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

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Highlights:

- An approach for ecosystem-services based image analysis is developed and tested.
- We leverage existing deep-sea video and an adapted trait-based approach.
- Three southern California methane seeps are qualitatively described and compared.
- Del Mar seep may have elevated contributions to local deep-sea ecosystem services.
- Steps are made towards quantifying ecosystem services of deep-sea habitats.

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 remotely-operated vehicle *Hercules* (operated by Ocean Exploration Trust), as well as adapted biological trait analysis, to develop an approach that characterizes ecosystem services. Specifically, fisheries services 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 along a gradient of seep activity and site-to-site comparisons that suggest the Del Mar seep and adjacent areas provide 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.

Keywords: Deep ocean, benthic ecology, carbon cycling, fisheries, Southern California Borderlands, methane seeps, ecosystem services, image analysis, biological trait analysis

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., 2019). 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 including education and outreach (Hoeberechts et al., 2015). 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 & 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 underwater observatories (de Leo et al., 2018), drop cameras (Clayton & Dennison, 2017), landers (Lavaleye et al., 2018; Gallo et al. 2020), autonomous underwater vehicles (AUVs; Mejia-Mercado et al., 2019), remotely-operated vehicles (ROVs; Myhre et al., 2018), and human-occupied vehicles (HOVs; Gallo et al., 2015). Deep-sea expeditions routinely collect imagery for scientific (e.g. National Deep Submergence Facility, NEPTUNE Ocean Observatory), 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 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., 2016; 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 nets (Ayma et al., 2016), and for minimizing disturbances associated with nets, dredges, grabs, or other means of sample collection.

With the multitude of deep-sea imagery being collected, there is opportunity to leverage existing data to characterize, and ideally quantify, ecosystem services. Visual data are often unanalyzed or only partially analyzed for specific applications. However, deep-sea imagery represents a repository of knowledge about, not only which organisms live there, but also how they interact with their environment, which 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. Investigators, however, 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 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. It should be noted that there are likely tens of thousands of hours of video and still-frame imagery available from international sea-going expeditions, spanning decades, that are available for further examination and study.

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 (USA) (Levin et al. 2016a). Methane seeps are found in every ocean from shallow to deep water depths (Judd, 2003) and are still being discovered today (Riedel et al., 2018; Seabrook et al., 2018). Geological processes lead to seepage of methane and sulfur-rich fluids from the seabed (Sibuet & Olu, 1997), which fuel chemoautotrophic microbial communities (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 et al., 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 & 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 low oxygen (< 22 umol/kg, < 0.5 ml/l). The OMZ can intersect benthic environments to shape local biological communities (Sellanes et al., 2010; Gallo & Levin, 2016; Neira et al., 2019), 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).

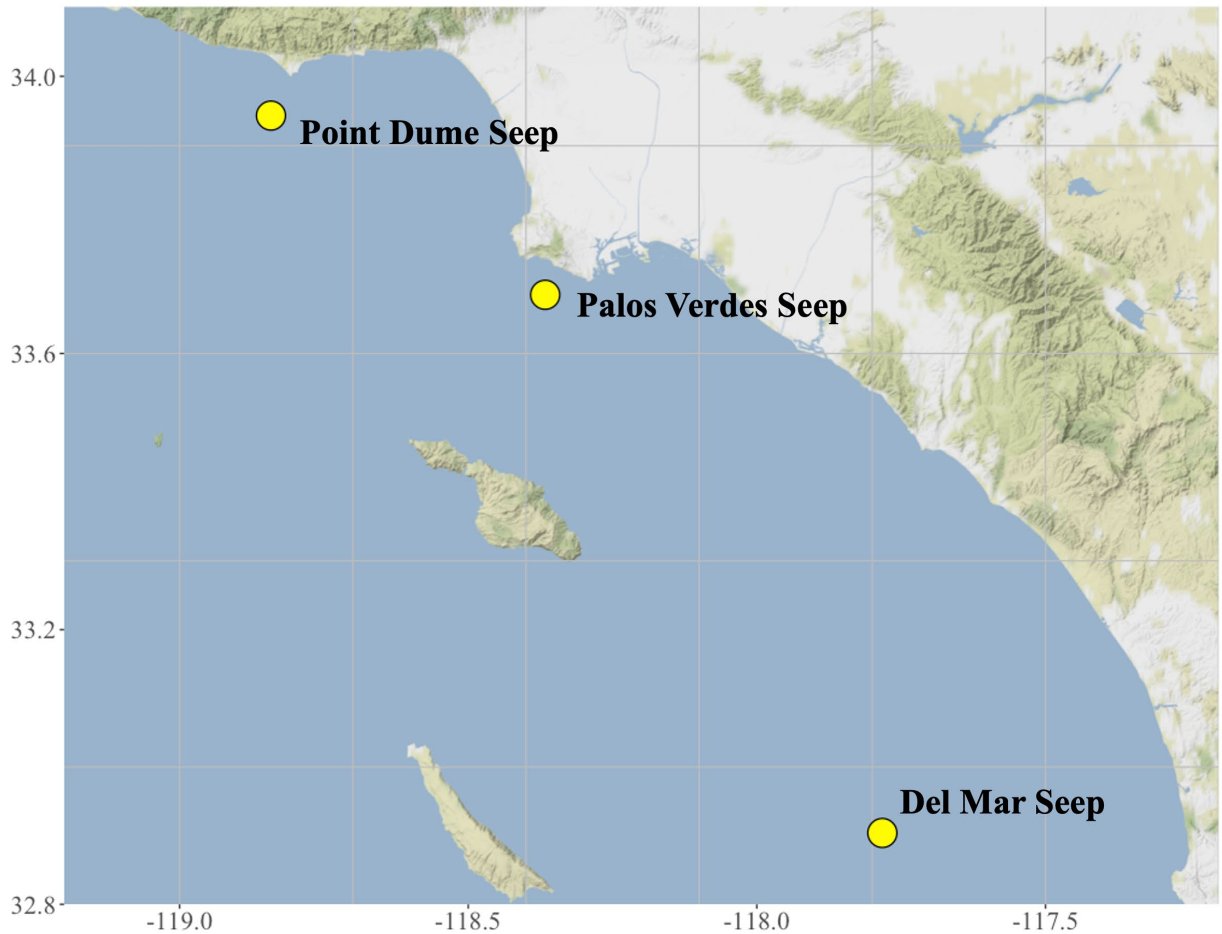
The objective of this paper is to develop an approach that characterizes deep-sea ecosystem services at and around methane seeps within the southern California OMZ using deep-sea images. We adapt biological trait analysis to target ecosystem services and focus specifically on fisheries and climate-regulating 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 whereas services such as element cycling are facilitated by microbes. However, we do discuss visual indicators of microbially-driven services where relevant. We use examples from three southern California upper slope methane seeps (from north to south): Point Dume (724.5 m), Palos Verdes (505.6), 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 & 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 approximately 450-1100 m (Helly & Levin, 2004; Stramma et al., 2010; Bograd et al., 2015). Our three study sites (Figure 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; Figure 1). Palos Verdes seep is less than 5 km from shore and characterized by large carbonate rocks covered by megafaunal aggregations (Levin et al., 2016a; Figure 1). Del Mar seep (mean depth 1023 m) was discovered by graduate students at Scripps Institution of Oceanography in 2015 (Maloney et al., 2015) and has since been visited several times (Figure 1).

