Distribution and community structure of deep-sea demersal fish assemblages across the central Pacific Ocean using ROV data

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Abstract

Four Marine National Monuments exist within the Pacific Islands region including the Papahānaumokuākea Marine National Monument, the Marianas Trench, Pacific Remote Islands, and Rose Atoll Marine National Monuments. Together these make up an area of 3,063,223 square kilometers; however significant knowledge gaps remain regarding the distribution and community composition of fishes, especially deeper than 500 meters. With the additional threats of global change, fishing, and deep-sea mining, there is a need to characterize these communities for conservation and management purposes. The remoteness of deep-sea habitats has resulted in deep-sea fishes being poorly sampled globally, with most descriptions of demersal fish communities focused along temperate continental margins. Demersal deep-sea fish communities from islands and seamounts are poorly described, even in the Hawaiian archipelago. Knowledge across all depths, in similar settings, is even more sparse for other archipelagos in the central Pacific. However, recent remotely operated vehicle (ROV) explorations of the central Pacific and archived video from submersible dives conducted by the Hawai`i Undersea Research Laboratory (HURL) provide an opportunity to explore the structure of these communities. Here we describe demersal fish communities from archipelagos across the tropical Pacific, including in multiple Marine National Monuments, and examine the relationship of the assemblages to depth and environmental conditions. We used data collected from 227 dives conducted by underwater vehicles resulting in the identification of 24,837 individuals belonging to 89 families and 175 genera across regions for depths ranging from 250-3000 m. The most frequently occurring genera between 250-500 m were *Epigonus*, *Setarches*, *Polymixia*, and *Antigonia*, between 500-1000 m were *Chlorophthalmus*, *Aldrovandia*, and *Neocyttus*, and between 1000-3000 m were *Synaphobranchus*, *Kumba*, *Halosaurus*, *Ilyophis,* and *Ipnops*. There are strong changes in the fish communities with depth, and communities become more similar between regions with greater depth. Depth explained the most variance in community composition followed by water mass distributions, seafloor particulate organic carbon flux (a food supply proxy), concentrations of dissolved oxygen, and salinity. The Line Islands and Tokelau Ridge had the highest values of seafloor particulate organic carbon flux for all depth zones investigated (250-3000 m) and the highest abundance of fishes at 250-500 m and 500-1000 m, respectively. Accumulation curves indicated that diversity at the genus level within all regions and depth bins (except 1000-2000 m and 2000-3000 m) had not been reached with the existing sampling effort. However, when combining samples from all regions, diversity generally appeared to decrease with depth. Overall, this study demonstrates that there are significant regional differences in the composition of the deep-sea fish fauna as well as differences across depth. Such distribution patterns suggest that existing Marine National Monuments are not replicates of diversity, but complementary components of the regional diversity. The effectiveness of the Monuments in protecting deep-sea fish communities will depend on the spatial distribution and depths of human-caused disturbances such as climate change and deep-sea mining, therefore we suggest further sampling in the regions to fully characterize the communities and better define boundaries and gradients of faunal change.

1. Introduction

Demersal fish living in association with the seafloor consist of numerous teleosts, sharks, eels, and rays (Froes and Pauly, 2013). Those of economic importance are concentrated on the continental shelf and slope to about 1500 m depths (Khedkar et al., 2003, Clark et al., 2016, Morato et al., 2007, Pitcher et al., 2007). World catches of demersal species increased rapidly during the 20th century and the limits of biological production have been reached in many areas

(Khedkar et al., 2003). Therefore, with the potential for changes in surface primary production induced by anthropogenic climate change to alter standing stocks in the food-limited deep-sea (Glover and Smith, 2003, Smith et al., 2008, Brito-Morales et al., 2020), it is important to understand demersal fish community structure as a key characteristic of these ecosystems.

There have been a few efforts across the globe to characterize demersal fish community structure, and these have been concentrated on continental shelves and upper slopes, with fewer studies for oceanic islands or seamounts (Clark et al., 2010, Drazen et al., 2021). Some studies have been conducted in the southwestern and southeastern Pacific Ocean (e.g., Drazen et al., 2021, Koslow et al., 1994; Francis et al., 2002; Tracey et al., 2004), off Japan (e.g., Fujita et al. 1995), the Nazca Ridge (Parin 1991; Parin et al., 1997), and in several areas of the North Atlantic (Colvocoresses and Musick, 1984; Haedrich and Merrett, 1990; Mahon et al. 1998; Menezes et al., 2006; Bergstad et al., 2008). These studies have found that depth is a strong driver of community structure and community structure was found to vary between the continental shelf (0-200 m), upper slope (200-600 m), mid-slope (600-800 m), and deep mid-slope (800-1200 m). These studies also found that species composition at shallow sites differed from deeper sites, with many deeper species having broad geographic distributions. However, the expense of sea-time has led to a tendency for research to be carried out near land masses and major oceanographic research institutions.

