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Variation in the structure of the deep-sea fish assemblages on Necker Island, Northwestern Hawaiian Islands

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ABSTRACT

Evidence is accumulating that within any given seamount, the abundance and diversity of fauna may vary strongly with environmental variability. Necker Island, located in the Northwestern Hawaiian Islands, has not been subject to commercial trawl fisheries and is currently protected from fishing activities as part of the Papahānaumokuākea Marine National Monument. The relatively pristine nature of this seamount makes it an excellent location to assess the abundance and diversity of the deep-sea fish fauna of a seamount and their variability relative to environmental parameters, with minimal confounding of natural patterns by human impacts. Using 51,988 AUV photos that showed 18,478 fishes, 92 species were identified from three study sites on different slopes of Necker Island at depths of 200–700 m. The deep-sea fish assemblages were dominated by Stomiiformes, Gadiformes, Myctophiformes, Aulopiformes, and Perciformes. From 250 to 700 m, relative abundance of fishes was significantly different among study sites, with the NE side having the lowest abundance. Species richness and rarefaction estimates of the expected species richness showed significant differences by study site, depth, and their interaction. The NE slope of the island had the lowest estimated richness. By depth, species richness showed two peaks, one at 350 m and the highest at 500 m, in which diversity was also very high with low dominance. The highest values of dominance were observed at 250 and 700 m. Community structure was significantly different by study site, depth, and their interaction. Variation by depth was observed in the NMDS plot, with three assemblages characterized by different dominant species. Fish assemblage structure was correlated with dissolved oxygen, salinity, percentage of sand, rugosity, slope, POC, and current vectors u and v. These results support significant variability in deep-sea fish abundance, diversity, and assemblage structure on seamounts over relatively narrow depth ranges and among sides of a seamount at the same depth. This variability should be considered in future ecological studies of seamounts as well as in the management and conservation of seamounts.

1. Introduction

Seamounts are undersea mountains found throughout the world's oceans. The broadest definition of seamounts includes oceanic islands and banks that have > 1000 m of relief from the surrounding seafloor (Staudigel and Clague, 2010). Seamounts are considered hotspots of biodiversity influenced by environmental conditions and under threat from human activities (reviewed in Rogers, 2018). These undersea mountains play an important role in marine ecology, being refugia for a high abundance and diversity of deep-sea species (Samadi et al., 2006; Rowden et al., 2010; McClain et al., 2010), with potentially high endemism (e.g., Hubbs, 1959; Wilson and Kaufmann, 1987; Parin et al., 1997; Richer de Forges et al., 2000; Koslow et al., 2001). However, evidence is emerging that this role may vary from one seamount to another, or within a given seamount, due to differences in the physical, chemical, and geological conditions (Richer de Forges et al., 2000; Tracey et al., 2004, 2012; McClain, 2007; Morato and Clark, 2007; Rowden et al., 2010; Clark et al., 2010a, 2010b; 2012; Schlacher et al., 2014). These conditions include the current regime, the surface water productivity, dissolved oxygen and salinity concentrations, temperature, and type of substrate (Pratt, 1967; White et al., 2007; Clark et al., 2010b). Some of these factors, such as temperature, salinity and oxygen, are strongly correlated with depth, which results in the community composition on a given seamount often showing depth-related patterns of change (Snelgrove and Haedrich, 1985; Carney, 2005; O'Hara, 2007; Rogers et al., 2007; Clark et al., 2010b, 2011; McClain et al., 2010; Schlacher et al., 2014; Long and Baco, 2014). Variation with depth may also be directly related to deep-sea water masses and

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their specific values of temperature, dissolved oxygen, salinity, and density (Koslow et al., 1994; Clark et al., 2010a; Tracey et al., 2012; Victorero et al., 2018). Water masses play two important roles: acting as a vertical barrier for many species (Koslow et al., 1994) and facilitating horizontal larval dispersal (Norcross and Shaw, 1984; Haedrich and Merrett, 1990; Koslow, 1993; Francis et al., 2002).

Variation in seamount communities may be further influenced by oceanic flow conditions that can interact with the topography and sediment type on different areas of a seamount (Boehlert and Genin, 1987; Rogers, 1994; Genin, 2004). Seamount flanks or summits can have asymmetric flow acceleration that enhances horizontal fluxes of organic material (White et al., 2007), but differences in the geology on a given seamount can also influence the intensity of current flow and thereby affect the food supply available for seamount fauna (Clark et al., 2010b).

In addition to being affected by these natural environmental conditions, community structure might also vary among or within seamounts based on the effect of human activities such as fishing, particularly trawling, which can decrease the abundance and diversity of seamount communities (e.g., Clark et al., 2010b).

A wide diversity of deep-sea fish species have been found on seamounts. The current number recorded from more than 60 seamounts is about 800 species (Morato and Clark, 2007), but this number is growing due to the increasing use of underwater vehicles such as AUVs, ROVs, and submersibles that have greatly increased imagery available for the identification of organisms. This diversity of fishes includes species endemic to specific seamounts (Koslow et al., 2001; Froese and Sampang, 2004) and others with a wide geographic distribution (McClain et al., 2009). In the Hawaiian Archipelago, the endemism and distribution of fish species, including deep-sea fishes, has been associated with physiography (Mundy, 2005) and oceanographic characteristics (Polovina et al., 1995). Mundy (2005) described the high islands and low atolls, or seamounts, at the southeastern end of the main Hawaiian Islands as the southeastern biogeographic boundary of the Hawaiian region, and the submerged seamounts of the Hawaiian Ridge to the northwest beyond the end of the emergent archipelago at Kure Atoll as the northwestern biogeographic boundary. Toonen et al. (2011) identified additional phylogeographic boundaries in shallow water in the Hawaiian Archipelago between Hawai‘i Island and Maui, O‘ahu and Kaua‘i, at Nihoa (Moku Manu) and Necker Island, and Pearl and Hermes Reef. Polovina et al. (1995) and Desch et al. (2009) found that within the Archipelago, north-south and east-west variation on the oceanographic variables correlated to a latitudinal partitioning of the deep-sea fauna, including endemic species of deep-sea fish.

Necker Island (Fig. 1) is the second smallest island of the Northwestern Hawaiian Islands (NWHI), but includes a diversity of deep-sea habitats, which are likely to host a great diversity of species. Unlike locations further northwest in the NWHI, Necker Island has not been subject to commercial trawl fisheries. This site is currently protected from fishing activities as part of the Papahānaumokuākea Marine National Monument, which allows it to be relatively free from human activities (Selkoe et al., 2008, 2009). The relatively pristine nature of this site makes it an excellent location to assess the abundance and richness of the deep-sea fish fauna of a seamount and their variability relative to environmental factors, with minimal confounding of natural patterns by human impacts.

The first and most significant effort to study the deep-sea fish communities on Necker was the Albatross expedition in 1882, in which several collections to depths approaching 3000 m were made using trawls or dredges (Bowers, 1903; Gilbert, 1903). The Tanager Expeditions in 1923 and 1924 visited Necker to study fish, among other organisms (Fowler and Ball, 1925). Other available information related to the taxonomy of deep-sea fish comes from the Hawai‘i Undersea Research Laboratory (HURL) which archives and catalogs images from all remotely operated vehicles (ROVs) and submersibles dives (Chave and Malahoff, 1998; Kelley et al., 2006). Some other studies have been conducted on a small portion of land and on a small fraction of the surrounding underwater area (to approximately l00 m depth) at Necker (Evenhuis and Eldredge, 2004), but focused on describing key organisms with some direct or indirect interaction with deep-sea fish (e.g., monk seals, Parrish and Polovina, 1994; Friedlander et al., 2009; Parrish, 2009). The most complete record of the deep-sea fishes present at Necker Island indicates that the species richness is close to 264 species, with 15 of these species having a geographic range beginning or ending on Necker (Mundy, 2005), although these estimates are biased by gaps in sampling.

The relatively pristine nature of Necker Island makes it an ideal location to expand our understanding of the distributions of deep-sea fishes on seamounts and to include baseline information on variability of these communities that can inform management of sites throughout the Hawaiian Archipelago. In order to generate information on the ecology of deep-sea fish assemblages inhabiting this area along upper slope depths (200–700 m), the objectives of this study were: 1) to characterize the composition, diversity and abundance of the deep-sea fish fauna on Necker Island, 2) to examine whether deep-sea fish assemblages change with study site and with depth, and 3) to determine which environmental variables are correlated with the assemblage structure across different study sites and depths.

2. Materials and methods

2.1. Study area

Necker Island, also known as a Mokumanamana, is a part of the Northwestern Hawaiian Islands (NWHI) about 740 km (400 nmi) from Honolulu and 287 km (155 nmi) northwest of Nihoa (the nearest island to the southeast), at latitude 23°34′N, longitude 164°42′W (Fig. 1). This small volcanic island, shaped like a fishhook, has an area of 0.2 km^2 and is approximately 150 m wide and < 1200 m long (Macdonald et al., 1970) with its highest point at 84 m above sea level (Evenhuis and Eldredge, 2004). Shallow water ecosystems and communities of Necker are described in Parrish and Polovina (1994) and Weiss et al. (2009). Below the euphotic zone, there are extensive deeper shelves that extend many kilometers from the island. Areas deeper than 200 m on Necker Island are virtually unexplored.

Although the NWHI are located near the center of an ocean gyre with oligotrophic conditions, the productivity in the area is influenced by local and regional factors such as currents, winds, and fronts (Desch et al., 2009). Necker Island is influenced by the North Hawaiian Ridge Current (NHRC), which flows northwestward along the north sides of the Islands from the Main Hawaiian Islands (MHI) towards the NWHI and the Hawaiian Lee Countercurrent (HLCC), which flows eastward along the southern sides. Both currents have a vertical extent from near the surface to at least 200 m (Firing and Brainard, 2006; Desch et al., 2009) (Fig. 1A). Additionally, these two currents are the likely mechanism of phytoplankton and zooplankton transport (Hirota et al., 1980), including larval transport, from the MHI toward the NWHI (Polovina et al., 1995; Kobayashi and Polovina, 2006) at least in shallow water.

