RESEARCH PAPER

Habitats and fish communities at mesophotic depths in the Mexican Pacific

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Abstract

Aim: Mesophotic ecosystems, found at the limit of light penetration in the ocean, are rich in biodiversity and harbour unique ecological communities. However, they remain among the least studied habitat zones on earth due to the high costs and technological limitations. Here, we characterize mesophotic communities in two marine reserves across a range of habitat types, depths and temperatures using submersible technologies, with the goal of understanding the processes that structure these communities across biogeographical regions.

Location: The Bay of La Paz and the Revillagigedo Archipelago, Mexico.

Taxa: Fish and algal species.

Methods: We used a small and inexpensive remotely operated vehicle (ROV) to conduct roving-swim surveys of major habitat types in depths from 12 to 94 m. With the resulting binary data on the presence of fish species, we used generalized linear mixed models and canonical correspondence analysis to determine whether biogenic habitat, depth and/or temperature best explained species richness and community structure across reef and non-reef substrate.

Results: We identified 72 species or genera, including new depth records for nine fish species and a new geographical record for one fish species. Our surveys included large undocumented rhodolith beds (free-living coralline algae) and mesophotic algal communities, in addition to diverse communities of soft corals and sponges. Fish species richness was positively associated with rocky substrate and warmer water, and reef fish communities differed significantly by depth, temperature and biogenic habitat.

Main conclusion: Our results highlight the importance of biogenic habitat in structuring communities across gradients of depth and temperature. We also demonstrate the effectiveness of a small and economical ROV for conducting mesophotic surveys in remote regions. Our methods and results provide a framework that can be used to greatly increase the biogeographical and taxonomic scope of mesophotic research, especially for readily identifiable taxa such as fish.

KEYWORDS

Baja California, canonical correspondence analysis, maërl, marine-protected areas, mesophotic algae, mesophotic zone, Mexico, Revillagigedo, rhodolith, ROV

1 | INTRODUCTION

The mesophotic zone, a region of low light found between approximately 30–150 m beneath the ocean surface, is largely unexplored and unstudied, especially in the eastern Pacific (Hinderstein et al., 2010; Kahng et al., 2010). The twilight depths of the mesophotic zone are beyond open-circuit diving limits and shallower than areas traditionally explored by large deep-sea submersibles. This results in a dearth of understanding of the ecology of these depths due to limitations in technology and research funding. Depending on the region and taxa surveyed, the mesophotic zone could serve as an important ecological refuge from overexploitation or climatic variability (Assis et al., 2016; Bongaerts, Ridgway, Sampayo, & Hoegh-Guldberg, 2010), or this depth range could represent a distinct ecosystem worthy of focused management and protection (Rocha et al., 2018; Semmler, Hoot, & Reaka, 2017). Understanding the identities of organisms occupying mesophotic ecosystems and what influences their distribution is crucial to managing near-shore marine resources, quantifying and monitoring ecosystem connectivity, and understanding the patterns and processes governing biodiversity in the ocean.

Our surveys focused on the biogeographical provinces of Cortez (Bay of La Paz [BLP]) and the Oceanic Islands (Revillagigedo Archipelago) in Mexico, according to the classification of fish fauna (Robertson & Cramer, 2009; Figure 1). Both regions are known for high marine biodiversity driven by complex hydrographic mixing of water from the California Current and the North Equatorial Current, as well as deep water masses that shoal to sunlit depths by the steep bathymetry and underwater canyons of both regions (Castro, Durazo, Mascarenhas, Collins, & Trasviña, 2006; Leon-Tejera, Serviere-Zaragoza, & Gonzalez-Gonzalez, 1996). This shoaling and mixing elevates the thermocline to the mesophotic zone, allowing tropical- and temperate-associated species to coexist in relative proximity. Due to this coexistence, the BLP is estimated to have among the highest species richness of fishes in the northeast Pacific (Castro-Aguirre, Balart, & Arvizu-Martínez, 1996). The Revillagigedo Archipelago has similarly high fish biodiversity, with species representing multiple comingling biogeographical regions (Fourriére, Reyes-Bonilla, Ayala-Bocos, Ketchum, & Chávez-Comparan, 2016). All islands in both regions, with the exception of Cerralvo Island in the BLP, are managed within the Mexican National Parks system (CONANP 2018).

Despite their status as biodiversity hotspots and national parks, no published field studies exist that document the habitats and fish communities found at depths >30 m in the BLP or the Revillagigedo Archipelago (Arreola-Robles & Elorduy-Garay, 2002; Castro-Aguirre & Balart, 2004; Chávez-Comparán et al., 2010). The current literature on mesophotic ecology is largely dominated by tropical coral reef studies, with the majority from the Atlantic Ocean and the Caribbean Sea (reviewed in Loya, Puglise & Bridge, 2019). Our goal, therefore, was to survey ecosystems in the mesophotic zone in a region of tropical and subtropical mixing and to characterize the diversity of fish species in the biogeographical provinces of Cortez (BLP) and the Oceanic Islands (Revillagigedo Archipelago). We intentionally targeted both reef and non-reef substrates to capture a wider diversity of habitats and associated species, and to assess the influence of biogenic versus abiotic substrate on fish diversity patterns at mesophotic depths. Our primary tool to conduct these surveys was a small, low-cost remotely operated vehicle (ROV), the expanded use of which could drastically increase our knowledge of mesophotic ecosystems, especially in remote areas.