Deep-sea demersal fish studies in the central Pacific have focused on the Hawaiian archipelago. Gilbert (1905) and Struhsaker (1973) were the first investigators to focus on demersal fishes in the region. Chave and Mundy (1994) synthesized a decade of submersible observations on more than 250 demersal fish taxa between depths of 40 and 2000 meters in the Hawaiian Archipelago, Johnston Atoll, and Cross Seamount from 1982 to 1992. Many of the recent studies on deep-sea demersal fishes in the central Pacific have taken place in the Hawaiian Islands (Oyafuso et al al., 2017, De Leo et al., 2012, Yeh and Drazen, 2009) and on seamounts in the Northwestern Hawaiian Islands (Mejía-Mercado et al., 2019). These studies and those from other regions document changes in community composition with depth. Some of the major environmental factors that could be driving these differences are changes in water mass properties (i.e., salinity, temperature, and density), substrate type, food, and oxygen availability (e.g., Labropoulou et al., 2000). Generalizing how these environmental gradients influence deep-sea fishes could be greatly expanded by surveying large spatial scales and depth gradients in different regions with different environmental characteristics. However, despite these studies from the Hawaiian Islands and other areas, there are no published studies, to the author's knowledge, that evaluate distribution and community structure across the central Pacific.

A recent expansion in ROV exploration throughout the central Pacific now provides a means to evaluate demersal fish community structure at a broad scale. NOAA's *CAPSTONE: Campaign to Address Pacific monument Science, Technology, and Ocean NEeds* used the NOAA Ship *Okeanos Explorer* to conduct ROV dives between 2015 and 2017 from the Marianas to American Samoa (Kennedy et al 2019). Data from other exploration expeditions from *EV Nautilus* Cruises between 2018 and 2019, as well as submersible surveys by the Hawai`i Undersea Research Laboratory (HURL) between 2005-2013, have also expanded available data. These datasets provide an opportunity to explore the relationships between geographic and environmental differences and demersal fish communities.

The objectives of this study were to elucidate how the community composition, total abundance, and diversity of demersal fish communities vary between archipelagos in the central Pacific. Since both physical and biological factors have been postulated to cause faunal zonation with depth, we consider the physical factors available to investigate the relationships between community structure and environmental drivers, i.e., temperature, POC flux (food supply), oxygen availability (e.g., Labropoulou et al., 2000), and water mass structure. These variables can influence biogeographic distributions of fish species by, in part, facilitating larval dispersal across large distances or by creating physiological barriers for dispersal (Norcross and Shaw, 1984; Richards et al., 1993; Grothues and Cowen, 1999; Galarza et al., 2009).

2. Methods

2.1.Underwater Vehicle Surveys

Opportunistic data were acquired from underwater vehicle surveys carried out during cruises from multiple ocean exploration expeditions in the central Pacific. We used data from NOAA's three-year Pacific-wide field campaign *CAPSTONE* that investigated the biodiversity of deep-sea taxa across multiple depths and feature types in American Samoa, Johnston Atoll, Line Islands, Main Hawaiian Islands, Musicians Seamounts, Northern Marianas, Northwest Hawaiian Islands, Southern Marianas, Tokelau Ridge, and Wake Island between July 2015 and September of 2017 (168 dives, 891.5 hours, 0-6000 m depth) (Kennedy et al., 2019).

In addition to the CAPSTONE dives, opportunistic data from four *EV Nautilus* cruises (NA101, NA110, NA112, and NA114) between 2018 and 2019 were used from multiple areas within the central Pacific (36 dives, ~218 hours, 0- 2459 m) (Kelley et al., 2019, Bell et al., 2020), and from from *Pisces 4* and *5* submersible dives conducted by HURL between 2005 and 2013 in the Main Hawaiian Islands (MHI) and Northwestern Hawaiian Islands (NWHI, the Papahānaumokuākea Marine National Monument) (96 dives,~576 hours, 0-2000 m depth).

Nearly all data occurred after 2007 when the use of a new Ultra-short Baseline acoustic positioning (USBL) was implemented to increase tracking accuracy. The US Line Islands and Phoenix Island surveys in 2005 (HURL) included the use of the Sonardyne USBL system which had a tracking accuracy of roughly 30 m at 1000 m and was therefore included. CAPSTONE and *EV Nautilus* dives were principally conducted for exploration and were not regular stratified transects. *Pisces* dives include a mixture of dives that conducted quantitative transects and opportunistic transits. The full list of dives used in the analysis is available in Table S1. The tracking data were unavailable for five of these dives, therefore they were not included in the abundance analysis because dive lengths along the seafloor could not be calculated.

The *Nautilus* and *Okeanos* cruises used the ROVs *Hercules* and *D2,* respectively. The ships followed the ROVs with USBL tracking systems as the ROVs traversed the seafloor at a slow speed (~0.05–0.1 m/s) and ~ 2 m altitude above bottom (Putts et al., 2019). The *Pisces* submarines used a Tracklink 500HA USBL (LinkQuest) system to calculate the position every 10 seconds (Putts et al., 2018) where *Hercules* and D2 calculated position at ≥1 scan per second (Quattrini et al., 2017). Due to the nature of ocean exploration, the dives were occasionally interrupted by stopping the ROV/HOV for sampling or for frequent adjustments of the wide-angle view on the forward-facing cameras to zoom in on animals (Quattrini et al., 2017).