2.2. AUV surveys

As a part of a project examining the recovery potential of deep-sea coral communities impacted by trawling in the NWHI (Baco et al., 2019; Baco et al., in review), three study sites on three different slopes of Necker Island (further referred to as “study site” to avoid confusion with the environmental parameter of “slope”) were surveyed in 2015 using the AUV *Sentry* (National Deep Submergence Facility (NDSF), 2019; https://ndsf.whoi.edu/sentry/) deployed from the RV Kilo Moana (Table 1, Fig. 1). At each site, 2–6 replicate photos transects of ~1000 m length were taken at 50-m depth intervals along the depth contour, from 200 to 700 m inclusive, for the W and SE study sites and

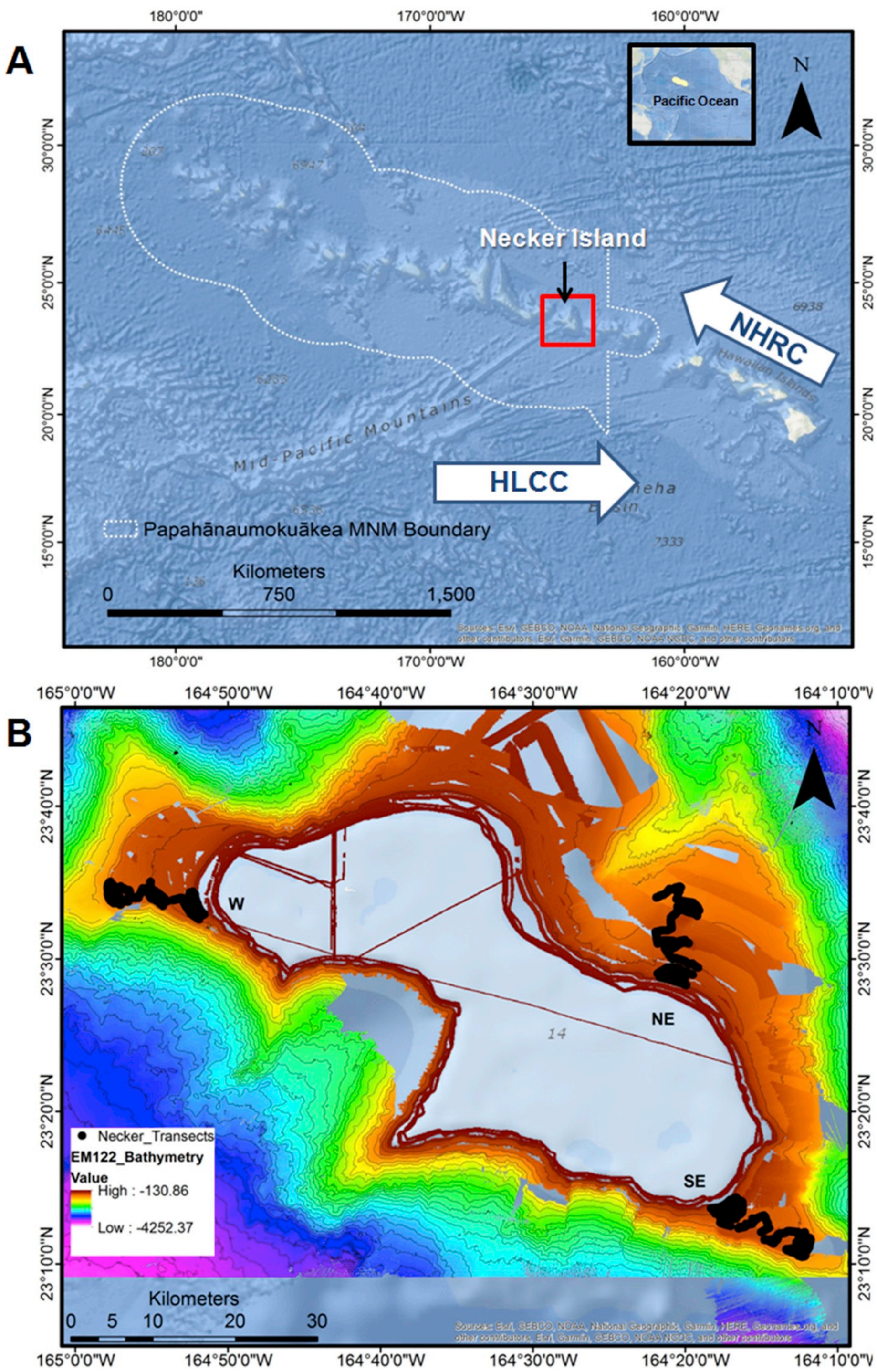

Fig. 1. A. Map of the Hawaiian Archipelago with the location of the Papahānaumokuākea Marine National Monument indicated by the white line and Necker Island by the red box. The North Hawaiian Ridge Current (NHRC) and the Hawaiian Lee Countercurrent (HLCC) described in Firing and Brainard (2006) and Desch et al. (2009) are also shown. B. Bathymetric map of Necker Island based on combined 10 m and 70 m resolution multibeam data. AUV dive tracks are indicated by the thick black lines (AUV *Sentry* dives number for each study site are W = S360, SE = S361 and NE = S362). Maps were created in ArcMap 10.4.1 (Esri, 2016). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1

Location and depth range of AUV dives on Necker Island. At each site 2–6 replicate transects of 1000 m were conducted along depth contours at 50 m depth intervals from ~250 to 700 m inclusive. Full data by transect are available in Table S1.

AUV *Sentry* Dive Number	Study site	Mean Latitude °N	Mean Longitude °W	Number of Transects
S360	W	23.567	164.919	33
S361	SE	23.208	164.252	37
S362	NE	23.523	164.343	38

from 250 to 700 m inclusive, for the NE (Fig. 1B). During imaging transects, the speed of the AUV was 0.5–0.7 m/s and the vehicle was between 3 and 8 m above the bottom (with an average of 6 m) with a down-looking Allied Vision Technologies Prosilica GE4000C camera. Images with a resolution of 96 dpi (4008 × 2672 pixels) were taken every 3–4 s.

2.3. Photo analyses

Images were viewed on a 24-inch (60.96 cm) computer monitor. After removing 1 cm on each side of each image (because it was dark and blurry), *Sentry* images were scanned for the presence of fishes. Photos with poor image quality (i.e. too high off the bottom or too close to the bottom, out of focus) were not analyzed. A small percentage of random photos did not present the best quality to taxonomically identify the individuals to the species level. For this reason, we were conservative in our assignment of taxonomic names and an identification confidence score was given to each photo identification on a scale of 1–4, as follows: (1) total certainty in the species or genus identification, (2) certainty in the family identification, (3) certainty in the order identification, and (4) certainty in the class. Observed fishes were taxonomically identified using Carpenter and Niem (1998, 1999a, 1999b, 2001a, 2001b), Chave and Malahoff (1998), Mundy (2005), Randall (2007), and taxonomic references for individual families cited in those works. More recent taxonomic publications, too numerous to list here, were also used, as were unpublished notes on the identification of fishes in the Hawaiian biogeographic region compiled by co-author Bruce Mundy. We follow the taxonomic classification of Nelson et al. (2016). All organisms were counted and included for the descriptive statistics, but only those with a confidence score of 1 were used for the univariate and multivariate analyses. All counts of fishes per transect were divided by the number of photos successfully analyzed in that transect to yield a standardized number of individuals per transect, which was then used for comparisons among transects.

2.4. Environmental data

Environmental data was collected from several sources. An Aanderaa optode (model 4330) oxygen concentration sensor on the AUV *Sentry* provided *in situ* temperature, conductivity, depth, and dissolved oxygen data that was linked directly to each image at the time of image capture. Conductivity was converted into salinity using an algorithm in MATLAB proposed by Fofonoff and Millard (1983).

As described in Baco et al. (2017), surface chlorophyll (chl-*a*) and particulate organic carbon (POC) were obtained from the National Oceanic and Atmospheric Administration's Environmental Research Division's Data Access Program (ERDDAP) Data Set (Simons, 2011). Monthly composites of surface Chl-*a* (0.025° resolution) and POC (4 km resolution) data were derived from Aqua-MODIS and NESDIS satellites from January 2008 to December 2016. Surface current (zonal (u, east-west) and meridional (v, north-south)) data were extracted from HYCOM (Hybrid Coordinate Ocean Model). Daily values of surface current data (1/12° resolution) were extracted from January 1, 2015 to January 1, 2016. All data (*.NetCDF) were imported into Matlab for quality control and then exported into ArcMap 10.4.1 (Esri, 2016) to calculate raster statistics (minimum, maximum, and average).

Substrate parameters were described for each transect using every fourth photo (3–4 m resolution) and based on simple categorical scale (Table S2). Rugosity and slope were estimated for each of these same photos, whereas substrate composition and substrate size were determined using the point-count method, with 15 random points placed on the photo using image J software (e.g. Mortensen and Buhl-Mortensen, 2004; Long and Baco, 2014; Morgan et al., 2015). Substrate categories were averaged within each transect, except for the substrate composition, which was expressed as the percentage (%) of sand.