Figure 1. Locations of the three methane seep study sites in southern California: Point Dume seep, Palos Verdes seep, and Del Mar seep. [single-column fitting image]



2.2. ROV dives

Exploration dives were conducted by *ROV Hercules* aboard the *EV Nautilus* in July and August 2015 as part of the OET southern California borderlands expedition NA066. High-definition video was taken continuously during each dive; dives ranged between 4-18 hours 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 altitude, zoom, and non-visible laser references. However, qualitative descriptions based on presence-absence and frequency of occurrence are useful, especially in deep-sea systems that are rarely visualized and expensive to study. Metadata from each dive are summarized in Table 1.

Table 1. Remotely-operated vehicle Hercules dive location and environmental data from Ocean Exploration Trust expedition NA066 off of the southern California borderlands.

Dive Number	**Date (2015)**	**Site**	**Latitude (ºN)**	**Longitude (ºW)**	**Average Water Depth (m)**	**Average Temperature (ºC)**	**Average 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

2.3. Video analysis

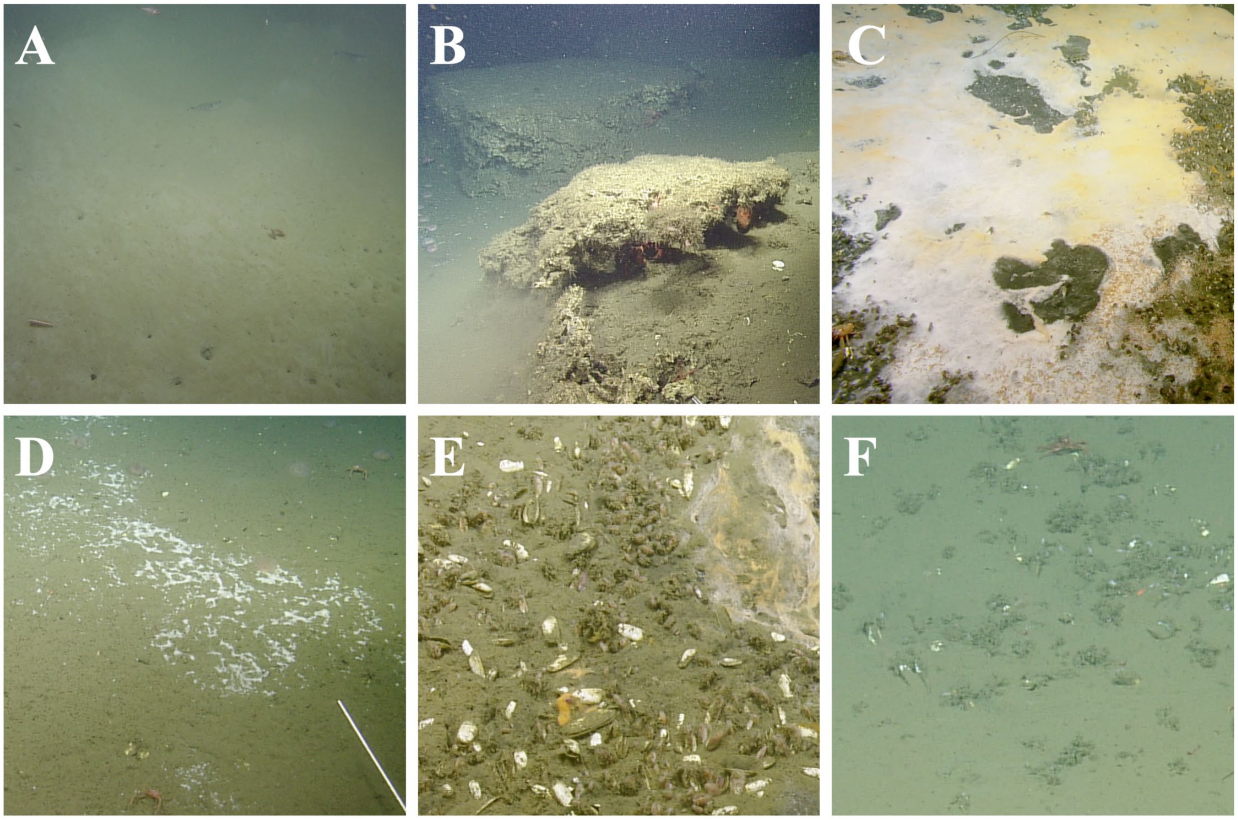
Videos from each dive were segmented into five-minute clips that were each treated as a "sample" and annotated by hand in Microsoft Excel™ (the full protocol can be found in Appendix A). Information regarding the ROV, surrounding environment (including seep activity), and megafauna encountered (morphotype, location, behavior) was also collected (Table 2; Figure 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, dead clam beds, carbonates without signs of seepage), and non-seep background areas generally associated with soft sediment habitats. 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 minute of each video, animals were counted and identified to the highest possible taxonomic resolution. For the remaining four minutes, a list of morphotypes was generated.