Cameras on all the dive systems were high definition. Putts et al., (2019) found that the fields of view of these different camera systems were comparable. Quattrini et al., (2017) combined dives from *Hercules* and *D2* to investigate demersal fish in the Caribbean; therefore, it was assumed that all vehicles were comparable in their ability to survey fish. All dives, regardless of vehicle, were annotated by the University of Hawai`i Deep-sea Animal Research Center (DARC), using VARS annotation software.

All vehicles collected temperature, DO, and salinity data from Seabird CTDs and Aanderaa oxygen optodes (Kelley et al., 2019). For every observation, the date, geographic position, depth, temperature, salinity, and dissolved oxygen concentration were recorded. There were 227 dives between 2005 and 2019 included in the analysis and they occurred on a variety of rugged features, predominantly rocky seafloor, but including seamounts, atolls, banks, and islands.

2.2. Demersal Fish Data

Taxa were identified to the lowest taxonomic resolution possible, which ranged from class to species. Identifications were made using a variety of taxonomic keys and reference images, and were sent to experts for ID verification. Due to the challenges of identification, many taxa were not identified to species level. Therefore, analyses were performed on data with identification to family and genus level. This enabled for the lowest taxonomic resolution possible while also providing an adequate number of fishes per sample for community structure patterns to emerge. Midwater taxa were removed, which included all Alepocephalidae, Barbourisiidae, Cetomimidae, Chiasmodontidae, Eurypharyngidae, Gonostomatidae, Myctophidae, Nemichthyidae, Phosichthyidae, Scombridae, Sternoptychidae, Stomiidae, Trichiuridae and the zoarcid, *Melanostigma* spp. Pelagic species were identified based on authors' experience or by reference to the scientific literature (Mundy, 2005).

The dives spanned ten different regions (Figure 1) and were split into five depth bins: 250-500 m, 500-750 m, 750-1000 m, 1000-2000 m, 2000-3000 m. The depth bins were chosen to provide higher resolution (250 m) in shallower water where community change is more rapid and lower resolution for depths below 1000 m (Zintzen et al., 2017, Carney, 2005). This depth resolution also corresponded with the Kennedy et al., (2019) analysis of the CAPSTONE data. The full range of data includes deep-sea fishes between depths of 100 and 5877 m; however, there were not enough observations above 250 m or below 3000 m for a robust analysis, so these observations were omitted. After filtering the data using the above criteria, the number of dives available were 138 from CAPSTONE, 33 from *E/V Nautilus*, and 56 from the HURL records.

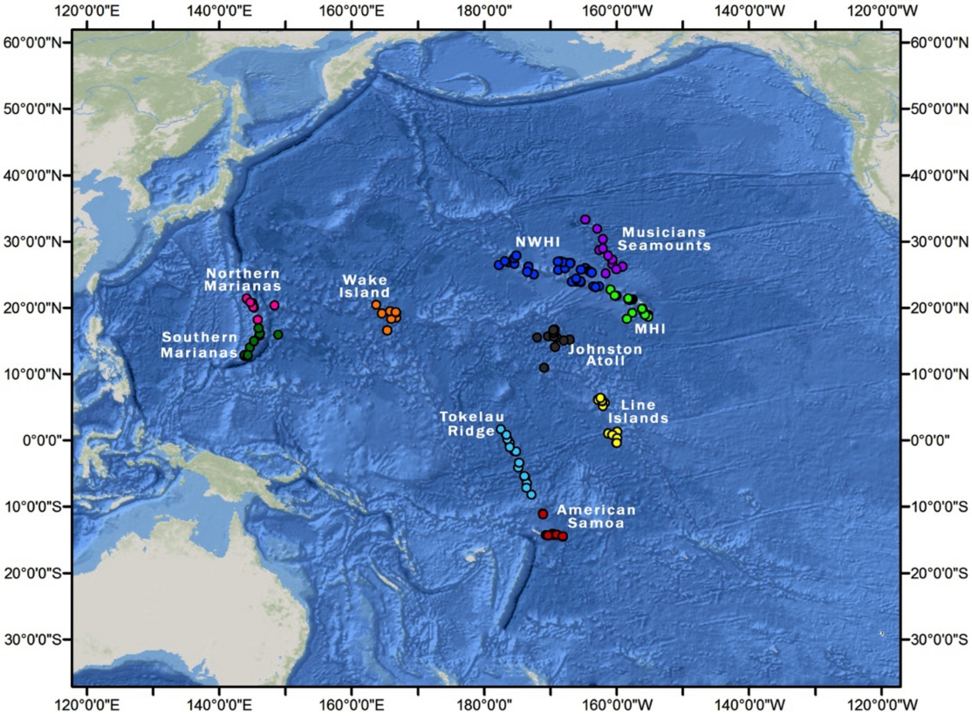


Figure 1) Locations of the 241 samples in the ten regions: American Samoa (AS), Johnston Atoll (JA), Main Hawaiian Islands (MHI), Musicians Seamounts (MS), Northern Marianas (NM), Northwestern Hawaiian Islands (NWHI, the Papahānaumokuākea Marine National Monument), Southern Marianas (SM), Wake Island (WI), Line Islands (LI), and Tokelau Ridge (TR) in the central Pacific.