Multibeam bathymetry and acoustic backscatter data (10 m resolution) were collected using a Kongsberg EM122 Multibeam Echosounder installed on the RV Kilo Moana. However, as this bathymetry information did not cover the entire surveyed area on Necker's slopes, it was complemented with 70 m resolution data extracted online from NOAA (2019). Sonar files were cleaned using Qimera 3D editor and the raster grid files were created in Fledermause (QPS software). These data were used to derive the contours in ArcGIS 10.4.1 for Desktop (Esri, 2016), and with the bathymetric data, to create a map of the seamount (Fig. 1B).

A combination of ultra-short baseline tracking of the AUV and Global Positioning System (GPS) tracking of the ship allowed for each transect to be mapped in ArcGIS 10.0 using XY layers. The length of each transect was measured using the Geospatial Modeling Environmental package for R (Beyer, 2012). Following the methodology in Long and Baco (2014), the aspect of the substrate was computed from the sine and cosine layers created from the original aspect raster by using the Map Algebra function within ArcView. With this information and using the equations described by Fisher (1995), the aspect of the substrate was converted to the mean direction of the substrate.

All environmental variables collected for each transect at each study site on Necker are presented in the Supplementary data (Table S1).

2.5. Statistical analyses

All statistical analyses were performed using the environmental and biological information obtained at the three study sites for transects from 250 to 700 m because of the lack of information at 200 m for the NE side. To asses variability in abiotic parameters among transects, Principle Components Analysis (PCA) was conducted with the environmental variables averaged by transect.

Species accumulation curves were constructed to evaluate how well the deep-sea fishes of Necker Island were surveyed. The expected richness was calculated using the nonparametric estimators Chao 2, Jackknife 1, and Jackknife 2. Plots were constructed with 10,000 permutations. All statistical analyses and calculations of diversity indices were performed using PRIMER V6 + PERMANOVA software (Anderson et al., 2008).

Spatial variation in deep-sea fishes was analyzed using relative abundance, calculated as the number of individuals divided by number of photos in a transect (individuals/# photos), species richness (S), rarefaction estimates of the expected species richness in a 300-individual sample [$E_{S(300)}$], Shannon diversity (H', nats) and Simpson dominance (D) indices. These indices were evaluated using a two-way crossed analyses of variance (ANOVA) and pair-wise tests constructed with Euclidean distance matrices testing with 10,000 residual permutations under a type III (partial) model (Anderson et al., 2008) using Monte Carlo (MC) tests due to the low number of permutations.

The structure of the deep-sea fish assemblages was evaluated using a Permutational Multivariate Analysis of Variance (PERMANOVA), constructed with the fourth-root transformed relative abundance and Bray-Curtis similarity matrices (Clarke and Warwick, 2001), and testing with 10,000 residual permutations under a type III (partial) model (Anderson et al., 2008). The fourth-root transformation (intermediate-level) was used to diminish the contribution of highly abundant species in relation to the less abundant, taking into account the rarer species (Clarke and Warwick, 2001). The differences in fish assemblage structure were tested as a function of the following factors: (1) depth (50-m depth intervals from 250 to 700 m) and (2) study sites (W, SE and NE) in a two-way crossed model with fixed levels for each factor.

Non-Metric Multidimensional Scaling (NMDS) ordination, based on the Bray-Curtis similarity matrix, was used to visualize the similarities in community structure among transects and depths. The contribution of individual species to the dissimilarity and similarity among the *a posteriori* groups obtained from the above analyses was determined using the Similarity Percentage Analysis (SIMPER) based on Bray-Curtis similarities (Clarke and Warwick, 2001).

Environmental variables available for each transect were salinity, dissolved oxygen, temperature, direction of the substrate, rugosity, substrate size, % of sand, slope, chl-*a*, POC, vector of currents u and v, and time of day (Table S1). After normalizing all the environmental variables, draftsman plots were used to detect high correlation. A correlation with an $r \geq \pm 0.90$ (Clarke and Warwick, 2001) between dissolved oxygen and temperature; between POC and chl-*a* (extracted from Modis and Nesdis); and between % of sand and substrate size (Table S3) was used to remove from the DistLM analysis temperature, chl-*a*, and substrate size. Nevertheless, a variance inflation factor (VIF) < 5 was also used to avoid high multicollinearity, taking into account that some authors suggest VIFs > 10 as severe (Neter et al.,

Table 2
Taxonomic identification and number of individuals of deep-sea fishes observed on three study sites (W, SE, and NE) on Necker Island. The taxonomic classification follows Nelson et al. (2016). The identification confidence scores (ICS) given to each taxonomic identification are presented as (1) total certainty in the species or genus identification, (2) certainty in the family identification, and (3) certainty in the order identification. Endemic species for the Hawaiian Archipelago (+) and new records for Necker Island (*) are indicated. Minimum and maximum observed depths are shown for each species.

Class Chondricthyes				Number of individuals				Depth (m)
Order	Family	Species	ICS	W	SE	NE	Total	Min.–Max.
Squaliformes	Centrophoridae	_Centrophorus_ cf. _Squamosus_*	1	1	4	4	9	289–630
	Etmopteridae	_Etmopterus pusillus_*	1	10	12	4	26	282–692
		Etmopteridae	2	1			1	577–577
	Squalidae	_Squalus hawaiiensis_+	1	14	43	14	71	216–595
Torpediniformes	Torpedinidae	_Tetronarce_ sp.*	1		1		1	465–465
Class Osteichthyes								
Anguilliformes	Congridae	_Ariosoma marginatum_+	1		29		29	214–553
		Ariosoma sp.	1	44	34	17	95	225–693
		Conger oligoporus+	1	3	2		5	282–444
		Gnathophis cf. _heterognathos_*	1	24	61		85	215–493
	Nettastomatidae	_Nettastoma parviceps_*	1	15	10	18	43	281–694
	Ophichthidae	Sp.1	1		2		2	279–293
		Ophichthus kunaloa+*	1	7	8	4	19	229–640
	Synaphobranchidae	_Ilyophis_ sp. 1*	1	95	79	31	205	282–695
		Ilyophis sp. 2*	1	4	18	11	33	386–694
		Meadia abyssalis	1	4	3		7	416–640
		Sp.2	1	71	2	5	78	281–690
		Synaphobranchidae	2		10		10	440–692
Argentiniformes	Argentinidae	_Glossanodon struhsakeri_+	1	81	8	403	492	229–487
Stomiiformes	Sternoptychidae	_Argyripnus_ sp.	1	361	3105	77	3543	213–525
Ateleopodiformes	Ateleopodidae	_Ijimaia plicatellus_+*	1	1	8	25	34	287–691
Aulopiformes	Chlorophthalmidae	_Chlorophthalmus imperator_+*	1	41	32		73	387–588
		Chlorophthalmus proridens+	1	236	510	857	1603	179–615
		Chlorophthalmidae	2	6	11	15	32	478–624
	Ipnopidae	_Bathypterois atricolor_	1		1	1	2	434–511
		Ipnopidae	2	8	1	2	11	189–545
	Synodontidae	_Synodus kaianus_	1	39	3	27	69	229–315
Myctophiformes	Myctophidae	Myctophidae	2	13	3	11	27	180–543
	Neoscopelidae	_Neoscopelus macrolepidotus_	1	1179	815		1994	249–695
		Neoscopelidae	2		45		45	237–508
Polymixiiformes	Polymixiidae	_Polymixia japonica_	1	6	42	15	63	233–539
Zeiformes	Grammicolepididae	_Grammicolepis brachiusculus_	1		3	7	10	292–534
	Parazenidae	_Stethopristes eos_	1	1	11	7	19	439–628
	Zeniontidae	_Cyttomimus stelgis_	1	3	40	41	84	390–543
Gadiformes	Macrouridae	_Coelorinchus aratrum_+*	1	31	29	39	99	387–695
		Coelorinchus gladius+*	1	31	78	32	141	282–543
		_Coelorinchus tokiensis_*	1	4	1	2	7	439–640
		Gadomus melanopterus	1	4		2	6	528–596
		Hymenocephalus antraeus+*	1	44	29	6	79	440–694
		Hymenocephalus sp. 1	1			1	1	486–486
		Sp.3	1	5	7	24	36	339–693
		Sp.4	1	20	17	4	41	339–683
		Malacocephalus cf. _hawaiiensis_+	1	322	213	73	608	332–692
		_Pseudocetonurus septifer_*	1	14	10	15	39	292–693
		Ventrifossa atherodon	1	255	174	89	518	390–693
		Macrouridae	2	272	32	37	341	177–693
		Gadiformes	3	42	88	87	217	280–694
	Moridae	_Laemonema_ sp.	1	91	200		291	214–688
		Laemonema rhodochir	1	83	71	8	162	336–539
		Physiculus grinnelli+	1		2		2	444–539
		_Physiculus nigripinnis_*	1	5	12	5	22	455–637
		Moridae	2		43	2	45	215–637
Trachichthyiformes	Trachichthyidae	_Hoplostethus_ sp.	1	1	4	1	6	340–551
		_Hoplostethus crassispinus_*	1	3	14	26	43	450–689
		Trachichthyidae	2		1		1	490–490
Beryciformes	Berycidae	_Beryx decadactylus_	1	37	145	12	194	475–684
		Beryx splendens	1	156	106	26	288	235–686
		Berycidae	2	1		2	3	530–623
Ophidiiformes	Carapidae	_Pyramodon ventralis_	1	28	30		58	282–542
	Ophidiidae	_Lamprogrammus_ cf. _brunswigi_*	1			5	5	513–642
		Sp.5	1		5	2	7	291–686
		_Ophidion muraenolepis_*	1		13		13	215–289
		Ophidiiformes	3	3	6	6	15	281–691
Carangiformes	Carangidae	_Seriola dumerili_	1	1			1	166–166
Pleuronectiformes	Bothidae	_Chascanopsetta crumenalis_+*	1		5	4	9	284–587
		Chascanopsetta prorigera+	1	9	14	36	59	234–537
		Parabothus cf. _coarctatus_	1	39	17	9	65	174–346
		Poecilopsetta hawaiiensis+	1	21	2	63	86	181–395
		Taeniopsetta radula+	1	59	23	6	88	181–640
		Bothidae	2	5	3	2	10	177–341