Table 2. Observation type, observation options, and percentage of time the ROV spent doing the activity, at seepage activities or seafloor 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
	Mobile: Transect	3.5	8.4	16.2

Seep activity	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

Figure 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. [two-column fitting image]



2.4. Trait analysis

Observable traits that support fisheries or carbon services were chosen (Table 3), and each morphotype was assigned a score for selected traits based on a literature review (Appendix B). We used fuzzy coding (Chevenet et al., 1994) to capture the extent to which each trait modality contributes to each service. 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.

Table 3. Traits and their modalities that contribute to fisheries and climate-regulating services related to carbon. Higher scores indicate modalities that contribute more to the respective service.

Ecosystem service	**Trait**	**Modality**	**Reference**
Fisheries – characteristic	Commercially valuable	Yes (1) No (0)	Koslow et al., 2000
Fisheries – trophic support	Predator Prey	Active (2) Passive (1) No (0) Yes (1) No (0)	Yang & Somero, 1993; Jacobsen & Vetter, 1996; Dufault et al., 2009; Hattori et al., 2009
Carbon – fixation and cycling	Feeding mode	Autotrophic (5) Predator (4) Filter feeder (3) Deposit feeder (2) Scavenger (1)	Doering et al., 1986; Reinthaler et al. 2010; Wilmers et al., 2012; Atwood et al., 2015
Carbon – transport	Mobility	High (3)	

		Medium (2) Low (1) None (0)	
Carbon – transport	Movement	Swim (1) Crawl (1) Burrow (1) Sessile (0)	
Carbon – transport	Bioturbation	High (3) Medium (2) Low (1) None (0)	Vardaro et al., 2009; Martinetto et al., 2016; Hou et al., 2017; Gogina et al., 2020
Carbon – transport	Diel vertical migration	Yes (1) No (0)	Hidaka et al., 2001; Hudson et al., 2014; 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)	

Each video was scored (both within the one-minute subset and the whole five-minute clip) for the morphotypes present that demonstrate the traits chosen. We were not able to calculate faunal densities from the videos due to unknown and variable camera field-of-view so we use presence-absence data. Scores were standardized by the number of morphotypes found in each clip. The maximum fisheries score a morphotype could have was four and the minimum score was zero. For carbon services, the maximum score was seventeen and the minimum score was two.

2.5. Statistical analysis

All statistical analyses were done in R (version 3.5.2.), using the base package unless otherwise noted. Data were tested for normality using a Shapiro-Wilk test. Because data did not meet normality conditions, non-parametric tests were used. The Kruskal-Wallis test-by-ranks was used to test for significant differences among groups (e.g. sites, seep activity, microhabitats), and a *post hoc* Dunn test with a Bonferroni correction (package 'dunn.test') was used to identify which groups were different. Correlations were tested using Spearman's rank coefficient. 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.

3. Results

We present here results from this methodology, including initial biological characterizations of several seep ecosystems. These 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 the videos and grouped into seven functional (mainly feeding) groups: scavengers, benthic filter feeders & microcarnivores, benthic deposit feeders & bacterivores, demersal predators, pelagic predators, gelatinous plankton, and symbiont-bearing taxa (Table 4; Figure 3). Demersal predators had the most morphotypes with 37, most of which were fish species (Figure 4A). Both pelagic predators and symbiont-bearing taxa had only three morphotypes observed.

Table 4. Functional groups used, morphotypes included in them, average fisheries or carbon score assigned to the morphotypes in the functional group, and frequency of occurrence throughout each dive as percentages.

Functional Group	**Morphotypes included**	**Average fisheries score**	**Average carbon score**	**Point Dume (%)**	**Palos Verdes (%)**	**Del Mar (%)**
Scavengers	Hagfish, shrimp, amphipods	2.00	10.53	9.1	4.3	16.2
Benthic filter feeders & microcarnivores	Sea anemones, sea pens, corals, sponges	1.63	5.71	15.4	14.6	6.0
Benthic deposit feeders & bacterivores	Sea cucumbers, urchins, snails, brittle stars	1.32	8.05	0.3	8.5	6.0
Demersal predators	Demersal and benthic fish, crabs, sea stars	3.09	11.40	43.0	40.9	29.6

Pelagic predators	Midwater fish, squid, chaetognaths	2.91	10.85	3.7	4.8	5.1
Gelatinous plankton	Jellies, ctenophores, siphonophores	1.01	7.26	23.9	26.9	35.6
Symbiont-bearing taxa	Vesicomyid clams, lucinid clams, folliculinids	0.93	10.60	4.6	0	1.5

Figure 3. Example morphotypes of each functional group: (A) scavengers – hagfish, shrimp; (B) benthic filter feeders & microcarnivores – carnivorous sponge, sea anemone, sea pen; (C) benthic deposit feeders – brittle star, sea cucumber, sea urchin; (D) demersal predators – groundfish, sea stars, crabs; (E) pelagic predators – midwater fish, squid; (F) gelatinous plankton – jellies, ctenophores, siphonophores; and (G) symbiont-bearing taxa – folliculinid ciliates, vesicomyid clams. [two-column fitting image]