Table 1) The number of samples (dive by depth) with fish observations. The number of samples are separated by a comma for identifications at the family and genus level, respectively. NAs indicate where no sampling was available.

Regions	**250-500 m**	**500-750 m**	**750-1000 m**	**1000-2000 m**	**2000-3000 m**	**Total Samples**
American Samoa (AS)	7,7	7,6	3,**NA**	3,2	1,**NA**	21,15
Johnston Atoll (JA)	2,2	2,2	**NA,NA**	9,9	5,3	18,16
Line Islands (LI)	10,10	9,9	9,8	9,9	2,2	39,38
Main Hawaiian Islands (MHI)	20,21	1,2	5,6	11,12	1,**NA**	38,41
Musicians Seamounts (MS)	**NA,NA**	**NA,NA**	**NA,NA**	3,1	8,6	11,7
Northern Marianas (NM)	6,6	1,1	1,1	**NA,NA**	2,1	10,9
Northwest Hawaiian Islands (NWHI)	7,7	6,6	5,5	21,15	13,7	52,40
Southern Marianas (SM)	6,5	3,3	**NA,NA**	2,1	2,**NA**	13,9
Tokelau Ridge (TR)	5,5	5,5	3,3	12,12	5,4	30,29
Wake Island (WI)	1,1	1,1	1,1	4,3	2,2	9,8
Total Samples in Depth Bin	64,64	35,35	27,24	74,64	41,25	241,212

Fish observations from each dive were aggregated into five depth bins (250-500 m, 500-750 m, 750-1000 m, 1000-2000 m, 2000-3000 m) that were used for statistical analyses (Table 1). These dive-by-depth counts will be referred to as samples throughout. Samples with five or less fishes observed were removed for the community composition analyses because there are inherently fewer similarities for samples with few individuals. This threshold was chosen based on non-metric Multidimensional Scaling (NMDS) and cluster analysis in which removing samples with five or less fishes produced the least number of outliers. The number of resulting samples at the genus level (n = 212 samples from 151 dives) and family level (n = 241 from 176 dives) varied between regions (Table 1). In some cases, no samples were available for a depth and region because no dives were conducted there, or no samples were possible due to local bathymetry. For example, in the Musicians Seamounts, summits reach no shallower than ~1000 m (Cantwell, 2020).

More data were available at the family level, so these were used to investigate trends in abundance. For abundance analysis, the number of samples varied between regions, ranging from 9 to 52 (Table 1). Sample sheets created at the family and genus level are available in Table S2. The length of each ROV dive track was used to standardize abundance (fish/ m) for each sample (depth bin within a dive). Track length distances varied from 85 m to 7.1 km (Table S1). Dive track distances were measured in ArcMap 10.8.2, consistent with the methods in Kennedy et al., (2019). There were six dives in the HURL archive that did not have dive tracking data available and were not included in the abundance analysis.

2.3. Environmental Covariates

Oceanographic data (depth, dissolved oxygen, salinity, and temperature) for each sample position were extracted from the observational data sets. Temperature (°C), salinity, and depth (m) were used to identify the water mass encountered by each ROV dive sample (Table 2, Figure 2). Fuhr et al. (2021), Kawabe and Fujio (2010), and Emery et al., (2001) were used to identify water masses in the upper waters (0-500m), intermediate waters (500-1500 m), and deep waters (≥1500 m). A map of the schematic circulation of intermediate and deep-water masses in the Equatorial and North Pacific was overlaid onto the sample locations using Fuhr et al., (2021) (Figure 3).

Table 2: Water masses found in the central Pacific. Approximate depth, potential density (kg/m3), and temperature ranges (°C) are included (ranges from Fuhr et al., 2021 and Schneider et al., 2003)

Layer	Water Mass	Abbreviation	Depth Range (m)	σ θ (kg/m3)	θ (°C)
Upper	Western North Pacific Central Water	WNPCW	0-500 m	25.2-26.4	10-22 (°C)
Intermediate	North Pacific Intermediate Water	NPIW	500-1300 m	26.6-27.4	3.5-13 (°C)
	Antarctic Intermediate Water	AAIW	500-1300 m	26.8-27.3	2-10 (°C)
Deep	North Pacific Deep water	NPDW	1500 – 3500 m	27.6-27.8	1.4-6.4 (°C)
	Upper Circumpolar Deep Water	UCDW	1000 - 3000 m	27.7-28.2	1.4-6.4 (°C)
	Lower Circumpolar Deep Water	LCDW	3000 m - bottom	27.7-28.2	0.98-1.2 (°C)

There were 15 *Pisces* dives that did not have depth information available and therefore were omitted. On top of that, there were 24 *Pisces* dives in the MHI that did not have CTD data, and 15 Pisces dives in the NWHI that did not have dissolved oxygen data. Therefore, CTD data from dives nearby (within ~50 km) were used to interpolate the dives that did not have dissolved oxygen data.