(*continued on next page*)

Table 2 (*continued*)

Class Chondricthyes				Number of individuals				Depth (m)
	Cynoglossidae	*Symphurus strictus**	1	9	73	86	168	281–692
Callionymiformes	Callionymidae	*Synchiropus kinmiensis*+*	1	4			4	338–339
Scombriformes	Gempylidae	*Rexea nakamurai**	1	9	19		28	234–678
		Ruvettus pretiosus	1		1		1	640–640
		Gempylidae	2		1		1	539–539
	Trichiuridae	*Benthodesmus* cf. *tenuis*	1	5	2		7	605–681
Trachiniformes	Percophidae	*Chrionema chryseres*	1	98	235	24	357	163–514
		Chrionema squamiceps+*	1	79	39	64	182	176–497
		Percophidae	2		5		5	186–339
	Pinguipedidae	*Parapercis roseoviridis*+	1	13	135	8	156	163–394
Perciformes	Acropomatidae	*Parascombrops argyreus*	1		6	25	31	248–542
	Epigonidae	*Epigonus* cf. *glossodontus*+*	1	57	104	19	180	435–655
		Epigonus devaneyi+	1	1	25	7	33	389–529
		Epigonidae	2	2	1		3	437–438
	Lutjanidae	*Etelis carbunculus*	1		2	13	15	230–342
		Etelis coruscans	1			2	2	289–341
		Pristipomoides filamentosus	1	777	1	104	882	180–540
	Serranidae	*Plectranthias kelloggi*	1			4	4	293–346
	Symphysanodontidae	*Symphysanodon maunaloae*	1	115	80	119	314	215–493
Scorpaeniformes	Bembridae	*Bembradium roseum*	1	31	47	11	89	235–471
	Hoplichthyidae	*Hoplichthys citrinus*	1	19	4	19	42	178–343
	Peristediidae	*Scalicus engyceros*	1	90	96	83	269	230–545
		Scalicus hians	1	15	37	6	58	286–675
	Scorpaenidae	*Pontinus macrocephalus*	1		9	4	13	175–345
		Scorpaena pele+*	1	51	27	14	92	175–483
		Sp.6	1	23	25	57	105	283–542
		Sp.7	1	12	7	22	41	336–543
		Sp.8	1	3	16	5	24	359–642
		Setarches guentheri	1	9	16	3	28	285–544
		Scorpaeniformes	3	10	23	13	46	188–627
Spariformes	Callanthiidae	*Grammatonotus laysanus*	1			1	1	340–340
Lophiiformes	Chaunacidae	*Chaunax* sp.	1	1	4		5	388–470
		Chaunax umbrinus+	1	1	6	2	9	345–494
	Lophiidae	*Lophiodes* cf. *bruchius*	1	15	20	5	40	336–648
		Lophiodes miacanthus	1		3		3	191–543
		*Sladenia remiger**	1	3	3	1	7	641–689
	Ogcocephalidae	*Halieutaea retifera*+	1	2	13		15	178–282
		*Malthopsis mitrigera**	1	12	83	28	123	178–641
		Solocisquama erythrina+*	1	14	9	2	25	578–693
		Ogcocephalidae	2	2	4		6	177–522
Tetraodontiformes	Triacanthodidae	*Hollardia goslinei*+	1	4	9	2	15	433–542
		Triacanthodidae	2		1		1	508–508

1996; Chatterjee et al., 2000; Zuur et al., 2010). This analysis was performed using the Vegan package (Oksanen et al., 2010) in the R statistical program (R Development Core Team, 2018). The remaining 10 variables were used to evaluate the most important environmental parameters correlated with the observed community structure patterns using Distance-based Linear Modeling (DistLM; Anderson et al., 2008), combined with redundancy analysis and the BEST model in conjunction with Akaike Information Criterion (AIC, Akaike, 1973).

3. Results

3.1. Summary statistics

A total of 18,478 individual fishes were observed in 51,988 photos taken on the three study sites on Necker from 200 to 700 m (Table S1). Of these, 15,856 (86%) individuals with a 1, 2 or 3 taxonomic certainty were identified in 22 orders with 44 families of bony fishes and 2 orders with 4 families of cartilaginous fishes (Table 2). The orders with the highest abundance of individuals were Stomiiformes (22.7%), Gadiformes (15.3%), Myctophiformes (13.3%), Aulopiformes (11.5%), and Perciformes (9.4%) (Fig. 2). Within these orders, Sternoptychidae, Macrouridae, Neoscopelidae, Chlorophthalmidae, and Lutjanidae represented the most abundant families, respectively (Fig. 2). Scorpaeniformes, Trachiniformes, Anguilliformes, and 14 other orders were each below 5.2% of individuals. Within cartilaginous fishes (not shown in Fig. 2 due to low relative abundance), sharks were represented by the order Squaliformes with three families, whereas rays were represented by the order Torpediniformes and one family (Table 2).

Using just the individuals with a taxonomic certainty of 1, we found 92 species. However, one of these species, *Seriola dumerili*, was identified only on a 200 m transect that was not included in further analysis.

3.2. Habitat description

The three study sites on Necker Island show similar average values of dissolved oxygen, temperature and salinity in the depth range of 250–700 m (Table S1). The NE side is characterized by having mostly sandy substrate with low rugosity, whereas the W side was mostly hard substrate with low average rugosity. The SE side had sandy and hard substrates in almost the same percentage with low average rugosity as well. The SE side showed the lowest average values of POC, chl-*a*, and surface current vector u, while the NE side had the highest values (Table S1). A PCA plot of environmental data for each transect showed a clear separation of transects on the three study sites along PCA axis 2, with some overlapping at deeper depths mainly on the NE side. Likewise, a depth gradient among all sites along axis 1 is observed, with the exception of the 700 m depth, with shallower depths on the left of the ordination and deeper depths moving to the right (Fig. 3). The separation of study sites was associated with current vector u, which was highly correlated with axis 2. Axis 1 showed a high correlation with chl-*a* Modis, % of sand, POC, temperature, dissolved oxygen, chl-*a* Nesdis, and substrate size (Fig. 3, Table S4).

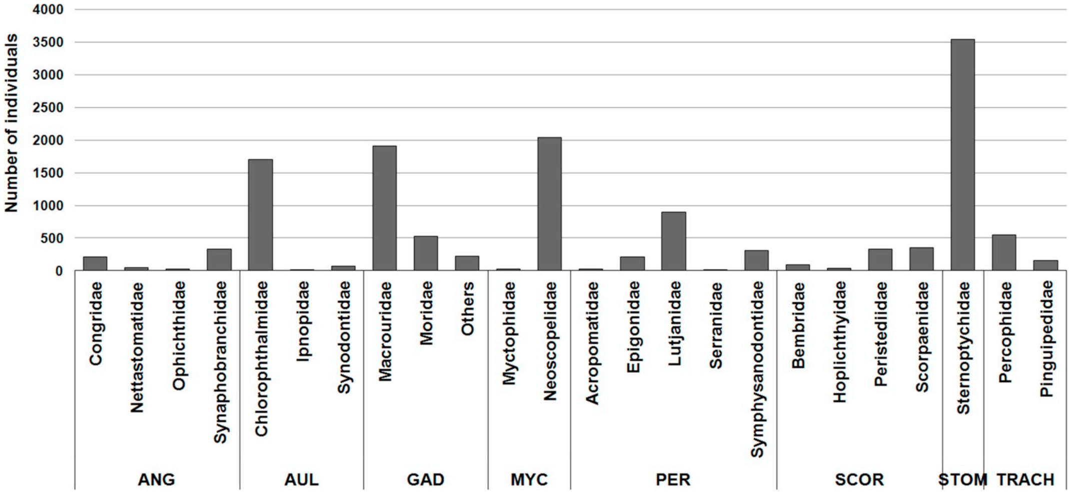

Fig. 2. Total number of individuals identified in the most abundant orders and families of deep-sea fishes inhabiting Necker Island from 200 to 700 m depth. ANG = Anguilliformes, AUL = Aulopiformes, GAD = Gadiformes, MYC = Myctophiformes, PER = Perciformes, SCOR = Scorpaeniformes, STOM = Stomiiformes, TRACH = Trachiniformes.

3.3. Statistical analyses

Based on the species accumulation curves by study sites, 72 species identified on the W side represented between 82.3 and 87.7% of the expected species richness, 82 species on the SE side represented between 89.2 and 94.2%, and 72 species on the NE side represented between 91.4 and 95.6%. For the W and SE study sites, Jackknife 2 showed the maximum expected richness as 88 and 92, respectively, while Chao 2 had the lower value of 82 and 87 species, respectively. In the NE side, Jackknife 1 showed the maximum expected richness as 79 species, and Chao 2 had a slightly lower value of 75 species (Fig. S1).

3.4. Univariate analyses

Relative abundance showed a significant difference among study sites with a two-way crossed ANOVA ($p = 0.0027$) (Table 3). The pairwise tests showed differences between the NE and the other two sites, with the NE side having the lowest abundance (Fig. S2). There was no difference by depth ($p = 0.9024$) or the interaction of site and depth ($p = 0.1482$) (Table 3).