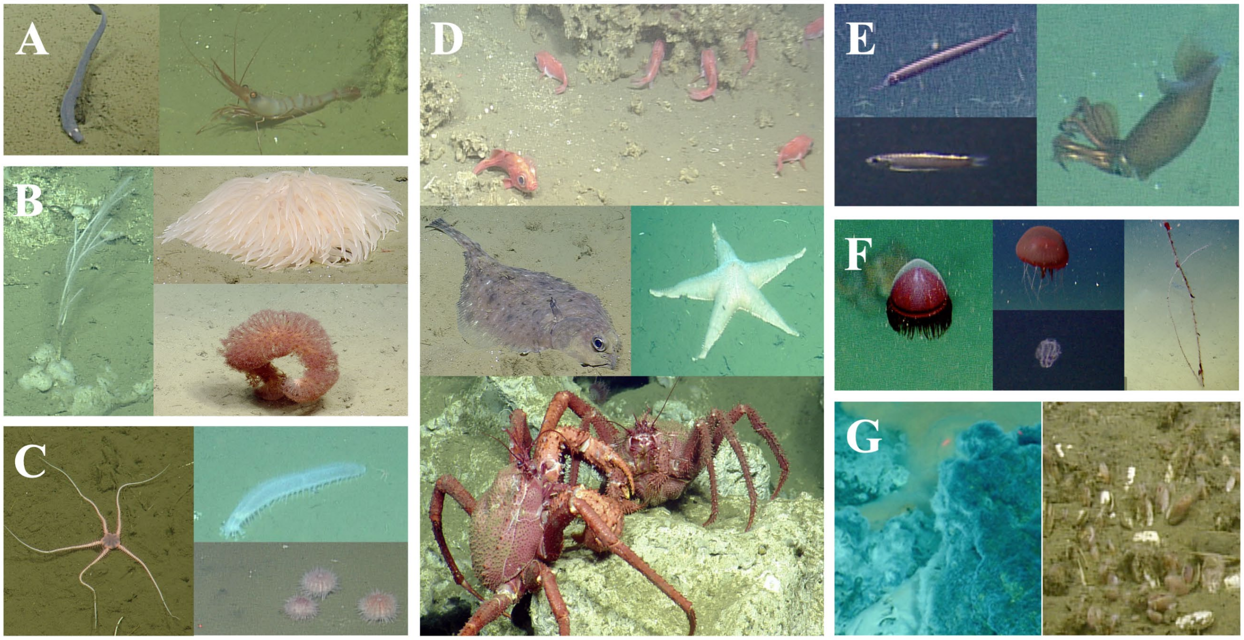
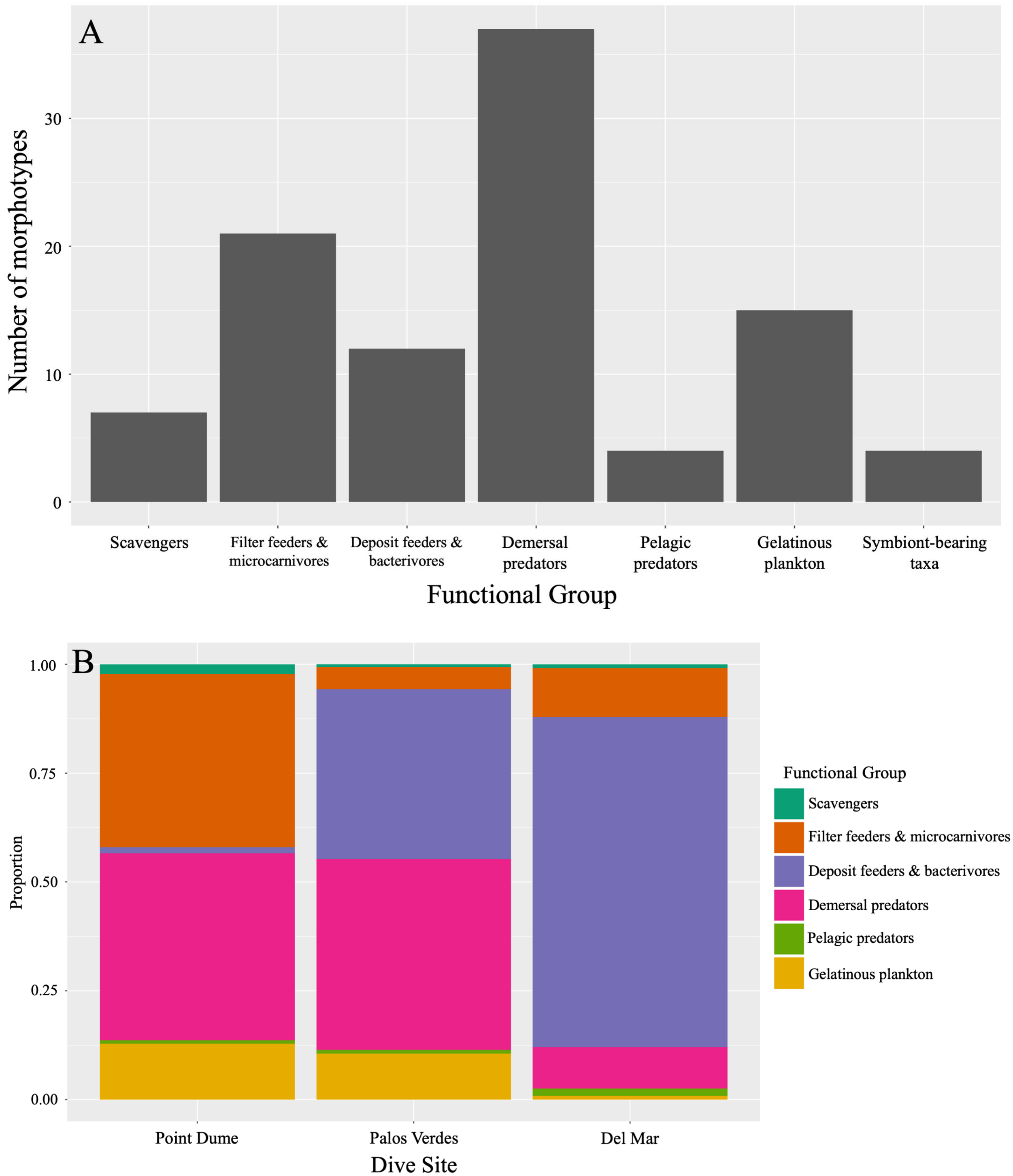


Figure 4. (A) The number of morphotypes included in each functional group, and (B) the relative abundance of each functional group at three methane seeps off southern California within the one-minute subset. [1.5-column fitting image]



The most frequently occurring morphotypes 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%) (Table 5). There was a significant difference among the biological communities at our sites (ANOSIM, $R = 0.356$, $p < 0.01$) (package 'vegan'). 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.