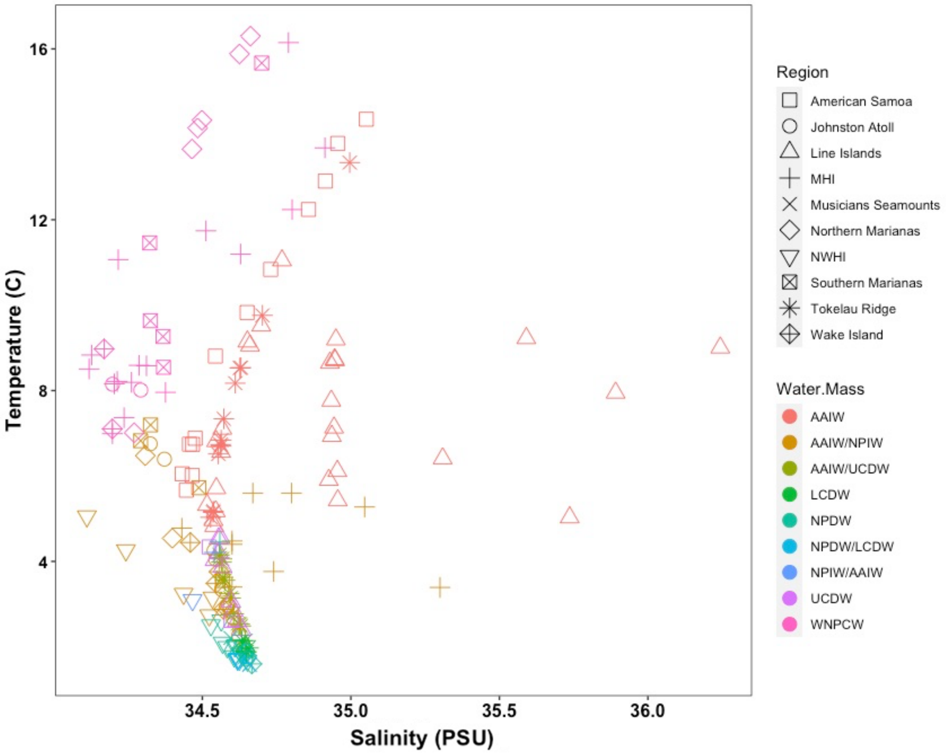


Figure 2) Salinity vs. temperature plot for all samples at the genus level (n = 212 samples). Regions and water masses are represented by the different shapes and colors respectively. The water mass classification is based on hydrographic properties defined in Table 2.