2 | MATERIALS AND METHODS

2.1 | Survey methodology

All surveys were conducted using a small (roughly 1 m^3 and 11 kg) and highly portable ROV (BlueRobotics BlueROV2) capable of diving to 100 m and equipped with four 1,500 lumen lights, two cameras that filmed in 1,080 p resolution (one 8MP Raspberry Pi v2 Camera and one GoPro HERO3 or HERO4), a Measurement Specialties MS5837-30BA sensor that measured depth and temperature, and a 250 m tether (see Appendix S1 in Supporting Information for image of ROV). The total cost of this device was under $5,000, making it a financially accessible tool for research groups with small budgets. Surveys were done while live boating from a small craft, with the exception of El Bajo where surveys were done at anchor. At each site, the ROV operator would descend the ROV directly to the benthos and begin roving-swim surveys, shown to be highly effective in quantifying species diversity (Schmitt, Sluka, & Sullivan-Sealey, 2002). The duration of surveys ranged from 7 to 65 min, depending on weather and ocean conditions, battery duration and cruise schedules. Video, depth and temperature were continuously recorded and saved for later analysis.

2.2 | Site selection

We surveyed nine sites in the El Bajo-Espíritu Santo National Park and around Isla Cerralvo in the BLP in October 2018, and 11 sites around the islands of Socorro, Clarión and San Benedicto in the Revillagigedo National Park (RNP) in December 2018 (Figure 1; Table S1). Sites were chosen based on sea surface clarity, bathymetry and day of swell conditions. To estimate sea surface clarity, we used data on sea surface net primary production from NASA's Moderate Resolution Imaging Spectroradiometer with a resolution of 0.0125°, and targeted regions that showed estimated chlorophyll *a* levels of <0.15 mg/m^3 for the months of our surveys. We used Navionics SonarChart maps to choose regions with rapid depth change to increase the likelihood of deep-water shoaling and therefore mixing of water masses. Since these bathymetric charts were often inaccurate, especially in RNP, we also used boat mounted or handheld depth sounders to measure depth once we reached the target region. Sites in Socorro and Clarión Islands were also chosen based on the results of the Graham, Kinlan, Druehl, Garske, and Banks (2007) model predicting locations of deep-water
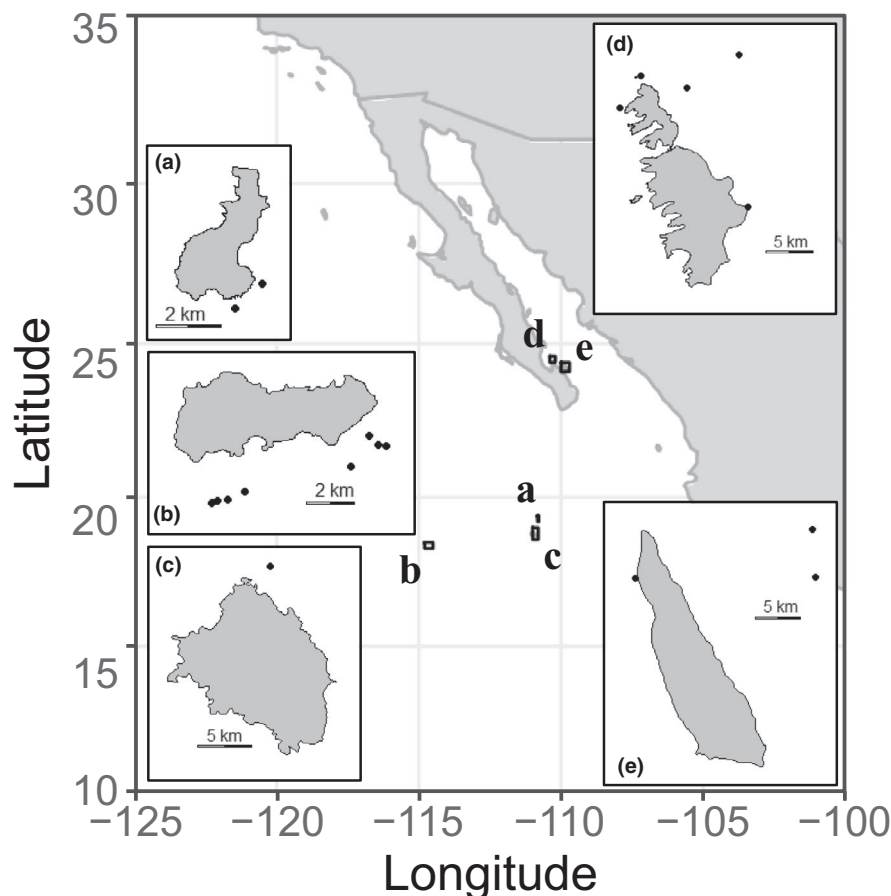
FIGURE 1 Study sites around the islands of the Revillagigedo National Park, including (a) San Benedicto, (b) Clarión and (c) Socorro; and the islands of the Bay of La Paz, including (d) El Bajo-Espíritu Santo National Park and (e) Cerralvo. Scale bars are included in each island inset

kelp ecosystems. Sites in San Benedicto focused on the lava flow of the 1952 Bárcena eruption. We conducted additional shallow water (<30 m) transects over this geological feature to document any recruitment of scleractinian coral since the Bárcena eruption.