Table 5. 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**
Alepocephalus tenebrosus	0	0	2	0.3
Anoplopoma fimbria	0	3.6	4.4	2.3
Bathyraja spinosissmia	0	0	0.4	0
Cataetyx rubirostris	0	0	0	0
Cladorhizidae	0	0	0.4	0
Coryphaenoides acrolepis	0.2	0	0	0.1
Embassichthys bathybius	0	0.1	0	0
Epatratus spp	2.6	0.8	4.2	1.9

Glyptocephalus zachirus	0	0.2	0.9	0.2
Liparidae	0	0.1	0	0
Lyopsetta exilis	0	0.1	0	0.1
Merluccius productus	0	0.5	0	0.3
Microstomas pacificus	4.6	4	0.7	3.8
Midwater fish	3.7	4.6	4.5	4.2
Nemichthyidae	0	0.8	0	0.4
Nettastomatidae	0	1.2	0	0.6
Nezumia liolepis	8	5.4	0.2	5.8
Ophiodon elongatus	0	0	0	0
Rajidae spp	0	0	0	0
Scyliorhinidae	5.2	1.4	0	2.7
Sebastes spp	0	0.5	0	0.2
Sebastolobus alascanus	0.2	0	0	0.1
Sebastolobus altivelis	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

Strongylocentrotus fragilis	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
Brisingidae	0	0.4	0	0.2
Hippasteria spp. 01	0	0.2	0	0.1
Gonatus sp	0	0.1	0	0
Octopus	0	0.6	0	0.3
Pteropod	0	0.1	0.5	0.1
Eusergestes similis	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
Pandalopsis 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
Alia permodesta	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
Provanna	0	0	3.1	0.4
Heteropolypus sp	0	0.7	0	0.3
Zoanthid	0	0.1	0	0
Umbellula 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
Bolocera spp	0	0.1	0	0.1
Liponema spp	14.6	2.5	0.2	6.9
Funiculina sp	0	1.7	0	0.8

Pennatulacea spp 01	0	0.1	0	0
Petalidium suspiriosum	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
Aeginura	0	0.5	0	0.3
Atolla spp	0	0.1	0	0
Jelly03	0	0.6	0	0.3
Poralia rufescens	18.5	10.8	0.2	12.5
Spinophiura jolliveti	0	0	2.4	0.3
Voragonema pedunculata	2.5	6.4	30	7.8
Dromalia alexandri	0	4	0	2
Siphonophore	2.4	4.1	2.4	3.2
Bolinopsis 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

Lampocteis cruentiventer	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

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 five-minute clip (scores for the one-minute subset are still shown in Table 6).

Table 6. Summary of ecosystem services scores, standardized by the number of morphotypes, for each site. Transition areas were not delimited for Del Mar. Significant differences across sites are noted with *a*, *b*, *c* (horizontally); significant differences within sites are noted with *x*, *y*, *z* (vertically).

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 one-minute	2.22 ± 0.59	2.42 ± 0.77	2.30 ± 1.30	2.32 ± 0.79
Fisheries – active	$2.38 \pm 0.78^{a,x}$	$2.35 \pm 0.76^{ab,x}$	2.98 ± 1.45^{b}	2.58 ± 1.09^{x}
Fisheries – transition	$2.52 \pm 0.45^{a,x}$	$2.84 \pm 0.66^{b,y}$	NA	2.52 ± 0.45^{xy}
Fisheries – background	$3.18 \pm 0.97^{a,y}$	$2.59 \pm 0.86^{b,x}$	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 one-minute	9.47 ± 1.71	10.53 ± 2.30	10.56 ± 3.51	10.08 ± 2.33
Carbon – active	$10.61 \pm 2.67^{a,x}$	11.63 ± 2.66	14.03 ± 5.93^{b}	11.94 ± 4.34
Carbon – transition	10.58 ± 1.54^{x}	11.75 ± 2.55	NA	10.58 ± 1.54

Carbon – background	13.57 ± 3.42^{a,y}	11.53 ± 3.45^{b}	13.84 ± 4.68^{a}	12.34 ± 3.73

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 µm O_2/kg (Table 1). During this dive, the most frequently occurring morphotypes were *P. rufescens* (18.5%), *Liponema* anemones (14.6%), galatheid crabs (11.7%), *S. altivelis* (8.2%), and *N. liolepis* (8.0%) (Table 5). These five 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 µm/kg to 4.55 µm/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 6). 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 scores than active and transition areas by 17.4% and 17.6%, respectively ($X^2 = 50.74$, df = 2, p <

0.01; Table 6). Oxygen negatively covaried with depth (ρ = -0.18, p = 0.01). Fisheries (ρ = 0.27, p < 0.01) and carbon scores (ρ = 0.38, p < 0.01) were also significantly positively correlated with depth. Fisheries scores were significantly positively correlated with temperature at this site (ρ = 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 *P. rufescens* (10.8%), *S. altivelis* (8.9%), *V. pedunculata* (6.4%), *N. liolepis* (5.4%), and a diversity of midwater fish (4.6%) (Table 5). The percentage of singletons, i.e. morphotypes that were observed exactly once, was 13.9%, which was the lowest of all sites. Oxygen (ρ = -0.97, p < 0.01) and temperature (ρ = -0.96, p < 0.01) significantly covaried with depth. Number of morphotypes was significantly positively correlated with depth (ρ = 0.60, p < 0.01) between 278 m to 799 m, and negatively correlated with oxygen (ρ = -0.59, p < 0.01), which ranged between 2.12 µm/kg to 54.76 µm/kg, and temperature (ρ = -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 6). 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 *V. pedunculata* (30.0%), *S. 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%) (Table 5). Neither the number of morphotypes nor functional groups were significantly correlated with depth, temperature, or oxygen.