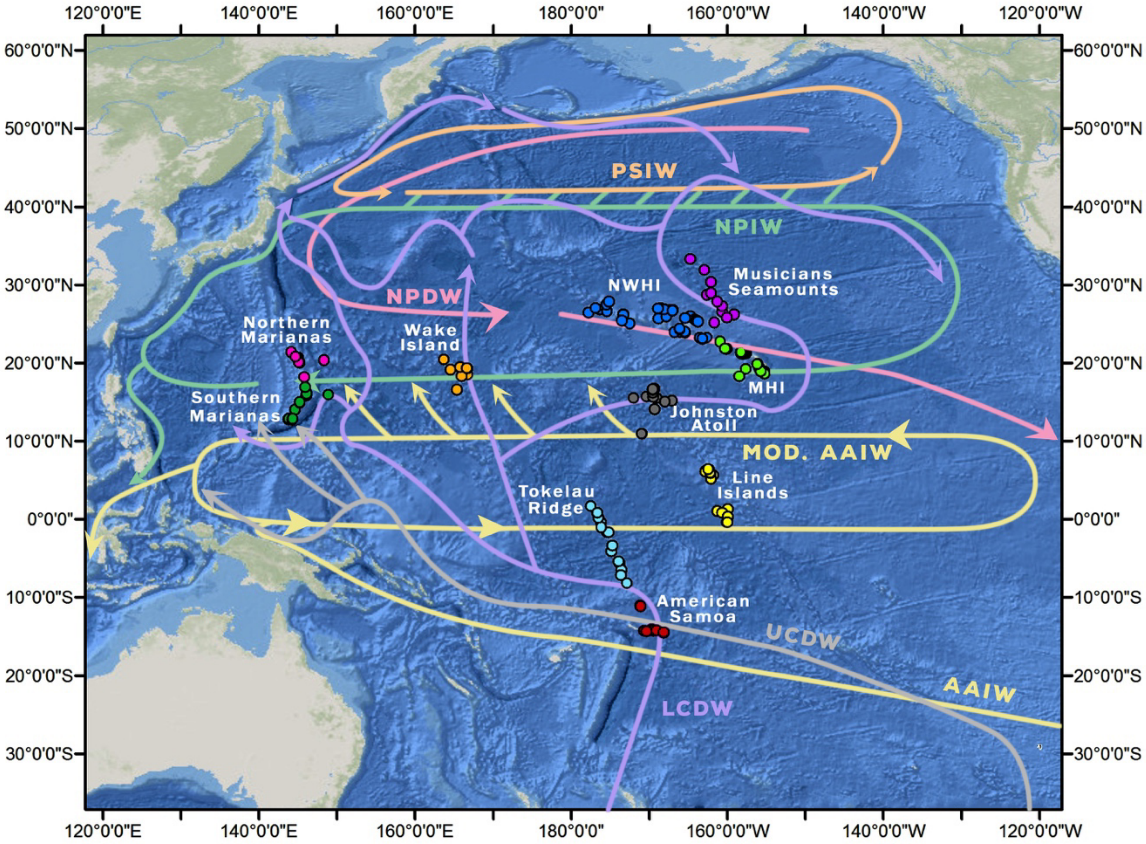


Figure 3) Schematic circulation of intermediate and deep-water masses in the Equatorial and North Pacific (Fuhr et al., 2021). The ten regions (sampling locations) are represented by the colored dots. The light orange and green lines depict mixing of the PSIW and NPIW respectively. The grey lines mark the approximate location of upwelling of UCDW into the intermediate layer. The purple lines mark upwelling of LCDW and its transformation into NPDW (pink line). The map was created using ArcMap 10.8.2 and further modified.

We used estimates of particulate organic carbon (POC) flux to the seafloor, following methods in Lutz et al. (2007), as a proxy for food supply. Net-Primary-Production (NPP) data were obtained from the Oregon State Ocean Productivity website (http://orca.science.oregonstate.edu/1080.by.2160.monthly.hdf.vgpm.v.chl.v.sst.php), which provided NPP based on the Vertically Generalized Production Model (VGPM). Monthly estimates of NPP data were averaged between 2007 and 2017 at a resolution of 1/6th of a degree. A fixed euphotic zone depth of 100 m (commonly used as noted in Palevsky et al., 2018) was used to calculate Lutz POC flux at the depth for each sample (midpoint of sample bin).

2.4. Data analysis

Differences in demersal fish community composition between regions and depths were evaluated using PERMANOVA in PRIMER v7 (Clarke and Gorley, 2006) and the program R (R Development Core Team, 2013). Community data were visualized using non-metric Multidimensional Scaling (NMDS) ordinations and unconstrained hierarchical clustering. A Mantel test was used to test if differences in community composition between samples covary with the geographic distance between samples. Samples were partitioned into upper bathyal, (250-500 m) intermediate (500-750, 750-1000 m), and deep samples (1000-2000, 2000-3000 m). Mantel tests are a common routine used to determine the correlation between two matrices and permutations are used to determine significance (Legendre et al., 2010). Genera contributing most to similarity between regions were examined using the Similarity Percentage (SIMPER) analysis with a 70% cutoff for low contributions (Clarke and Gorley, 2006).

We calculated similarities in fish assemblages between all samples in the community composition analysis using a Bray Curtis similarity matrix. A square-root transformation was used to normalize the variance. As rare genera are expected to be over-represented on geographic features with many samples compared to those with fewer, a wisconsin double standardization was used to make genera of different abundance equally important (Gauch et al., 1977).

The relationship between community composition and environmental variables was investigated using a constrained distance-based ordination method, Canonical Analysis of Principal Coordinates (CAP) which uses an *a priori* hypothesis to relate a matrix of response variables, Y (genera) with predictor variables, X (quantitative environmental variables). CAP has the advantage of allowing any distance or dissimilarity measure (e.g., Bray-Curtis) to be used. It looks for multivariate axes in predictor space that explain community similarity, incorporating the fact that environmental variables may covary. The CAP was performed on the community data using the function capscale() in the R package vegan (Oksanen et al., 2016) and the significance of each environmental variable was determined.

To understand how the abundance of fish varies between regions, we modeled the total fish count within each depth bin from each dive. We used a General Additive Model (GAM) to investigate the response of total fish abundance to different environmental variables fit with the "mgcv" package (Hastie, 2020) in R (R Development Core Team, 2013). Average depth, dissolved oxygen, and salinity were calculated for each sample and used as predictors. The GAM used a negative binomial error distribution with a log link function, and the length of the dive track within the depth bin was included as an offset to account for variation in sampling effort across samples. The "deviance explained" is analogous to variance in a linear regression. The effective degrees of freedom (edf), an approximation of how many parameters the smoother represents were all calculated. The spread of the data (y axis maxima) change between plots because the plots are showing partial residuals and unexplained variation is added on top of the smoother.

We investigated diversity at the genus level using several metrics. First, we used genera accumulation curves. Since there were not enough samples to parse the data by region and depth bin, we separated the samples by region and depth bin respectively. We are aware that in shallower depths, there are more individual fishes than at the deeper depths, which can cause there to be more accumulated diversity at the shallower depths simply because more individuals were sampled. We therefore used Chao-1 and Chao-2 estimators to further estimate generic richness for regions and depth bins. Samples were also rarefied using the iNEXT package (Chao et al., 2014) in the R program (R Development Core Team, 2013) with the Hill number of order q=0 (genera richness). Lastly, we used Pielou's evenness which is the count of individuals of each species (genera in our case) to get a thorough description of the community's structure (Pielou et al., 1966) where values range from 0 (no evenness) to 1 (complete evenness).