2.3 | Data collection from video transects

Footage from the GoPro and Raspberry Pi cameras were synchronized for each dive and cut into 5-min transects, starting at the time the ROV reached the benthos. In each video, all fish were identified to the lowest possible taxonomic level using Robertson and Allen (2015). To determine the known depth distributions for species we identified, we compiled information from records in Robertson and Allen (2015), Ocean Biogeographic Information System (OBIS, 2019) and FishBase (Froese & Pauly, 2009). Algae were identified using herbarium records via the University and Jepson Herbaria Specimen Portal (v5.2.0) and with assistance from Dr. Kathy Ann Miller (University of California, Berkeley). Biotic and abiotic habitat characteristics of each transect were also noted. Biogenic habitat represented the dominant foundation species group (sensu Dayton, 1972) that contributed to three-dimensional habitat, including coral, unidentified filamentous algae, rhodolith beds (also termed maërl, comprised of colonies of slow-growing, free-living coralline algae; Foster, 2001), turf (broadly encompassing encrusting organisms such as algae, bryozoans, hydroids and crustose coralline algae) and

burrows in sand (see Appendix S2 for representative images of habitat classifications). Substrate classifications included reef (continuous hard substrate or large semi-continuous boulders) and non-reef (small patches of unconsolidated hard substrate over sand, or sand). Depth (m) and temperature (°C) for each transect were averaged and rounded to the nearest integer.

2.4 | Fish species richness

We tested whether environmental variables (fixed effects of depth, temperature and reef vs. non-reef substrate) predicted patterns of species richness using generalized linear mixed effects models with a Poisson distribution and a random effect of dive site. Analysis was done using the LME4 package in R v. 3.5.2 (Bates, Maechler, Bolker, & Walker, 2015).

2.5 | Fish community analyses

All statistical analyses were based on the presence or absence of fish species. We used canonical correspondence analysis (CCA), a multivariate constrained ordination technique, to assess the significance of environmental variables (depth, temperature and habitat) to explain community composition. Community composition in the model was defined as presence or absence of a binary matrix of

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TABLE 1 Family, genus and species of organisms observed in our transects, depth range (m), number of transects in which the species was observed in each region (Cer, Cerralvo; Esp, Espíritu Santo; Cla, Clarión; Soc, Socorro; San, San Benedicto), diet (Herb, Herbivore; Invert, Invertebrates; Omniv, Omnivore; Pisc, Piscivore; Zoo, Zooplankton) and IUCN status of each species if available (DD, data deficient; EN, endangered; LC, least concern; NT, near threatened; VU, vulnerable)

Group	Family	Species	Depth range	Cer	Esp	Cla	Soc	San	Diet	IUCN status
Fish	Acanthuridae	Acanthurus nigricans	18–57	0	0	0	0	5	Herb.	LC
Fish	Acanthuridae	Acanthurus xanthopterus	42–67	0	1	0	1	0	Herb.	LC
Fish	Acanthuridae	Prionurus laticlavius	30–49*	2	3	0	0	0	Herb.	LC
Fish	Aulostomidae	Aulostomus chinensis	31–82	0	0	5	0	1	Pisc.	LC
Fish	Balistidae	Balistes polylepis	45–82	0	5	4	1	0	Invert.	LC
Fish	Balistidae	Sufflamen verres	20–76	0	2	1	1	1	Invert.	LC
Fish	Balistidae	Xanthichthys mento	18–90	0	0	12	3	9	Zoo.	LC
Fish	Carangidae	Caranx caballus	45	1	1	0	0	0	Pisc.	LC
Fish	Carangidae	Caranx lugubris	34–94	0	0	12	3	6	Pisc.	LC
Fish	Carangidae	Caranx melampygus	18–80	0	0	3	3	7	Pisc.	LC
Fish	Carangidae	Elagatis bipinnulata	67	0	0	0	1	0	Pisc.	LC
Fish	Carangidae	Seriola rivoliana	45–94	2	2	13	0	0	Pisc.	NA
Fish	Carcharhinidae	Carcharhinus albimarginatus	20–90	0	0	5	2	6	Pisc.	VU
Fish	Carcharhinidae	Carcharhinus falciformis	34–84	0	0	4	0	8	Pisc.	VU
Fish	Carcharhinidae	Carcharhinus galapagensis	66–72	0	0	0	3	1	Pisc.	NT
Fish	Carcharhinidae	Triaenodon obesus	20–73	0	0	1	3	4	Pisc.	NT
Fish	Chaetodontidae	Chaetodon humeralis	60–62	0	2	0	0	0	Omniv.	LC
Fish	Chaetodontidae	Forcipiger flavissimus	31–72	0	0	0	2	6	Invert.	LC
Fish	Chaetodontidae	Johnrandallia nigrirostris	42–74*	0	3	0	0	0	Omniv.	LC
Fish	Chaetodontidae	Prognathodes falcifer	41–94	4	7	6	1	3	Invert.	NA
Fish	Dasyatidae	Hypanus longus	64	0	0	0	0	1	Invert.	DD
Fish	Diodontidae	Chilomycterus reticulatus	38–74	1	0	1	1	1	Invert.	LC
Fish	Diodontidae	Diodon holocanthus	20–94	1	4	9	1	2	Invert.	LC
Fish	Diodontidae	Diodon hystrix	30	1	0	0	0	0	Invert.	LC
Fish	Fistulariidae	Fistularia commersonii	31–69	1	1	2	1	1	Pisc.	LC
Fish	Haemulidae	Anisotremus interruptus	18–76*	2	3	5	2	5	Invert.	LC
Fish	Haemulidae	Haemulon sexfasciatum	30–55	2	3	0	0	0	Pisc.	LC
Fish	Labridae	Bodianus diplotaenia	20–84*	1	5	7	3	11	Invert.	LC
Fish	Labridae	Halichoeres dispilus	62	0	1	0	0	0	Invert.	LC
Fish	Labridae	Halichoeres melanotis	67*	0	1	0	0	0	Invert.	LC
Fish	Labridae	Semicossyphus pulcher	69	0	1	0	0	0	Invert.	VU