Species richness and $E_{S(300)}$ showed significant differences among study sites ($p = 0.0001$), depths ($p = 0.0001$) and their interaction ($p = 0.0005$ and $p = 0.0007$, respectively) (Table 3). Both attributes indicated that the SE of the island has the highest estimated richness, whereas the NE has the lowest estimated richness. By depth, 350, 500, and 550 m were the most diverse depths and 250, 400, and 700 m had the lowest diversity (Fig. S2). Shannon diversity and Simpson Dominance were not significantly different among study sites, but depth and the interaction were significant for both (Table 3). For species richness, pairwise tests showed these differences primarily between the NE side and the other two study sites of the island. The highest species richness was found at 500 m depth, in which diversity was also high with low dominance. The lowest species richness and diversity were observed at 250 and 700 m depth, with dominance also the highest at 250 m depth (Fig. S2).

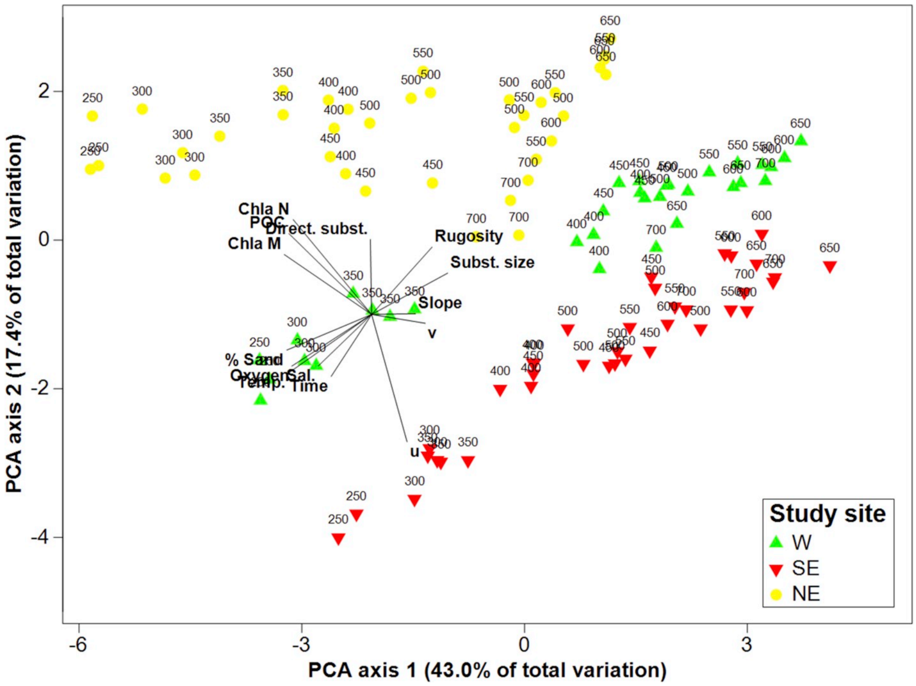

Fig. 3. Principal Component Analysis (PCA) of the environmental variables per transect obtained at Necker Island from 250 to 700 m. The first two axes of the PCA accounted for 60.4% of the total variance. Vectors show the direction and strength of each environmental variable to the overall distribution. Study sites on Necker Island are indicated with colored symbols and depth values are shown for each transect.

Table 3

Univariate PERMANOVA analysis of fish assemblages from Necker Island based on two-way crossed model with two factors: study sites and depths. Comparisons of each variable among study sites and depths were made with $p < 0.05$, using Euclidean distance and 10,000 permutations.

Factors	Study site df = 2		Depth df = 9		Study site x Depth df = 18	
	Pseudo-F	P	Pseudo-F	P	Pseudo-F	P
Abundance (ind./# photos)	6.4267	**0.0027**	0.4517	0.9024	1.4227	0.1482
Species richness (S)	26.644	**0.0001**	9.8003	**0.0001**	3.3133	**0.0005**
Estimated species richness ($E_{S(300)}$)	20.706	**0.0001**	10.545	**0.0001**	2.7917	**0.0007**
Shannon diversity (H′)	0.0833	0.9169	3.0554	**0.0043**	2.7681	**0.0013**
Simpson dominance (D)	0.4706	0.6351	2.0209	**0.0463**	2.8695	**0.0015**

Table 4

Multivariate PERMANOVA analysis of fish assemblages from Necker Island based on fourth-root transformed relative abundance data (ind./# photos), Bray-Curtis similarity matrices and 10,000 residual permutations. Two-way crossed model with two factors: study sites and depth were used.

Multivariate PERMANOVA	df	Pseudo-F	p
Study site	2	14.455	**0.0001**
Depth	9	18.727	**0.0001**
Study site x Depth	18	3.1353	**0.0001**

3.5. Multivariate analyses

The multivariate PERMANOVA results showed significant differences in the fish assemblage structure among study sites, depths and their interaction ($p = 0.0001$) (Table 4). The pair-wise comparisons for the interaction showed that within a given site most depths were significantly different, but the majority of differences among study sites were observed in comparison to the NE side. That is, within a given depth, it was common for the NE side to be different from either the W or SE side (Table S5).

The pattern of significant differences in assemblage structure by study sites found with the PERMANOVA analyses is not evident in the Cluster (Fig. S3) or NMDS outputs (Fig. 4). However, there is a noticeable horseshoe effect in the NMDS, corresponding with variation along a depth gradient, which shows three clusters defined at 30% similarity, roughly corresponding to depth ranges of 250–300 m, 350–500 m, and 550–700 m with some overlap among them (Fig. 4, Fig. S3). Two transects grouped separately from these, both at 250 m on the SE side (Fig. 4).

With a cumulative percentage of 50%, the results of the SIMPER analysis revealed that the most important species contributing to the dissimilarities among the NE and the other two sites were *Neoscopelus macrolepidotus*, *Malacocephalus* cf. *hawaiiensis*, *Laemonema* sp., *Argyripnus* sp., *L. rhodochir*, *Beryx splendens*, *Epigonus* cf. *glossodontus*, and *Ilyophis* sp.1 with higher abundances in the SE and W side, and *Glossanodon struhsakeri*, *Pristipomoides filamentosus*, *Scalicus engyceros*, *Ijimaia plicatellus*, and *Symphurus strictus* showing higher abundances in the NE side.

Based on SIMPER similarity, group 2 with mostly the intermediate depth range (350–500 m) had the highest average similarity (43.82%) among the three groups, with the fish assemblage mainly characterized by *Argyripnus* sp. and *Chlorophthalmus proridens* with contributions of 15.10% and 14.11%, respectively. The fish assemblage in group 1, the shallower depth range (250–300 m), had the greatest contributions to similarity from *Scalicus engyceros, Poecilopsetta hawaiiensis, Glossanodon struhsakeri* and *Hoplichthys citrinus* with contributions from 12 to 15%. The assemblage observed in the third group that includes the deeper depth range (550–700 m) had the greatest similarity contributions from *Ventrifossa atherodon* with a 17.93% contribution and *Malacocephalus* cf. *hawaiiensis* with 13.08%.

According to the DistLM marginal tests, of the included variables, oxygen explains the highest proportion of variation (24%). Salinity, percentage of sand, rugosity, slope, POC, u, v, and time also explain a small (4–15%), but statistically significant amount of the variation ($p < 0.05$, Table 5). The top 10 models from the DistLM had AIC values with a range of only 2.0 and included 7–10 variables. The BEST model from DistLM analyses uses nine variables, but the model with eight variables has an AIC value only 0.29 more than the 9 variable model. The eight variables are: dissolved oxygen, salinity, % of sand, rugosity, slope, POC, v, and u (Table 5). The first two axes of the fitted model ordination (dbRDA, Fig. 5) explained 74.2% of the fitted variation of the structure of the deep-sea fish assemblages on Necker Island. The supplementary data (Table S6) showed that oxygen was highly positively correlated with the first axis. With the second dbRDA axis salinity was highly negatively correlated.

Bubble plots corroborate the correlation between assemblage structure and the eight environmental variables recognized as important by DistLM (Fig. 6). A pattern is observed in Fig. 6A, C, and F where transects on the left of the ordination (which corresponds to shallower depths) are characterized by higher average values of oxygen concentrations, sandy areas, and higher concentrations of POC. In contrast, average rugosity and slope show higher values at deeper depths than shallower depths (Fig. 6D and E). Average salinity shows high values at shallower depths that decrease to intermediate depths and increase again to deeper depths (Fig. 6B). Average current factors u and v do not show an obvious pattern relative to the assemblage structure (Fig. 6G and H).

4. Discussion

Increasingly, studies of seamounts show variability within a single seamount and among seamounts in the same chain, making it necessary to study seamounts at finer scales. At the same time, studies of individual seamounts must be integrated with regional environmental variables that may influence the local abundance and distribution of the seamount species. The result of this variability is that no single model can be utilized to manage all seamounts (e.g., Clark et al., 2010b). Furthermore, management strategies must recognize natural variability in the diversity and endemism in seamounts over time and space, building information from specific locations into a broader framework (Probert et al., 2007). The current study contributes to our understanding of the degree of variability in deep-sea fish assemblages found on individual seamounts because it is one of the most extensive surveys ever conducted on a single seamount and encompasses multiple slopes of a seamount at multiple depths with replicate transects as well as environmental data. The seamount is also comparatively pristine, thus natural patterns are unlikely to be confounded by anthropogenic impacts.