There were no significant differences in fisheries or carbon scores among areas with different seep activity or microhabitats at Del Mar seep. However, fisheries scores were significantly negatively correlated with oxygen (ρ = -0.40, p <0.01) between 14.85 µm/kg to 15.56 µm/kg.

3.4. Across all three sites

Overall, fisheries and carbon scores were significantly positively correlated with each other (ρ = 0.86, p < 0.01). The number of morphotypes was also positively correlated with fisheries (ρ = 0.19, p < 0.01) and carbon scores (ρ = 0.18, p < 0.01). However, neither service score was correlated with the number of functional groups present nor the number of morphotypes present within any one functional group.

With respect to fisheries scores, Del Mar had significantly higher scores than Palos Verdes by 12% (X^2 = 8.83, df = 2, p = 0.01). 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, $p < 0.01$). 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) and carbon scores ($X^2 = 12.35$, df = 2, $p < 0.01$) 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), 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, $p < 0.01$). This was also the case for carbon scores ($X^2 = 33.46$, df = 2, $p < 0.01$).

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 and had the highest mean overlying oxygen concentration of 20.24 µm/kg (Table 1). This could be an artefact of the larger distance and wider depth range (~278–799 m) covered by the dive. However, 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 µm/kg (Sperling et al., 2016; Gallo et al. 2020). However, within the Palos Verdes dive, the number of morphotypes observed in each video was negatively correlated with oxygen ($\rho = -0.59$, $p < 0.01$), with the highest number of morphotypes

(> 20) found in videos with oxygen levels ranging from 2.18-2.26 µm/kg. Number of morphotypes was also positively correlated with depth ($\rho = 0.60$, $p < 0.01$). Because oxygen and depth covaried ($\rho = -0.97$, $p < 0.01$), 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 & 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 1500-3000 m has been documented in several taxa (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).

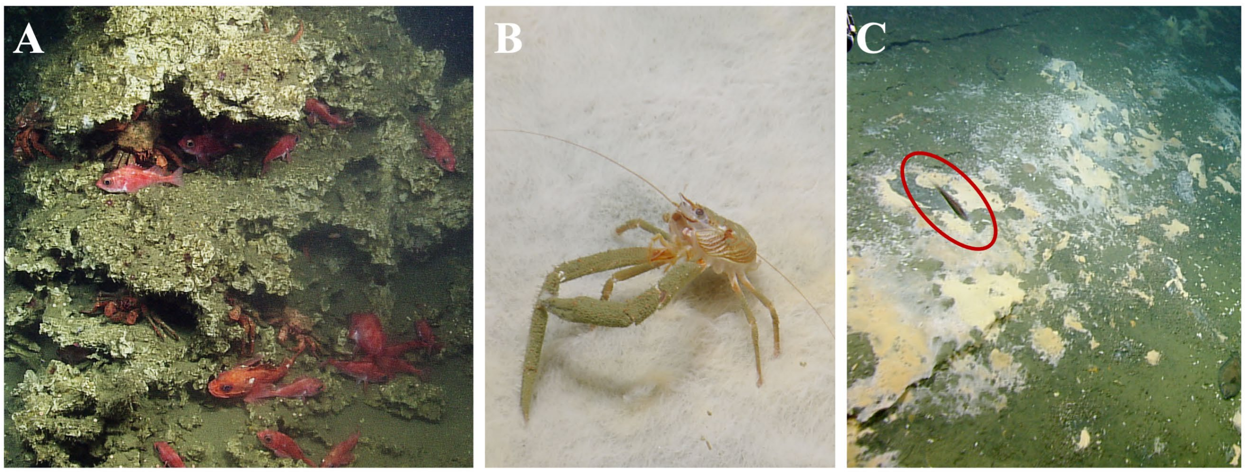
In contrast to Palos Verdes, the entire Point Dume dive occured within the core of the California OMZ with mean oxygen levels of 2.76 µm/kg. Here, the number of morphotypes was significantly positively correlated with oxygen ($\rho = 0.21$, $p < 0.01$) and negatively with depth ($\rho = -0.27$, $p < 0.01$). Because the Point Dume seep field is 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 and Deutsch et al., 2015). As oxygen deoxygenation continues to expand and intensify the OMZ (Bograd et al., 2008; Stramma & Schmidtko, 2019), animals that cannot tolerate low oxygen conditions will lose available habitat, while those that are more tolerant will distribute accordingly (Netburn & Koslow, 2015). The decrease in number of morphotypes with depth observed at Point Dume ($\rho = -0.27$, $p < 0.01$) may be driven by the significant negative correlation between oxygen and depth

(ρ = -0.18, p = 0.01). 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 (Figure 5), likely indicating microbial sulfide oxidation and possibly some methane oxidation. Sulfide-oxidation by microbes can reduce the concentration of sulfide in the overlying water (Lavik et al., 2009), such detoxification could facilitate occurrence of morphotypes that contribute to ecosystem services. Biotic and abiotic sulfide oxidation, however, also consumes oxygen, and active seep areas consume two orders of magnitude more oxygen than non-seep areas (Boetius & Wenzhofer, 2013). However, seep influence on sediment macrofauna communities, on which megafauna could be feeding, seems to be limited (Levin et al., 2000; Demopolous et al., 2018). Only 25% of morphotypes occurred on the bacterial mat, most frequently *Liponema* anemones (13.4%), *P. rufescens* (11.6%), and galatheid crabs (10.2%). One morphotype of polychaete was found exclusively on bacterial mats with two occurrences. Our results suggest that the active seep areas of Point Dume have lower fisheries and carbon scores than transition and background areas (Table 6). Intense seepage with hydrogen sulfide may act synergistically with exceptionally low oxygen to reduce the occurrence of functional traits that generate ecosystem services. 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 bacterial mats represent elevated levels of local primary chemosynthetic production, which likely comprises a significant process in the carbon cycle (Rothschild & Mancinelli, 1990).

