidae spp 02	0.8	0.5	1.1	0.7
Actiniidae spp 03	0	0.4	0	0.2
<i>Bolocera</i> spp	0	0.1	0	0.1
<i>Liponema</i> spp	14.6	2.5	0.2	6.9
<i>Funiculina</i> sp	0	1.7	0	0.8
Pennatulacea spp 01	0	0.1	0	0
<i>Petalidium suspensum</i>	0	0	0	0
Sessiliflorae spp	0	1.6	0	0.8
Scyphozoa spp 01	0	0.2	0	0.1
Scyphozoa spp 02	0	0.1	0	0
<i>Aeginura</i>	0	0.5	0	0.3
<i>Atolla</i> spp	0	0.1	0	0
Jelly03	0	0.6	0	0.3
<i>Poralia rufescens</i>	18.5	10.8	0.2	12.5
<i>Spinophiura jolliveti</i>	0	0	2.4	0.3
<i>Voragonema pedunculata</i>	2.5	6.4	30	7.8
<i>Dromalia alexandri</i>	0	4	0	2
Siphonophore	2.4	4.1	2.4	3.2
<i>Bolinopsis</i> spp	0.1	1.4	0	0.7
Ctenophora spp 01	0.1	1.5	0	0.8
Ctenophora spp 02	0.3	0.5	0	0.4
Ctenophore03	0	0.1	0	0.1
<i>Lampocteis cruentiventer</i>	0	0.5	0.7	0.3
Serpulid Polychaete	0	0.1	0	0.1
Flatworm01	0	0.2	0.5	0.2
Flatworm02	0	0.1	0	0
Polychaete01	1.8	0.3	0.2	0.8
Polychaete02	0	0	0.4	0
Polychaete03	0	0	0.2	0
Polychaete04	0	0	0.2	0
Polynoidae	0.5	0.9	0	0.6
Siboglinidae	0	0	0.2	0
Encrusting Sponge	0	0	0.5	0.1
Porifera sp 01	0.1	0	0	0
Porifera sp 02	0	0.1	0	0
Porifera sp 03	0	0.2	0	0.1
Sponge	0	0	0	0
Folliculinidae	0	0	1.1	0.1
Foram01	0	0.5	0	0.2
Foraminifera	0	0	0.5	0.1
Tunicate01	0	0.1	0	0

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