TABLE 1 (Continued)

Group	Family	Species	Depth range	Cer	Esp	Cla	Soc	San	Diet	IUCN status
Fish	Labridae	*Thalassoma lucasanum*	57	0	0	0	0	1	Invert.	LC
Fish	Lutjanidae	*Lutjanus argentiventris*	20–70	2	4	0	0	1	Pisc.	LC
Fish	Lutjanidae	*Lutjanus guttatus*	50–55	0	2	0	0	0	Invert.	LC
Fish	Lutjanidae	*Lutjanus jordani*	50–86	4	4	0	0	0	Pisc.	LC
Fish	Lutjanidae	*Lutjanus novemfasciatus*	49–55	0	2	0	0	0	Pisc.	LC
Fish	Lutjanidae	*Lutjanus viridis*	20–67	0	0	0	1	4	Pisc.	LC
Fish	Mocanthidae	*Cantherhines dumerilii*	34–69	0	0	0	2	2	Omniv.	LC
Fish	Mullidae	*Mulloidichthys dentatus*	30–45	2	0	0	0	0	Invert.	LC
Fish	Muraenidae	*Gymnothorax castaneus*	66*	0	0	0	1	0	Pisc.	LC
Fish	Muraenidae	*Muraena argus*	56–84	1	1	0	0	0	Pisc.	LC
Fish	Ophichthidae	*Quassiremus evionthas*	60–80*	0	0	2	0	0	Pisc.	VU
Fish	Ostraciidae	*Ostracion meleagris*	42	0	1	0	0	0	Invert.	NA
Fish	Pomacanthidae	*Holacanthus clarionensis*	31–90	0	0	8	2	8	Invert.	VU
Fish	Pomacanthidae	*Holacanthus passer*	30–74	2	9	0	0	0	Invert.	LC
Fish	Pomacentridae	*Chromis alta*	48–94	0	1	8	0	2	Invert.	LC
Fish	Pomacentridae	*Chromis limbaughi*	41–80	0	11	0	0	0	Zoo.	LC
Fish	Pomacentridae	*Stegastes leucorus*	34–58*	0	0	0	2	3	Herb.	VU
Fish	Priacanthidae	*Heteropriacanthus cruentatus*	57–94	0	0	4	0	2	Invert.	LC
Fish	Priacanthidae	*Pristigenys serrula*	62–86	4	2	3	0	0	Zoo.	LC
Fish	Scaridae	*Scarus ghobban*	42–45	0	2	0	0	0	Herb.	LC
Fish	Scorpaenidae	*Scorpaena guttata*	62–86	1	1	0	0	0	Invert.	NA
Fish	Serranidae	*Cephalopholis panamensis*	42–62	0	1	0	0	2	Pisc.	LC
Fish	Serranidae	*Dermatolepis dermatolepis*	34–76*	0	0	3	2	3	Pisc.	LC
Fish	Serranidae	*Epinephelus cifuentesi*	62–94	0	0	6	0	2	Pisc.	LC
Fish	Serranidae	*Epinephelus clippertonensis*	34–81	0	0	2	0	5	Pisc.	LC
Fish	Serranidae	*Epinephelus labriformis*	31–94	0	3	8	1	4	Pisc.	LC
Fish	Serranidae	*Liopropoma fasciatum*	41–86	3	10	0	0	0	Invert.	LC
Fish	Serranidae	*Mycteroperca rosacea*	30–55	2	3	0	0	0	Pisc.	LC
Fish	Serranidae	*Paranthias colonus*	18–94	1	11	12	2	12	Zoo.	LC
Fish	Serranidae	*Serranus psittacinus*	30–70	1	6	0	0	0	Pisc.	LC
Fish	Serranidae	*Serranus socorroensis*	74–79*	0	0	2	0	0	Pisc.	VU
Fish	Synodontidae	*Synodus lacertinus*	62–83	1	5	0	0	0	Pisc.	LC

TABLE 1 (Continued)