4.1. Fish assemblage diversity and biogeographic affinities

Estimates of species richness and endemism on seamounts can be affected by the tool used to sample and the level of sampling effort (e.g. Stocks and Hart, 2007; Clark et al., 2010b). The observation of seamount communities with photographic or video material collected with AUVs, ROVs, and submersibles has allowed an improved estimation of species diversity in seamount environments (e.g., Chave and Malahoff,

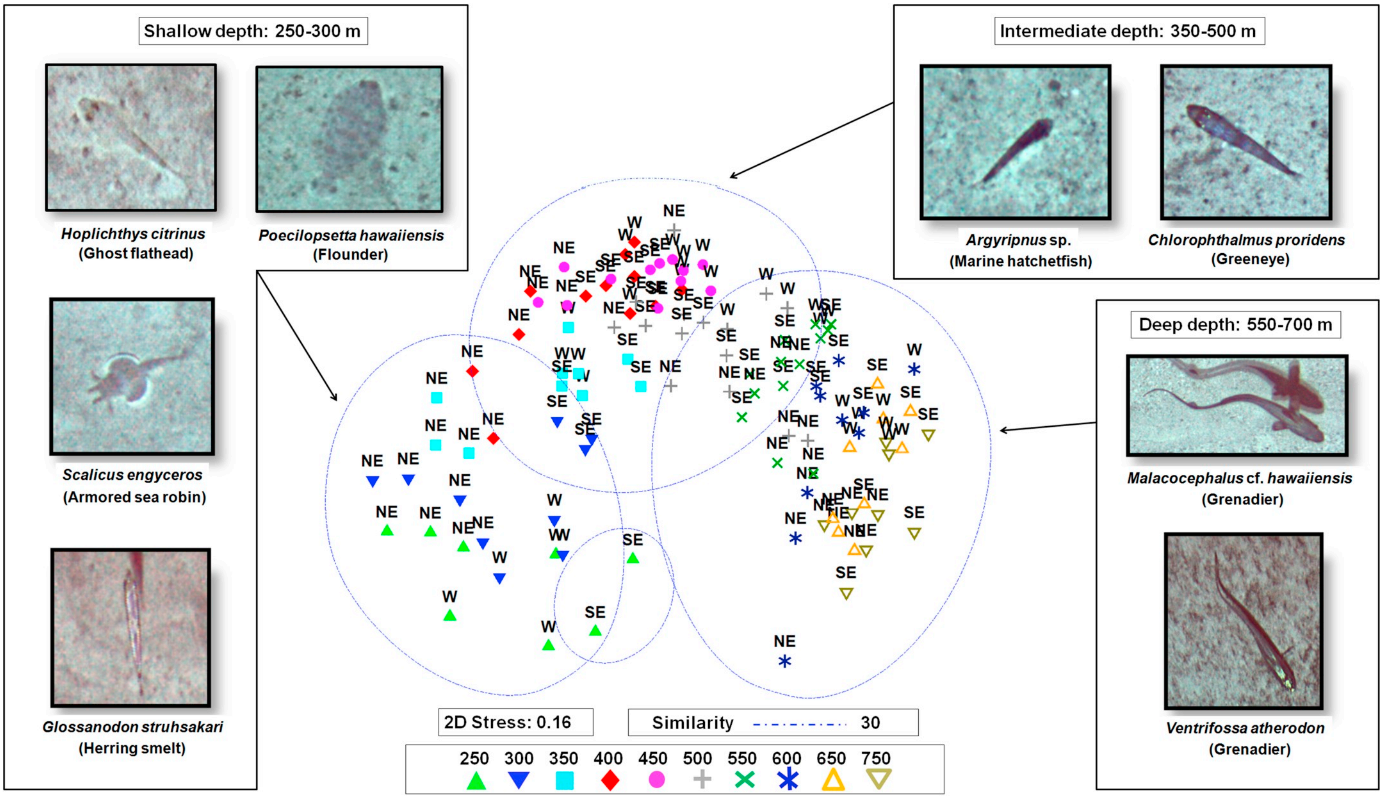

Fig. 4. Distribution of the assemblage structure by study sites and depth in a non-metric multidimensional scaling ordination based on Bray Curtis similarities calculated on fourth-root transformed relative abundance data. Each point represents a single transect. W, SE, and NE indicate study sites on the island as in Table 1. Circles represent depth groups and the most abundant species shared in each depth group are shown.

Table 5
Distance-based Linear Model (DistLM) marginal test results and model selection based on the environmental variables used to evaluate correlation with the deep-sea fish community structure patterns on Necker Island.

Var. No.	Variable	SS(trace)	Pseudo-F	p	Proportion of variation
1	Oxygen	77,163	32.82	0.0001	0.2364
2	Salinity	42,607	15.92	0.0001	0.1306
3	Direction substrate	5179.8	1.711	0.0948	0.0159
4	% Sand	48,198	18.37	0.0001	0.1477
5	Rugosity	47,517	15.07	0.0001	0.1456
6	Slope	12,210	4.120	0.0002	0.0374
7	POC	48,040	18.30	0.0001	0.1472
8	v	23,314	8.155	0.0001	0.0714
9	u	12,952	4.381	0.0008	0.0397
10	Time of day	21,433	7.451	0.0001	0.0657

Overall best solutions

Var. No.	AIC	R^2	RSS	Selections
9	796.54	0.56,108	1.43E+05	1, 2, 4–10
8	796.83	0.55,166	1.46E+05	1, 2, 4–9
8	797.39	0.54,932	1.47E+05	1, 2, 4, 5, 7–10
10	797.58	0.56,494	1.42E+05	All
7	797.82	0.53,909	1.50E+05	1, 2, 4, 5, 7–9
8	797.90	0.55,551	1.45E+05	1–9
9	798.27	0.54,564	1.48E+05	1, 2, 4, 6–10
7	798.29	0.54,554	1.58E+05	1, 2, 5–10
9	798.34	0.55,369	1.46E+05	1–5, 7–10
8	798.54	0.53,597	1.51E+05	1, 2, 4, 6–9

1998; Kelley et al., 2006; Baco, 2007; Lundsten et al., 2009; Long and Baco, 2014; Morgan et al., 2015). AUVs are useful tools to study deep-sea fish communities (e.g., Tolimieri et al., 2008; Milligan et al., 2016) since they are not tethered to the vessel (Griffiths, 2003), allowing the acquisition of data in very complex terrain. AUVs can also survey a large area and take high quality digital color photographs of the sea floor (Wynn et al., 2014), from which the identification of species can be obtained. However, there are some disadvantages when using AUV photos for identifications (Tolimieri et al., 2008). For example, the focus of image for identification purposes is affected when the AUV is too high off the bottom. Height off the bottom also affects light, with not enough light when the vehicle is too high and strong light reflection when the vehicle is too low. Light reflection can also impede the view of the organisms depending on the substrate type, especially on very white sand or very dark manganese crusts. We avoided several of these limitations by discarding, prior to the taxonomic identification of the individuals, photos that were too dark, out of focus, or too high or too close to the bottom. Another challenge with AUV imagery is the down-facing angle of the camera. This provides an excellent dorsal view of the organisms, but other characteristics such as body shape, position of the mouth, or coloration patterns, which are fundamental in taxonomic identifications, are often not in the field of view. Despite these difficulties, at the order level, 86% of the total individuals observed from 200 to 700 m were able to be identified. In addition, the number of species observed in each study site represented more than 82–96% of the expected species richness on each side (Fig. S1), indicating that a reasonable representation of the species at the three sites was acquired. Thus, these results represent a baseline for deep-sea fishes at Necker Island that can be enriched with future studies in the same area.

Benthic and demersal deep-sea fish assemblages at 200–700 m on the slopes of Necker Island were dominated by high abundances of the Sternoptychidae, Macrouridae, Chlorophthalmidae, Neoscopelidae, and Lutjanidae (Fig. 2). Other families such as Myctophidae and Scorpaenidae, also previously recorded on Necker (Mundy, 2005), were identified in this study but were not dominant. From the dominant families,

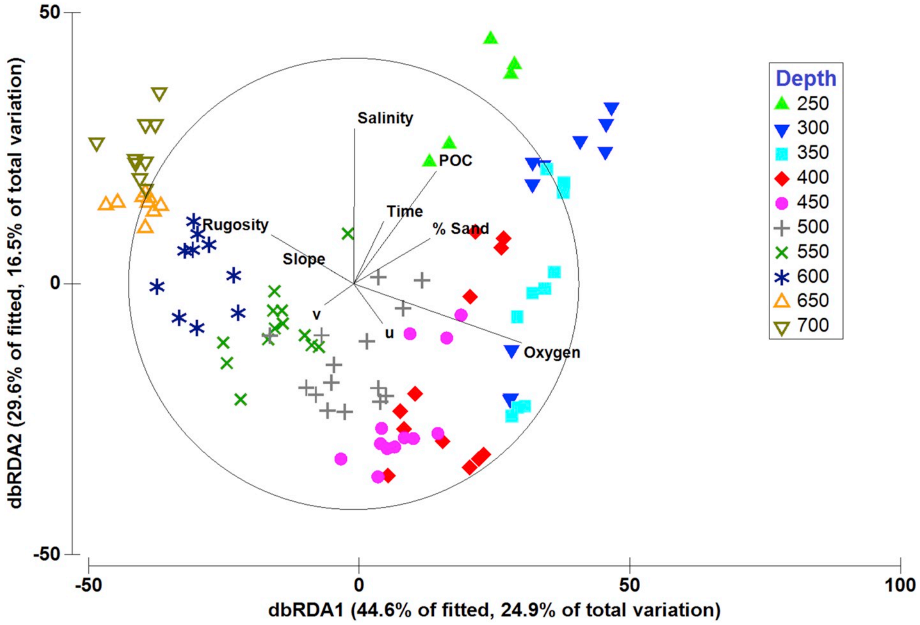

Fig. 5. Biplot of the distance-based redundancy analysis (dbRDA) of multiple environmental variables influencing the structure of the deep-sea fish assemblage on Necker Island. The environmental covariates were superimposed onto the dbRDA plot as vectors whose direction and length are related to their partial correlation with the dbRDA axes.

Macrouridae, previously noted as one of the 10 families with the highest number of registered species in the Hawaiian Archipelago by Mundy (2005), was the most diverse, with 11 species.