Figure 5. 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.



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 et al., 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 ($p > 0.05$), which ranged from 2.01-4.73 µm/kg, and ecosystem services scores at Point Dume. However, scores were significantly correlated with water depth which negatively covaried with oxygen (ρ = -0.18, p = 0.01). Unfortunately, separating these effects with our dataset 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 6). As mentioned before, this is likely driven by the large aggregations of fish found on carbonate rocks in transition areas (Figure 5). 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 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 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. 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. Application of this trait-based approach could provide additional guidance for development of spatial protections. The focus on ecosystem services provides a targeted effort that can help establish research and management priorities.

One drawback to using deep-sea imagery for trait-based ecosystem services assessment is the need for visual evidence. 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 metatranscriptomics could (e.g. 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 (Figure 5). 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

Deep-sea expeditions with submersible dives should always start with good base maps of an area (Raineault et al., 2012). Bathymetry and information from other sonar systems (e.g., 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. Ideally, each science submersible would have its own standalone imaging system with fixed focal length cameras and orientation to better allow for quantitative image analysis. In order to achieve this, standards regarding how to collect pictures and videos from deep-sea sampling instruments could be useful (e.g. **Error! Hyperlink reference not valid.**). The resulting data from transects with consistent altitude, 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 & Lauermann, 2016).

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).

Environmental parameters should be measured in association with imagery. Physical and chemical properties, such as temperature, oxygen, and hydrogen sulfide at seeps, are important factors that help shape the biological communities (Levin et al., 2005). Porewater chemistry 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). Scientific tools exist to assess water chemistry such as *in situ* mass spectrometers that can be mounted on ROVs and Niskin bottles that can be used to sample water at discrete depths. These environmental properties can help explain differences in diversity and distribution, and provide insight on how communities may change with human impact such as climate change (Sperling et al., 2016).

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 score but, as we learn more about trophic support and food web dynamics, prey can be scored 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 of 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. seeps with active bubbling) and sinks (e.g. non-active 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. It is a first step required to uncover the value of natural resources that the deep ocean has to offer.

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. Although standardized sampling would increase the capacity for quantification and comparison of ecosystem services across space and time, this study highlights how the plethora of existing dive videos and analysis tools can be leveraged to generate useful information on ecosystem services, such as fisheries and climate-regulating services related to carbon. 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 human activities such as fishing, oil and gas extraction, waste disposal, and climate change (Armstrong et al., 2019). Mapping of ecosystem services is a popular method of identifying vulnerable areas in shallow waters (Burkhard et al., 2018), and could help with marine spatial planning in deep water when making decisions and creating priorities.

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Appendices

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

ROV: For each observation, fill out the video file name. Fill out the observation type: activity, habitat, substrate, lebenspurren (if applicable). Each file should have AT LEAST one of each of these observations. Then fill out the observation (e.g. stationary: inactive, soft sediment, etc.) and record the start and end times for each. Please use these characterizations unless something out of the ordinary comes up; then let Jen know. Note whether the observation is within the first minute of the video or not (Y/N).

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 lebenspurren: lots of pits and burrows, ampharetids, etc.

FAUNA:

4. Please check and update the fauna identification document regularly. Name new fauna with an identifier (e.g. color), number, or both. Also be careful to avoid typos, which will make it difficult to sort later in the process: be consistent! 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. Scores assigned to individual morphotypes found within this study.

Taxa	Common name	Commercial	Predator of target	Prey of target	Feeding mode	Mobility	Bioturbation	Diel vertical migration	Calcification	Body size	Sum_Fish	Sum_Carbon	References
Amphipod	Amphipod	0	0	1	1	1	2	1	1	1	1	7	
Actinaria sp 01	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell, 1977
Actiniidae sp 01	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell, 1977
Actiniidae sp 02	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell, 1977
Actiniidae sp 03	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell, 1977
Bolocera sp	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell, 1977
Liponema sp	Anemone	0	1	1	3	0	0	0	0	2	2	5	Purcell, 1977
Asteronyx sp	Brittlestar	0	1	1	4	1	3	0	0	3	2	11	Pearson & Gage, 1984; Fujita & Ohto 1988
Brisingidae	Brittlestar	0	1	1	3	1	3	0	0	3	2	10	Pearson & Gage, 1984; Fujita &

													Ohto 1988
Ophidiidae sp	Brittlestar	0	1	1	4	1	3	0	0	1	2	9	Pearson & Gage, 1984; Fujita & Ohto 1988
Ophiurida sp 01	Brittlestar	0	1	1	4	1	3	0	0	1	2	9	Pearson & Gage, 1984; Fujita & Ohto 1988
Spinophiura jolliveti	Brittlestar	0	1	1	4	1	3	0	0	1	2	9	Pearson & Gage, 1984; Fujita & Ohto 1988
Cataetyx rubirostris	Brotula	0	2	0	4	3	3	0	0	3	2	13	
Cladorhizidae	Carnivorous sponge	0	1	1	3	0	0	0	0	2	2	5	Vacelet & Duport, 2004
Scyliorhinidae	Catshark	0	2	1	4	3	1	0	0	3	3	11	
Chaetognath	Chaetognath	0	0	1	4	2	0	1	0	1	1	8	Alvarez-Cadena, 1993
Lucinidae	Clam	0	0	1	5	1	3	0	1	1	1	11	Peek, 1998