Group	Family	Species	Depth range	Cer	Esp	Cla	Soc	San	Diet	IUCN status
Fish	Tetraodontidae	*Arothron meleagris*	31–57	0	0	0	0	3	Invert.	LC
Fish	Urotrygonidae	*Urobatis concentricus*	45	0	1	0	0	0	Invert.	DD
Fish	Zanclidae	*Zanclus cornutus*	34–69	0	1	0	1	2	Invert.	LC
Algae	Codiaceae	*Codium* sp.	43–60	0	0	2	0	0		
Algae	Dasycladaceae	*Neomeris* sp.	18–31	0	0	0	0	2		
Algae	Dictyotaceae	*Padina* sp.	60	0	0	1	0	0		
Algae	Dictyotaceae	*Spatoglossum* sp.	60	0	0	1	0	0		
Algae	Halimedaceae	*Halimeda* sp.	43–60	0	0	2	0	0		
Algae	Palmophyllaceae	*Palmophyllum* sp.	67–92	0	0	10	3	0		
Algae		Unidentified red blade	58–80	0	0	5	0	0		
Algae		Unidentified encrusting red	23–92	4	17	23	3	9		
Algae		Unidentified rhodolith	43–92	0	0	22	0	0		
Algae		Unidentified filamentous	16–80	0	0	2	0	12		

Note: Asterisks indicate new depth records or new geographical records based on data from FishBase (Froese & Pauly, 2009), OBIS (2019) and Robertson and Allen (2015).

species for each transect. The explanatory variables included standardized depth and temperature (mean = 0, *SD* = 1) recorded at the beginning of each transect, biogenic habitat (coral, algae, rhodolith, turf and burrows) and substrate (reef and non-reef). To determine the environmental variables that best explained the ordination, we conducted permutation analyses to test the significance of the CCA models, the marginal effects of each variable and the significance of the first two axes of each model. Statistics were conducted using the VEGAN package in R v. 3.5.2 (Oksanen et al., 2019).

3 | RESULTS

We completed a total of 81 transects around the islands and seamounts in BLP (El Bajo, Espíritu Santo and Cerralvo) and RNP (Socorro, San Benedicto and Clarión), covering depth ranges from to 12–94 m and temperature ranges from 18 to 29°C (see Appendix S2). We identified 72 species or genera representing 38 families, including 66 fish species and six algal genera (Table 1). Some organisms could not be identified given the quality of our videos or due to mobile organisms appearing only transiently in the periphery of the ROV's light field, and these were not included in our analysis. Our observations extended the observed depth range of nine species and the geographical range of the Galapagos snake eel (*Quassiremus evionthas*). *Quassiremus evionthas* was previously only registered in the Galapagos and Cocos Islands but was observed in two of our surveys around Clarión Island (see Appendix S3 for video). Of the fish species, 25%, or 17 species, were observed in both BLP and RNP. The most species-rich family was Serranidae (10 species), followed by Carangidae, Labridae, Lutjanidae and Pomacanthidae (five species). Most fish species were found throughout the depths surveyed, though of the fish observed on more than one transect, some appeared to have affinities for either shallower (<40 m) or deeper (>60 m) depths (Figure 2). Shallower species included the surgeonfish *Acanthurus nigricans* and pufferfish *Arothron meleagris* while deeper species included the snapper *Heteropriocanthus cruentatus*, the grouper *Epinephelus cifuentesi* and the bigeye *Pristigenys serrula*. Non-filamentous macroalgae were observed from 18 to 60 m in RNP and extensive rhodolith beds were observed at Clarión Island from 42 to 81 m. Of the algal species we could identify to genus, half were calcifying species (*Neomeris*, *Padina* and *Halimeda*).

Habitat types varied across biogeographical regions and depths. Coral habitats represented the majority of transects and were found around Clarión Island and the BLP islands at depths of 30–94 m. We observed limited numbers of encrusting scleractinian coral colonies along the San Benedicto lava flow at depths <30 m (see Appendix S5 for additional discussion). No stony or soft coral was observed on the lava flow below 30 m. The deeper coral habitats were exclusively around Clarión and were dominated by sea fan species (*Pacifigorgia*, *Eugorgia*) with occasional black corals (*Antipathes*), compared to the soft corals (*Lophogorgia*, *Leptogorgia*, *Muricea* and others) and black coral (*Athipathes galapagensis*) that characterized BLP mesophotic reefs. The reefs of Clarión had scattered populations of *Palmophyllum*, a genus of green alga of ancient origin found in deep waters (Zechman
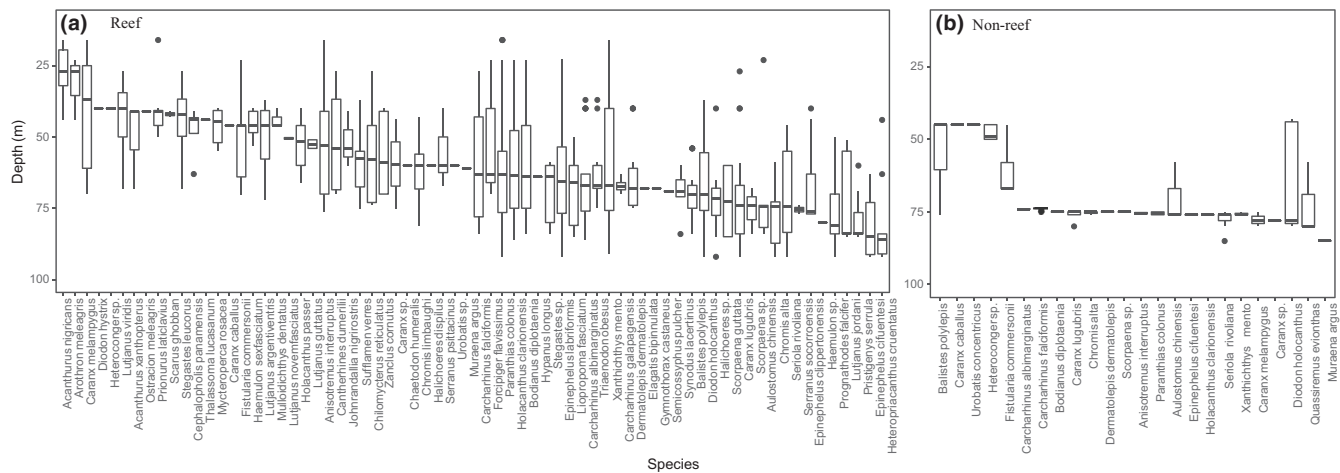
FIGURE 2 Depth observations of fish species in (a) reef and (b) non-reef habitats in the Bay of La Paz and the Revillagigedo Archipelago. For each species, horizontal lines represent mean value for depth, boxes represent 25th and 75th quartile values, error bars represent 1 *SE* and points represent outlier values