3. Results

3.1. Frequently occurring genera

Between 250 and 3000 m, 22,162 individual fishes were recorded in the 212 samples with six or more fishes (Table 1). The average fish per sample was 104 with the minimum number of fishes in one sample being six and the maximum being 2,689 fishes. Across depths, more samples were available between 250-500 m (n = 64) and 1000-2000 m (n = 64). The 750-500 m depth range had the least number of samples (n = 24). The regions with the most samples were the MHI (n = 41), the NWHI (n = 40), and the Line Islands (n = 38). The regions with the least samples were the Musicians Seamounts (n = 7), Wake Island (n = 8), the Southern Marianas (n = 9), and the Northern Marianas (n = 9).

The most frequently occurring fishes varied between regions with some similarity between depth bins (Table 3, Figure 4). *Epigonus* occurred frequently in the upper and intermediate bathyal depths within American Samoa, Johnston Atoll, the Main Hawaiian Islands, Southern Marianas, and Wake Island. *Neocyttus* occurred frequently in Tokelau Ridge and the Line Islands in intermediate depth bins. At about 1000 m, the taxa transitioned to genera, such as *Aldrovandia,* with a deeper depth range*,* which occurred frequently between 1000 and 3000 m within American Samoa, the Main Hawaiian Islands, and Northwestern Hawaiian Islands and Wake Island.

Table 3) Most frequently observed taxa (genus level) between region and depth bin (m).

Regions	**250-500 m**	**# individuals**	**500-750 m**	**# individuals**	**750- 1000 m**	**# individuals**	**1000-2000 m**	**# individuals**	**2000-3000 m**	**# individuals**
AS	*Epigonus*	287	*Chlorophthalmus*	34	**NA**	**NA**	*Aldrovandia*	4	**NA**	**NA**
JA	*Epigonus*	347	*Epigonus*	27	**NA**	**NA**	*Halosaurus*	28	*Kumba*	4
LI	*Setarches*	6014	*Setarches*	1420	*Neocyttus*	449	*Neocyttus*	83	*Bathypterois*	9
MHI	*Epigonus*	565	*Hymenocephalus*	40	*Aldrovandia*	170	*Aldrovandia*	202	**NA**	**NA**
MS	**NA**	**NA**	**NA**	**NA**	**NA**	**NA**	*Kumba*	2	*Ilyophis*	18
NM	*Grammatonotus*	2692	*Chlorophthalmus*	70	*Synaphobranchus*	22	**NA**	**NA**	*Bassozetus*	2
NWHI	*Polymixia*	123	*Synaphobranchus*	4	*Aldrovandia*	16	*Aldrovandia*	54	*Kumba*	23
SM	*Epigonus*	205	*Epigonus*	46	**NA**	**NA**	*Synaphobranchus*	2	**NA**	**NA**
TR	*Antigonia*	189	*Neocyttus*	491	*Neocyttus*	742	*Neocyttus*	86	*Bathypterois*	13
WI	*Epigonus*	11	*Beryx*	12	*Aldrovandia*	10	*Aldrovandia*	14	Bassozetus	5


A


B

Figure 4) The most frequently observed taxa between depth and region. A) Most common genera between 250-500 m. Top to bottom and left to right, *Epigonus, Setarches, Polymixia,* and *Antigonia*. B) Most common genera between 500-1000 m, *Chlorophthalmus*, *Aldrovandia, Synaphobranchus,* and *Neocyttus*. C) Most common genera between 1000 and 3000 m, *Kumba, Halosaurus, Ilyophis* and Bathyptoris. Depth bins combined due to lack of space for photograph panels. See Table 2 for a complete list of frequently observed fishes by region and depth bin. Images courtesy of the NOAA Office of Ocean Exploration and Research.

3.2 Differences in community composition with region and depth, water mass, and geographic distance

Overall, fish community composition at the genus level varied significantly between region (pseudo-*F*= 2.6, *P*=0.001), and depth bin (pseudo-*F*= 6.4, *P*= 0.001), with a significant region by depth interaction (interaction term pseudo-*F*= 1.9, *P*= 0.001). Pairwise tests for each region and depth bin (Table 4) revealed that community composition differed by depth and region, but differences lessened with depth (communities become more similar with depth). Regional variation was also apparent across depth, however there were some regions that frequently clustered together. The Line Islands and Tokelau Ridge had distinctly different communities compared to the rest of the regions (Figure 5A) in upper and intermediate depths between 250 - 1000 m. The MHI and the NWHI also had distinctly different communities between 250 - 750 m. The Northern Marianas and Southern Marianas clustered together as well in the upper bathyal depths; however, they are not as closely matched as the Line Islands and Tokelau Ridge and MHI and NWHI. Further, a deep sample (2000-3000 m) was unavailable for the Southern Marianas. Across all regions, there were more significantly different groups in the upper bathyal and intermediate depth bins indicating that there was more community structure in the shallower depths compared to the deep.