Vesicomyidae	Clam	0	0	1	5	1	3	0	1	1	1	11	Peek, 1998
Zoanthid	Coral	0	0	1	3	0	0	0	1	1	1	5	
Galatheid sp	Crab	0	1	1	2	1	3	0	1	2	2	9	Cartes, 1993
Lithodidae sp	Crab	0	1	1	2	1	3	0	1	3	2	10	Cartes, 1993
Lithodidae sp 02	Crab	0	1	1	2	1	3	0	1	3	2	10	Cartes, 1993
Paguroidea	Crab	0	1	1	2	1	3	0	1	2	2	9	Cartes, 1993
Bolinopsis sp	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Mills, 1995
Ctenophora spp 01	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Mills, 1995
Ctenophora spp 02	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Mills, 1995
Ctenophore03	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Mills, 1995
Lampocteis cruentiventer	Ctenophore	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Mills, 1995

Embassichthys bathybius	Deep sea sole	0	2	1	4	3	3	0	0	3	3	13	
Microstomas pacificus	Dover sole	1	2	1	4	3	3	0	0	3	4	13	
Dromalia alexandri	Dromalia	0	0	1	3	2	1	0	0	2	1	8	Hissmann, 2004
Zoarcid	Eelpout	0	2	1	4	3	3	0	0	3	3	13	
Folliculinidae	Folliculinid	0	0	0	5	0	0	0	0	1	0	6	Pasulka et al., 2017
Foram01	Foram	0	0	0	2	0	2	0	1	1	0	6	
Foraminifera	Foram	0	0	0	2	0	2	0	1	1	0	6	
Coryphaenoides acrolepis	Grenadier	0	2	1	4	3	3	0	0	3	3	13	
Nezumia liolepis	Grenadier	0	2	1	4	3	3	0	0	3	3	13	
Epatratus spp	Hagfish	0	1	1	1	3	3	0	0	3	2	10	
Merluccius productus	Hake	1	2	1	4	3	3	0	0	3	4	13	
Aeginura	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991
Atolla spp	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991

Jelly03	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991
Poralia refescens	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991
Scyphozoa spp 01	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991
Scyphozoa spp 02	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991
Voragonema pedunculata	Jelly	0	0	1	3	2	0	0	0	2	1	7	Angel, 1982; Larson, 1991
Ophiodon elongatus	Lingcod	0	2	1	4	3	3	0	0	3	3	13	
Midwater fish	Mid water fish	0	2	1	4	3	1	1	0	2	3	11	
Heteropolypus 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	Angel & Pugh, 2000

Bathyraja spinosissmia	Ray	0	2	1	4	3	3	0	0	3	3	13	
Rajidae spp	Ray	0	2	1	4	3	3	0	0	3	3	13	
Glyptocephalus zachirus	Rex sole	1	2	1	4	3	3	0	0	3	4	13	
Sebastes spp	Rock fish	1	2	1	4	3	3	0	0	3	4	13	
Anoplopoma fimbria	Sable fish	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	Miller et al., 2000
White Sea Cucumber	Sea cucumber	0	0	1	2	1	3	0	0	2	1	8	Miller et al., 2000
Funiculina sp	Sea pen	0	0	1	3	0	0	0	0	3	1	6	Best, 1988
Pennatulacea sp 01	Sea pen	0	0	1	3	0	0	0	0	3	1	6	Best, 1988
Sessiliflorae sp	Sea pen	0	0	1	3	0	0	0	0	3	1	6	Best, 1988
Asteroidea sp 01	Seastar	0	1	1	4	1	3	0	0	2	2	10	Lauerman, 1998
Hippasteria sp 01	Seastar	0	1	1	4	1	3	0	0	2	2	10	Lauerman, 1998
Eusergestes similis	Shrimp	0	1	1	4	3	1	1	1	1	2	11	Cartes, 1993
Pandalopsis sp	Shrimp	0	1	1	4	2	1	1	1	1	2	10	Cartes, 1993
Peracarid sp 01	Shrimp	0	1	1	4	3	1	1	1	1	2	11	Cartes, 1993

Petalidium suspiriosum	Shrimp	0	1	1	4	2	1	1	1	1	2	10	Cartes, 1993
Sergestidae sp	Shrimp	0	1	1	4	1	1	1	1	1	2	9	Flock & Hopkins, 1992
Siphonophore	Siphonophore	0	0	1	3	2	0	1	0	3	1	9	
Lyopsetta exilis	Slender sole	1	2	1	4	3	3	0	0	2	4	12	
Alepocephalus tenebrosus	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	
Alia snail	Snail	0	0	1	2	1	2	0	1	1	1	7	
Buccinidae 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	
Liparidae	Snail fish	0	2	1	4	3	3	0	0	2	3	12	
Nemichthyidae	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	
Sebastolobus alascanus	Thornyhead	1	2	1	4	3	3	0	0	3	4	13	
Sebastolobus altivelis	Thornyhead	1	2	1	4	3	3	0	0	2	4	12	
Tunicate 01	Tunicate	0	0	1	3	2	0	0	0	3	1	8	
Umbellula sp	Umbellula	0	0	1	3	0	0	0	0	3	1	6	
Strongylocentrotus fragilis	Urchin	0	1	1	2	1	3	0	1	2	2	9	
Nettastomatidae	Witchface eel	0	2	1	4	3	1	0	0	3	3	11	Merret, 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	
Polynoidae	Worm	0	0	1	4	1	2	0	0	1	1	8	Chevaldonné, 1998
Serpulid Polychaete	Worm	0	0	1	2	1	0	0	0	1	1	4	Bornhold & Milliman, 1973

Siboglinidae	Worm	0	0	1	2	1	2	0	0	1	1	6	Hilario et al., 2011