TABLE 2 Generalized linear mixed effects model results describing the relationship between fish species richness and environmental variables, including depth, temperature and substrate (reef vs. non-reef). Site-level variance was 0.14 with *SD* of 0.38

	Estimate	SE	z	Pr (>|z|)
Depth (m)	0.01	0.01	0.95	0.34
Temperature (°C)	0.14	0.04	3.13	0.002
Substrate – Reef	1.28	0.18	7.24	< 0.001

et al., 2010). Turf habitat was found at depths from 62 to 81 m around Espíritu Santo, Socorro and in deeper regions of San Benedicto. The turf habitat around Socorro also had populations of *Palmophyllum*. Burrow habitat was found in regions of sandy bottoms in Clarión and the islands of BLP from depths of 37–86 m. Rhodolith beds were widespread around the Clarión Island sites surveyed from 70 to 80 m. Rhodolith beds surveyed on the southeast coast of Clarión co-occurred with green and brown algae (*Halimeda*, *Padina*, *Codium* and *Spatoglossum*) while those on the south coast co-occurred mainly with erect, fleshy red algae that we were unable to identify (see Appendix S4 for images of algae). Sponge habitats were limited to deep transects (83–87 m) around Cerralvo Island. Substrate dominated by filamentous algae was only observed surrounding the Bárcena eruption lava flow at San Benedicto at depths from 18 to 62 m, though we observed smaller colonies of the filamentous algae up to 80 m.

3.1 | Fish species richness

Fish species richness was best predicted by temperature and substrate (Table 2). Richness increased with temperature and was greater in reef habitats than non-reef habitats (Figure 3).
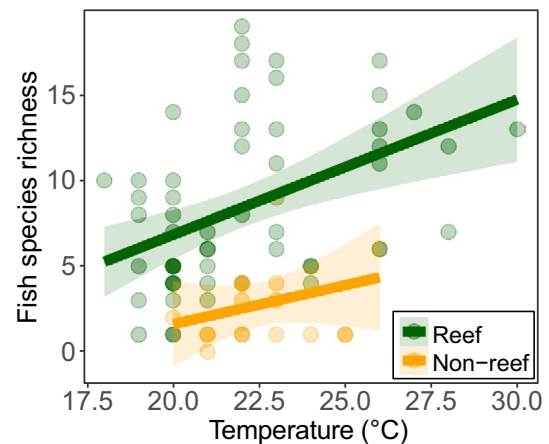

FIGURE 3 Fish species richness by temperature (°C) and habitat, including reef (green) and non-reef (yellow). Points represent transects, lines represent a linear least squares regression of richness by habitat and shading indicates 95% confidence interval [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Fish community analyses

Fish communities found in reef and non-reef habitats significantly differed from one another (χ^2 = 0.25, *p* = 0.001; Figure 4a).

Among fish communities in reef habitat, we found that the constraining variables of temperature, depth and biogenic habitat (algae, coral, sponge and turf) all significantly explained community composition (Figure 4b; Table 3). The first CCA axis explained 34% of the total model inertia and differentiated communities by biogenic habitat with the algal and turf group loading negatively and the coral and sponge group tending more positively. Both groups contained diverse trophic assemblages, including herbivores such as the damselfish *Stegastes leucorus*, omnivores such as the filefish *Cantherhines*
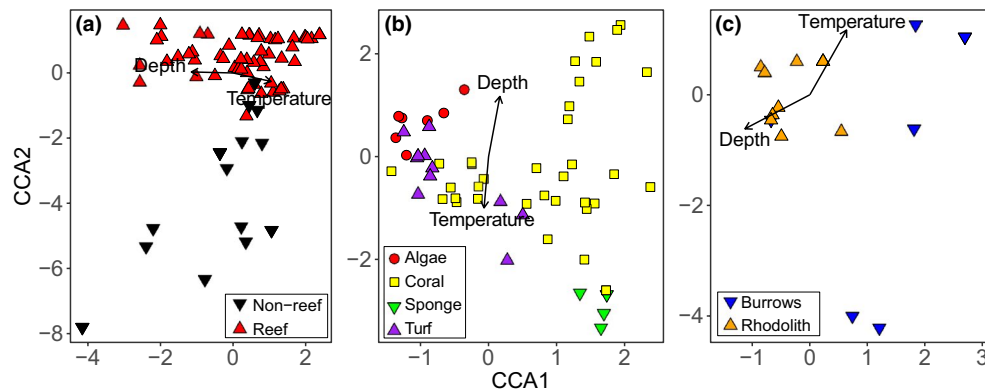
FIGURE 4 Canonical correspondence analysis (CCA) of binary fish community data as predicted by temperature, depth and habitat, including (a) reef and non-reef habitat, (b) reef-associated habitat only, including algae, coral, sponge and turf reefs and (c) non-reef-associated habitat only, including sand burrows and rhodolith beds. Each point represents a transect [Colour figure can be viewed at wileyonlinelibrary.com]