Of the 92 species identified in this study with taxonomic certainty of 1, 78 could be assigned a full scientific name or compared with the species in the Hawaiian Archipelago. From these 78 species, 49 had already been reported with ranges in the Hawaiian Ridge that included Necker Island (Evenhuis and Eldredge, 2004; Mundy, 2005; Daly-Engel et al., 2018) and are the 18.6% of the 264 species documented by Mundy (2005) with a high probability of being found in upper bathyal depths on Necker Island. Of the other 29 species, 19 were previously known to occur only in the Main Hawaiian Islands (MHI), 2 in the MHI and in the NWHI beyond Necker Island, and 4 on seamounts in the NWHI beyond Necker Island (Mundy, 2005). The remaining 4 (*Coelorinchus tokiensis*, *Ilyophis* sp.1, *Ilyophis* sp.2, and *Physiculus nigripinnis*) had not been reported for the Hawaiian Archipelago before this study, but were known from other parts of the Pacific.

High endemism has been noted in the deep-sea fishes of the Hawaiian-Emperor seamount chain (ESC) and Johnston Atoll (Mundy, 2005). Johnston is part of the larger Hawaiian biogeographic region (Mundy, 2005) and is located ~800 km from the Hawaiian Ridge (Kosaki et al., 1991). This endemism has been tied to the physiographic (Mundy, 2005) and oceanographic (Polovina et al., 1995) characteristics of the region that, together with life history characteristics, provide connectivity between locations for some taxa and isolation for others. Out of the 78 species identified on Necker Island in this study, 27 (34.6%) are known to be endemic to the Hawaiian Archipelago and Johnston Atoll region (Table 2). Before this study, some of these species (*Ophichthus kunaloa, Ijimaia plicatellus, Coelorinchus gladius, C. aratrum, Hymenocephalus antraeus, Scolicisquama erythrinus, Epigonus* cf. *glossodontus, Chrionema squamiceps, Chascanopsetta crumenalis, Plectranthias kelloggi, Synchiropus kinmeiensis* – a senior synonym of *S. hawaiiensis* according to Randall (2007) – and *Scorpaena pele*) had been previously reported with their biogeographic boundaries in the MHI (Mundy, 2005). Thus, the records of these species at Necker Island expand their known ranges within the Archipelago and support the regional endemism listed before for the area by Mundy (2005).

A few of the species observed on Necker have a wider distribution, connected to the western Pacific Ocean and influenced by oceanographic conditions. According to Mundy (2005), there are 57 species of deep-sea fish in the Hawaiian Archipelago that overlap with the Western Pacific. The species *Lophiodes miacanthus, Scalicus hians, S. engyceros*, and *Bembrops filifera* reported in this study for Necker Island and found through the MHI, the NWHI, and the ESC, are part of these species that have also been recorded outside the Archipelago. The connection from the western Pacific to the Archipelago seems to be influenced by the Kuroshio Current from Japan or Taiwan to the Hawaiian Islands (Howell et al., 2012).

4.2. *Fish assemblage patterns*

The abundance of fishes, from 250 to 700 m, showed significant differences between the NE side compared to the other two study sites at Necker, but not among depths (Table 3, Fig. S2). Abundance of organisms generally decreases with depth from 0 to at least 5500 m (Rowe, 1983; Merrett and Haedrich, 1997; Rex and Etter, 2010). This pattern of abundance is generally explained by the decrease in the food input available for organisms inhabiting deeper depths (Johnson et al., 2007; Ramirez-Llodra et al., 2010). Nevertheless, our results showed that depth does not affect the abundance of deep-sea fishes inhabiting 250–700 m at Necker. It is possible that small depth ranges, such as the one surveyed in this study, do not show significant differences in the abundance of benthic megafauna with depth. However, similar results were found by McClain et al. (2010) in a study conducted at depths of 1246 to 3656 m on benthic megafauna on a seamount in the northeast Pacific.

Instead of decreasing with depth, the abundance of deep-sea fishes varied with geographic location on Necker. The NE slope had a lower abundance of deep-sea fishes than either of the other two study sites (Fig. S2). Geographic location on a seamount can result in different topographic and oceanic conditions on each side of the seamount. These conditions interact and can affect the food supply (Boehlert and Genin, 1987; Rogers, 1994; Genin, 2004) that could supports high abundances of organisms. Although the values of POC were higher in the NE compared to the other two study sites (39.54 mg/m^3-NE, 31.60 mg/m^3-SE and 35.18 mg/m^3-W) (Table S1), the surface currents on the NE side may affect horizontal transport of surface productivity and therefore the amount of POC that reaches the benthic habitats in our target depths. Additionally, the NE side of Necker has an extended shelf and the amount of POC arriving to the sea floor may also be influenced by deeper currents that make the food supply less available to the organisms on this side of the seamount. Another explanation for the low

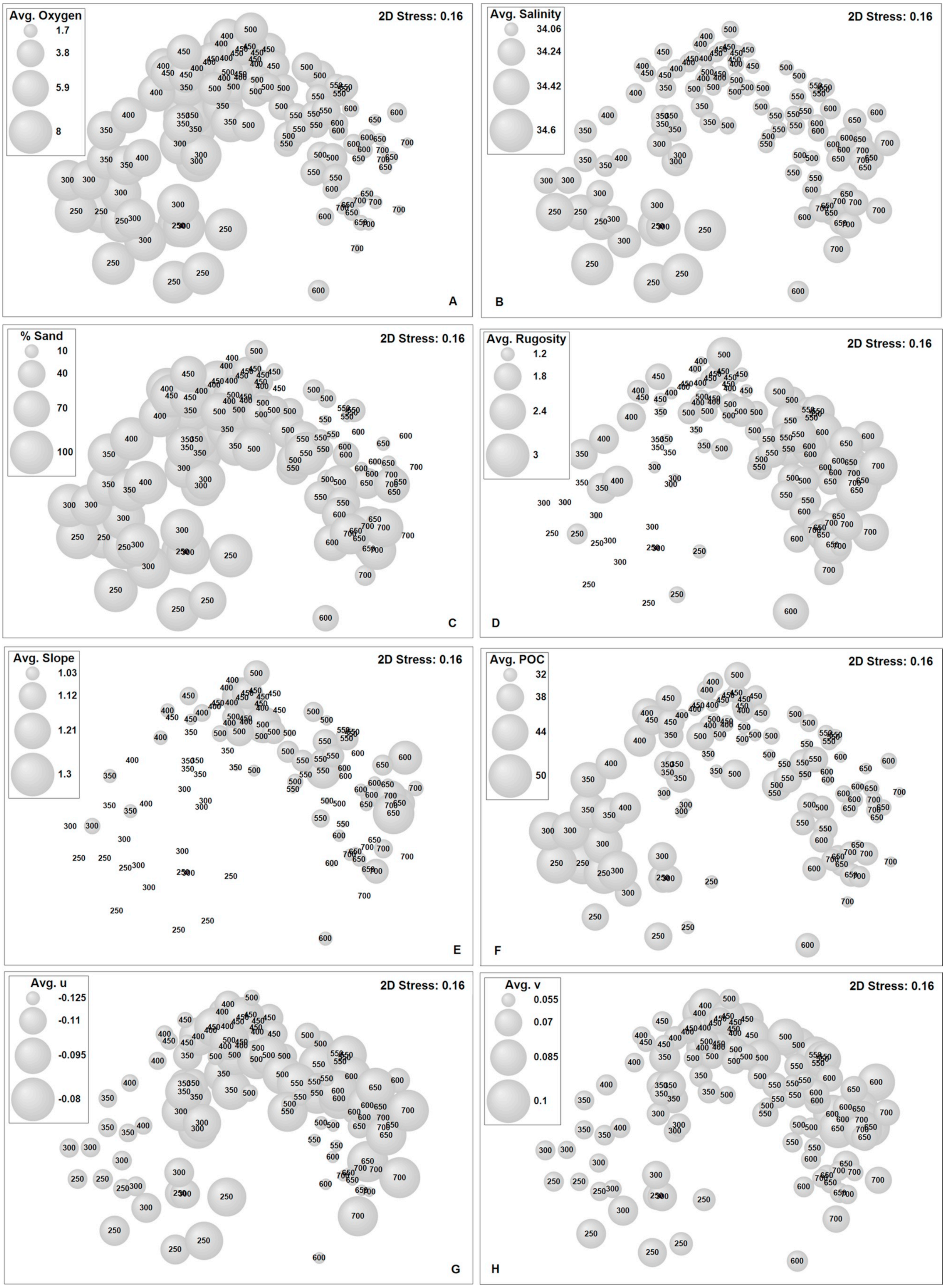

Fig. 6. NMDS from Fig. 4 (assemblage structure) with bubble plot overlays for the environmental variables included in the top model in the DistLM analysis. Bubble size is proportional to the value of the environmental variable and each point is an AUV transect represented by its depth.

abundances on the NE study site can be related to the high percentage of sand observed on this site (74.67%) that might affect the abundance of fishes due to habitat preferences and fewer available hiding places. Nevertheless, more studies that measure the speeds of deep-currents and the amount of POC that reaches the sea floor are necessary to corroborate our interpretations.