dumerilii, and carnivores such as jacks (*Caranx* spp.; see Appendix S6 for CCA axes loadings). The second CCA axis explained 29% of the total model inertia and differentiated communities by temperature and depth. This axis also differentiated sponge habitat, found only in deep zones (>80 m), from the other biogenic habitats. These deepest and sponge-dominated sites were characterized by carnivorous species, including the snapper *Lutjanus jordani*, the soldierfish *P. serrula* and the scorpionfish *Scorpaena guttata*. Herbivorous species, such as surgeonfish (*Acanthurus* spp.), sawtails (*Prionurus laticlavius*) and parrotfish (*Scarus ghobban*), all loaded strongly positively on the second CCA axis, suggesting a strong association with warmer and shallower regions.

Among non-reef habitats, including rhodolith beds and sand, neither temperature and depth nor biogenic habitat significantly explained community composition. However, the first CCA axis was significant, explaining 44% of the total model inertia. This axis generally differentiated communities by biogenic habitat (Figure 4c; Table 3, see Appendix S6 for CCA axes loadings). Burrow habitat grouped on the positive CCA1 axis which was most characterized by garden eels (*Heteroconger* sp.) that create the burrow habitat, the stingray *Urobatis concentricus* and the green jack *Caranx caballus* which are associated with soft or rubble bottoms near reefs, and the moray *Muraena argus* which is known to be associated with reefs and rocky bottoms but was only observed in sandy habitat. Rhodolith habitat grouped around zero on the CCA1 axis which was characterized by carnivores, including the Galapagos snake eel (*Q. evionthas*).

4 | DISCUSSION

It is generally accepted that biogenic habitat and temperature structure fish communities in shallow water, but most studies of mesophotic depths focus only on the ecological effects of depth (e.g. Coleman, Copus, Coffey, Whitton, & Bowen, 2018; Garcia-Sais, 2010; Sih, Cappo, & Kingsford, 2017) or discuss temperature and habitat without explicit testing (e.g. Fukunaga, Kosaki, Wagner, & Kane, 2016; Pinheiro et al., 2016; Simon et al., 2016; but see Baldwin, Tornabene, & Robertson, 2018). Using survey data spanning multiple habitat types, depths and temperatures, we found that biogenic habitat, temperature and depth were all important factors in shaping patterns of species richness and community composition in mesophotic zones across two east Pacific biogeographical provinces. Depth was an influential factor regarding community composition but not species richness. These patterns were apparent in spite of the fact that our findings represent conservative estimates of richness and community structure due to our limited ability to identify the more cryptic species that often define some habitats (Steller, Riosmena-Rodríguez, Foster, & Roberts, 2003). Considering the dominance of scleractinian coral reefs in the mesophotic literature, our results highlight the importance of surveying across multiple

TABLE 3 Canonical correspondence analysis (CCA) permutation test results for reef and non-reef models

	df	χ^2	F_{perm}	$Pr(>F_{perm})$
Reef				
Total model	5	1.45	2.51	0.001
Axis 1	1	0.50	4.29	0.001
Axis 2	1	0.42	3.64	0.001
Marginal effects				
Temperature	1	0.23	1.98	0.001
Depth	1	0.23	1.99	0.01
Habitat	3	0.89	2.56	0.001
Non-reef				
Total model	3	1.62	1.71	0.009
Axis 1	1	0.72	2.28	0.05
Axis 2	1	0.54	1.71	0.15
Marginal effects				
Temperature	1	0.46	1.46	0.11
Depth	1	0.41	1.31	0.11
Habitat	1	0.45	1.45	0.07

habitat types to better understand regional community composition (Kahng, Copus, & Wagner, 2014).

Despite observing significant changes in fish community composition with increasing depth and decreasing temperature in reef habitat, we did not find assemblage breakpoints as have been identified in other mesophotic studies (e.g. Baldwin et al., 2018; Bejarano, Appeldoorn, & Nemeth, 2014; Semmler et al., 2017). Rather, we observed a gradient in fish depth distributions. This lack of faunal breakpoints in the studied depth range could be due to the complex vertical mixing of water masses around the islands surveyed, especially in areas of rapid depth change (Aburto-Oropeza & Balart, 2001), which can dampen the segregation of communities by providing similar habitat conditions and resources along a wide gradient of depth.

Food availability likely drove our observed patterns in fish species richness. We found that species richness was higher in reef habitat and warmer waters, which is consistent with observations in shallow fish communities in BLP (Aburto-Oropeza & Balart, 2001; Pérez-España, Galván-Magaña, & Abitia-Cárdenas, 1996), where a higher number of species were observed at vertical walls and boulder habitat in the warm season (June–November, T° > 20°C) compared to rhodolith and sand habitat or the cold season. Reef habitat tends to be more complex than non-reef and thus shelters a greater number of species and provides a wider variety of food resources compared with more homogeneous habitat, such as rhodolith beds, which tend to be dominated by specialist organisms (Cúrdia et al., 2015; Foster, 2001). Likewise, cold water in BLP is often associated with lower primary production and recruitment, and therefore less food (Pérez-España et al., 1996). While our surveys only took place during the warm season, our deepest transects registered similar temperatures as are observed during the cold season (<20°C), suggesting fewer food resources. These deep low-light environments were seemingly devoid of photosynthesizing species, including zooxanthellate corals, and dominated by carnivorous fish species which suggests little to no primary production occurring at these depths and temperatures.

The fish communities we observed at mesophotic depths also differed from published shallow water (<30 m) species assemblages. Our dataset for BLP had a 65% overlap (28 species) with the shallow water fish surveys of Arreola-Robles and Elorduy-Garay (2002), while our dataset for Socorro Island in RNP overlapped 80% (21 species) with shallow water surveys in Socorro by Chávez-Comparán et al. (2010). A comparable proportion of overlapping species were observed between shallow and mesophotic reefs in Hawaii (79%; Fukunaga et al., 2016), though these proportions are lower than the 95% overlap reported from Puerto Rican reefs (Garcia-Sais, 2010) and higher than the 27% reported from multiple sites in the Pacific and western Atlantic by Rocha et al. (2018). This range of proportions emphasizes the difficulties in generalizing the interchange between shallow and mesophotic communities across different biogeographical regions due to oceanographic differences. The fact that there is not a 100% overlap between shallow and mesophotic fish fauna indicates that the reservoir hypothesis, which considers

deep reefs to be refugia for overexploited or threatened species (e.g. Lindfield, Harvey, Halford, & McIlwain, 2016), should be considered with caution in these regions. Much research is still needed to identify which species are depth generalists versus specialists so management strategies can be adjusted accordingly, especially in highly managed coastal ecosystems such as these National Parks.

In addition to novel depth and geographical records for some fish species, our observations of mesophotic algal species in RNP add to the growing body of literature on photosynthetic organisms residing at depth (reviewed in Spalding et al., 2018). Notably, we observed no algae in any of the BLP sites surveyed at comparable depths and temperatures. Around the islands of RNP, we observed at least eight genera of mesophotic algal species, including vast rhodolith beds undescribed in the literature (Foster, 2001; Spalding et al., 2018). Rhodoliths had been previously collected in the region from bottom trawls (e.g. Taylor, 1939) and our data reveal the geographical extent and biodiversity of this habitat around Clarión Island. The spherical growth morph we encountered is generally associated with areas of intermediate water motion and bioturbation (Foster, 2001; Marrack, 1999). We observed high currents and species such as the Mexican hogfish (*Bodianus diplotaenia*) and the pink flower sea urchin (*Toxopneustes roseus*) feeding in the rhodoliths, which together could provide the necessary level of disturbance to maintain these free-living algae (James, 2000).

The associated macroalgal communities in the rhodolith beds differed substantially between the south and southeast shores of Clarión, possibly due to different light regimes. Fleshy red macroalgae, which could not be identified beyond phylum, predominated in south-shore sites while green and brown species, including large meadows of *Halimeda*, were abundant on the southeast side of the island. Deep-water meadows of *Halimeda* have been found throughout the tropics, including but not limited to Hawaii (Spalding, 2012), Australia (Drew, 2001) and the Caribbean (Jensen, Gibson, Littler, & Littler, 1985; Leichter, Stokes, & Genovese, 2008) but had never been reported in RNP. Interestingly, the southeast side of Clarión Island was a region predicted to have favourable conditions for mesophotic kelp due to hypothesized high nutrient levels from deep-water shoaling and high irradiance at depth due to clear surface waters (Graham et al., 2007). While we did not find any kelp species, the algal assemblages here were markedly more diverse than all other sites surveyed, supporting the hypothesis that mesophotic light and nutrient conditions were more favourable for macroalgal growth.

Our study was made possible by rapidly improving submersible technologies that drastically increase the accessibility of mesophotic depths by precluding the need for specialized dive training and closed- or open-circuit diving equipment. As is common in mesophotic studies in poorly known regions, our observations increased the known depth and geographical ranges of multiple species and identified previously undocumented habitats. By including multiple habitat types in our survey efforts, our findings highlight the importance of foundation species in structuring communities even in the mesophotic zone. While human divers using

closed-circuit diving technology remain the gold standard for mesophotic surveying and collections (Sherman et al., 2009), we hope that expanded use of small and affordable ROV technology can improve monitoring efforts to ensure the appropriate habitat-specific management and conservation of these unique and diverse ecosystems.

DATA AVAILABILITY STATEMENT

All data used for analysis, including presence data for fish and algae, and site metadata, are available in a public repository hosted by Dryad, found at the following link: https://doi.org/10.5061/dryad.pnvx0k6j3.

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BIOSKETCH

Jordan A. Hollarsmith is broadly interested in how environmental heterogeneity influences ecosystem resilience and management strategies. This work represents a component of her PhD research at UC Davis on species adaptation to and refugia within heterogeneous environments.

Author contributions: JAH, GRO, TW and KD conceived the ideas; JAH, GRO, TW, MVL, KD, KCN and HRB conducted the fieldwork and analysed video footage; JAH, KD and EDG analysed the data; and JAH led the writing with assistance and edits from all authors.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.