In contrast to abundance, species richness and $E_{S(300)}$ were significant different by study site, depth, and by their interaction, while diversity and dominance were significantly different by depth and the interaction term (Table 3, Fig. S2). As with other organisms, species richness of benthic fishes generally increases with depth at bathyal depths and then decreases through abyssal depths (Rex, 1981). However, the tendency at bathyal depths has been observed to vary from one place to other (see Pearcy et al., 1982). According to Froese and Sampang (2004), above 1000 m species richness of seamount fishes peaks at approximately 400–600 m deep and then decreases until it reaches values close to 0 at 7000 m, which can be the result of under sampling. The distributions of deep-sea species result from the adaptation to specific environmental conditions that, besides the geomorphological ones affecting the food supply (Boehlert and Genin, 1987; Rogers, 1994; Genin, 2004), also include oceanographic conditions related to water masses (Koslow et al., 1994; Clark et al., 2010a; Tracey et al., 2012) that determine the presence of a particular species in a particular depth range based on its physiology. The pattern we found on Necker Island is very similar to what Froese and Sampang (2004) described for seamount fishes. The lowest species richness of fishes on Necker was observed at 250 and at 700 m depth, where the diversity was also the lowest and the dominance the highest, while the highest species richness, high diversity and low dominance were found at 500 m depth (Fig. S2). The depth of 500 m seems to be a barrier for many species that are characterized by remaining mostly in and above 500 m (i.e., the marine hatchetfish *Argyripnus* sp. and the duckbill *Chrionema chryseres*) and those species that mostly range from 500 to deeper depths (i.e., the macrourids *V. atherodon* and *M.* cf. *hawaiiensis*, and the large-scaled lantern fish *N. macrolepidotus*). Physiological adaptation of the species to specific values of temperature and oxygen (Thistle, 2003) can influence their distribution and presence on Necker along the depth range sampled. For example, oxygen minimum zones (< 2 mg/l) were found from 650 to 700 m in the three study sites of the island (Table S1) where only 42% and 30% of 91 species identified in this study were found, respectively. The barrier at 500 m may also be related to the change in water masses at this depth. In Hawaii there is a changeover in water masses at 500 m from Western North Pacific Central Water (WNPCW) and Eastern North Pacific Central Water (ENPCW) at 0–500 m to the Pacific Subarctic intermediate water (PSIW) from 500 to 1500 m (Emery, 2001).

4.3. Environmental variables influencing assemblage structure

The fish assemblage structure on Necker Island showed differences by study sites, by depths and by the interaction between sites and depths (Table 4). These results are consistent with previous studies in terms of the variation of deep-sea assemblages on seamounts (Richer de Forges et al., 2000; Tracey et al., 2004, 2012; McClain, 2007; Morato and Clark, 2007; Rowden et al., 2010; Bo et al., 2011; Clark et al., 2010a, 2010b; 2012; Schlacher et al., 2014; Long and Baco, 2014; Morgan et al., 2015). In New Zealand, Francis et al. (2002) found that the assemblage structure of fishes in many seamounts depends on latitude and depth. Tracey et al. (2012) mentioned that the proximity of the seamounts in their study did not allow recognition of latitude as an important variable for the structure of the assemblage, but depth was correlated as it was also for other studies in the area (Donovan, 1998; Jacob et al., 1998). Despite the fact that we found variations in the structure of the assemblage by study site and depth, it is difficult to affirm assertively whether the variation is based on vertical or horizontal differences in the structure. Substantial variation over the vertical scale was observed in the NMDS plot, which illustrates a horseshoe effect in the assemblage structure with a depth-gradient implication (Fig. 4). A pattern of strong variation in assemblage structure with depth is common and has been observed previously on seamounts (Baco, 2007; McClain et al., 2010; Long and Baco, 2014; Victorero et al., 2018; Morgan et al., in review).

Seamounts and oceanic islands are not homogenous habitats; each study site presents different physical, chemical, and geological conditions that have the potential to affect assemblage structure. The variation with site and depth observed in fish assemblages that inhabit the seafloor at the studied depths on Necker was correlated most strongly to oxygen, percentage of sand, POC, salinity, and rugosity (Fig. 5, Table 5).

Oxygen explained the highest proportion of variation in the fish assemblage structure on Necker Island (Fig. 5, Table 5). In the oceans, oxygen is highly correlated with temperature. Oxygen generally decreases with depth and reaches very low concentrations between 300 and 1000 m depth (Thistle, 2003). This pattern was clearly observed on Necker where oxygen concentrations showed high values in shallower depths that decreased with depth (Fig. 6A), presenting minimum oxygen concentrations from 650 to 700 m depth (Table S1). Likewise, temperature decreased with depth but was removed from the DistLM test because it was highly correlated to dissolved oxygen (Table S3). Salinity also explained a high proportion of the variation in the assemblage structure (Fig. 5, Table 5). Therefore, our results showed that the structure of the fish assemblages on Necker, in terms of the species composition, is highly influenced by depth, potentially through differences in environmental parameters in the vertical water masses found in the area as mentioned above. Oxygen and temperature, which are some of the variables that change the most in these vertical water masses, are known to have an influence on the physiology and life cycle of organisms (Thistle, 2003; Clark et al., 2010b) and also affect their distribution in the water column. These results have been previously documented by other studies in deep-sea fishes; in some oxygen was found to influence the structure of the community (Wishner et al., 1990; Yeh and Drazen, 2009), but in others temperature was found to have the stronger effect (Koslow et al., 1994; Jacob et al., 1998; McClain et al., 2010; Clark et al., 2010a, 2011).

The percentage of sand and rugosity were also important in explaining the assemblage structure of deep-sea fishes on Necker as well as the slope, but with a lower proportion of variation explained by these variables (Fig. 5, Table 5). The substrate of seamounts and islands slopes varies from soft sediment to continuous hardpan. Soft sediments are commonly detected on the top of the deep guyots as well as in topographic depressions, while extensive hard-bottom areas and rocky outcrops are characteristic of the abrupt flanks and the tops of shallow guyots (Karig et al., 1970; Lonsdale et al., 1972; Raymore, 1982; Genin et al., 1986). Additionally, sediments on seamounts can vary in grain size and are greatly affected by the interaction between topography and the current regime (Roberts et al., 1974). The substrate parameters determine the occurrence, distribution and diversity of species when they are directly related to the species habitat. Our results show that at least two of the three observed assemblages (Fig. 4) were associated with the type of substrate. One is characterized by the high abundance of benthic and demersal species dwelling on soft bottoms in the shallower end of our surveyed depth range (i.e, *G. struhsakeri*, *S. engyceros*, *Hoplichthys citrinus*, and *Poecilopsetta hawaiiensis*), and the other is formed by high abundance of demersal species inhabiting deeper depths (i.e., *V. atherodon* and *M.* cf. *hawaiiensis*), where there was a lower percentage of sand and higher rugosity (Fig. 4, Fig. 6C and D). Similar results were found by Francis (1976) in shallow fish assemblages (4–74 m) in the Hauraki Gulf in New Zealand where the author found nine fish assemblages that were related to sediment type. At deeper depths, Jacob et al. (1998) analyzed data in southeast New Zealand (80–787 m) and did not find sediment type to be an important structuring variable, arguing that its variability was too small.

Another important parameter explaining the variation in fish assemblage structure was particulate organic carbon (POC) (Fig. 5, Table 5). POC generally decreases with depth (Suess, 1980) because the detritus arriving to deeper depths is the remains of organic matter that is not consumed in shallower depths (Carney, 2005). On the other hand, primary productivity may increase around some seamounts (Dower et al., 1992) due to internal waves that produce a turbulent mixing of the water, and bring nutrient-rich water from the bottom (White et al., 2007). Although POC values used in the analyses were based on surface POC, transects closer to the summit showed higher concentrations (Fig. 7F). POC at a site on the seafloor will be influenced by the amount of POC descending from the surface as well as by the movement of that POC by surface and deeper currents. These processes may contribute to the differences among study sites as well as among depths. Consistent with this explanation, both surface current vectors (u and v) came out as significant in this study (Table 5). Desch et al. (2009) mentioned that productivity in the NWHI is influenced by wind and bathymetric characteristics, which also determine the upwelling in specific areas. The location and extent of the shelf on each study site on Necker (Fig. 1) may affect local oceanic flow conditions that influence the productivity in the surface and determine the spatial scale of species distributions and abundances. Although flow has been shown to be one of the most important environmental factors influencing the organic material fluxes and the heterogeneous assemblage structure on seamounts (Genin et al., 1986), there are no studies that have investigated the effect of POC on the deep-sea fish assemblage structure in seamounts for comparison. Studies focused on other underwater features such as canyons have found a direct relationship among diversity of benthic megafauna and amount of organic material, where the decrease in diversity is exponential with depth because of the consumption of organic material (Vetter and Dayton, 1998). However, unlike seamounts, but like the emergent Necker Island, canyons are strongly influenced by coastal organic detritus (De Leo et al., 2012).

4.4. Conclusions and management implications

With observations of variation in abundance by site on a seamount, and variations in species richness, dominance, diversity, and assemblage structure with both study site and depth, this study adds to the growing body of evidence supporting natural variation in seamount communities at the scale of a single seamount. Three main assemblages of fishes were observed corresponding to depths of 250–300, 350–500, and 550–700 m. This variability of the assemblage structure was correlated with dissolved oxygen (and its correlate temperature), salinity, % of sand, rugosity, slope, POC, and current vectors u and v. This study documents variability in deep-sea fish assemblages inhabiting Necker Island that can be considered in the management of this seamount and, with some caution, in the management of other seamounts in the NWHI.

The confluence of variability in environmental parameters and anthropogenic impacts can result in variability in the assemblage inhabiting a single seamount, and can create local dynamic responses in the structure of seamount assemblages. Understanding this variation within a seamount is an important tool for managing and conserving areas where these underwater features are present. As environmental characteristics and biological communities can vary on a local scale within a single undersea mountain, threats can affect communities in different ways at different depths and locations on a single seamount. Hence, management strategies designed to protect a given seamount should recognize natural variability over space (Probert et al., 2007) and include basic ecological knowledge about the species present, allowing better control of the status of seamount resources. Seamount conservation efforts should not be restricted by limited knowledge or data (Clark et al., 2010b). Future studies should focus on the examining variability of deep-sea assemblages over time that can be used to compare to the present data and to monitor assemblage structure.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2019.103086.

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