Although there were six water masses identified across the ten sampling regions (WNPCW, NPIW, AAIW, NPDW, UCDW, LCDW), we found eight different combinations as some samples occurred at the nexus of two water masses and could not be differentiated (i.e., AAIW/NPIW, NPDW/LCDW, AAIW, UCDW). The intermediate depths encompassing American Samoa, Tokelau Ridge, Line Islands and Johnston Atoll, and the MHI are mainly occupied by Antarctic Intermediate Water (AAIW) whereas the NWHI, Musicians Seamounts, Wake Island, and the Mariana Islands are mainly occupied by North Pacific Intermediate Water (NPIW/AAIW) (Figure 3). Communities at sites that included WNPCW in the MHI, Northern Marianas, Southern Marianas, and Johnston Atoll were similar within 250-500 m. There were moderate similarities between assemblages in the NPIW/AAIW and AAIW within 500-1000 m. Overall, water mass generally followed depth strata with shallow samples on the far right, intermediate in the middle and deep samples on the far left (Figure 5B).

Table 4) Community composition similarity between regions and depth. Numbers indicate the average similarity with bolded values indicating a significant difference between regions (PERMANOVA, *P*<0.05). NA: too few samples were available for a test to be conducted.

250-500 m

	AS	JA	LI	MHI	MS	NM	NWHI	SM	TR	WI
AS	16.3									
JA	15.1	41.5								
LI	**10.9**	**16.3**	32.2							
MHI	**8.6**	**12.5**	**14.8**	13.5						
MS	NA	NA	NA	NA	NA					
NM	13.4	13.0	**12.1**	**7.2**	NA	15.5				
NWHI	**8.1**	**8.6**	**9.0**	**12.2**	NA	**4.0**	23.4			
SM	19.1	17.3	19.2	**10.8**	NA	23.8	**9.3**	30.7		
TR	**11.7**	**6.5**	**19.0**	**10.2**	NA	**9.4**	**10.0**	**14.0**	16.1	
WI	13.5	43.2	11.0	7.0	NA	19.0	4.9	25.3	7.6	0.0

500-750 m

	AS	JA	LI	MHI	MS	NM	NWHI	SM	TR	WI
AS	12.8									
JA	5.1	11.5								
LI	**5.3**	**4.1**	30.2							
MHI	7.9	8.4	**6.0**	10.0						
MS	NA	NA	NA	NA	NA					
NM	13.7	3.0	0.2	7.1	NA	0.0				
NWHI	**3.9**	**0.7**	**7.2**	5.1	NA	6.1	13.9			
SM	10.5	10.9	**13.2**	6.0	NA	18.1	**5.7**	13.0		
TR	**9.4**	**3.1**	**20.6**	**7.4**	NA	2.2	**7.5**	**12.6**	30.8	
WI	9.5	2.3	0.6	8.2	NA	34.6	19.3	21.3	3.7	0.0

750-1000 m

	AS	JA	LI	MHI	MS	NM	NWHI	SM	TR	WI
AS	NA									
JA	NA	NA								
LI	NA	NA	24.9							
MHI	NA	NA	**4.8**	25.0						
MS	NA	NA	NA	NA	NA					
NM	NA	NA	6.6	6.7	NA	0.0				
NWHI	NA	NA	**5.7**	17.9	NA	29.5	20.4			
SM	NA	NA	NA	NA	NA	NA	NA	NA		
TR	NA	NA	17.4	**6.7**	NA	9.6	9.8	NA	18.2	
WI	NA	NA	12.0	8.9	NA	14.0	8.7	NA	14.1	0.0

1000-2000 m

	AS	JA	LI	MHI	MS	NM	NWHI	SM	TR	WI
AS	0.0									
JA	32.0	21.2								
LI	11.5	**14.0**	24.8							
MHI	20.1	**21.9**	**5.1**	41.1						
MS	53.4	33.3	14.7	11.6	0.0					
NM	NA	NA	NA	NA	NA	NA				
NWHI	30.6	21.4	**9.2**	**20.8**	29.2	NA	22.5			
SM	12.1	22.6	7.3	16.2	33.9	NA	17.3	0.0		
TR	14.3	**16.6**	21.6	**10.2**	24.6	NA	**12.2**	14.5	21.4	
WI	**43.1**	23.6	**6.9**	22.6	35.1	NA	25.6	14.3	**12.1**	22.5

2000-3000 m

	AS	JA	LI	MHI	MS	NM	NWHI	SM	TR	WI
AS	NA									
JA	NA	16.3								
LI	NA	16.7	13.5							
MHI	NA	NA	NA	NA						
MS	NA	14.8	14.3	NA	24.2					
NM	NA	14.6	8.3	NA	4.4	0.0				
NWHI	NA	**15.6**	**12.4**	NA	31.2	5.2	39.0			
SM	NA	NA	NA	NA	NA	NA	NA			
TR	NA	21.1	22.1	NA	13.6	9.9	**8.1**	NA	19.8	
WI	NA	24.8	15.6	NA	21.4	33.0	32.0	NA	8.0	57.9

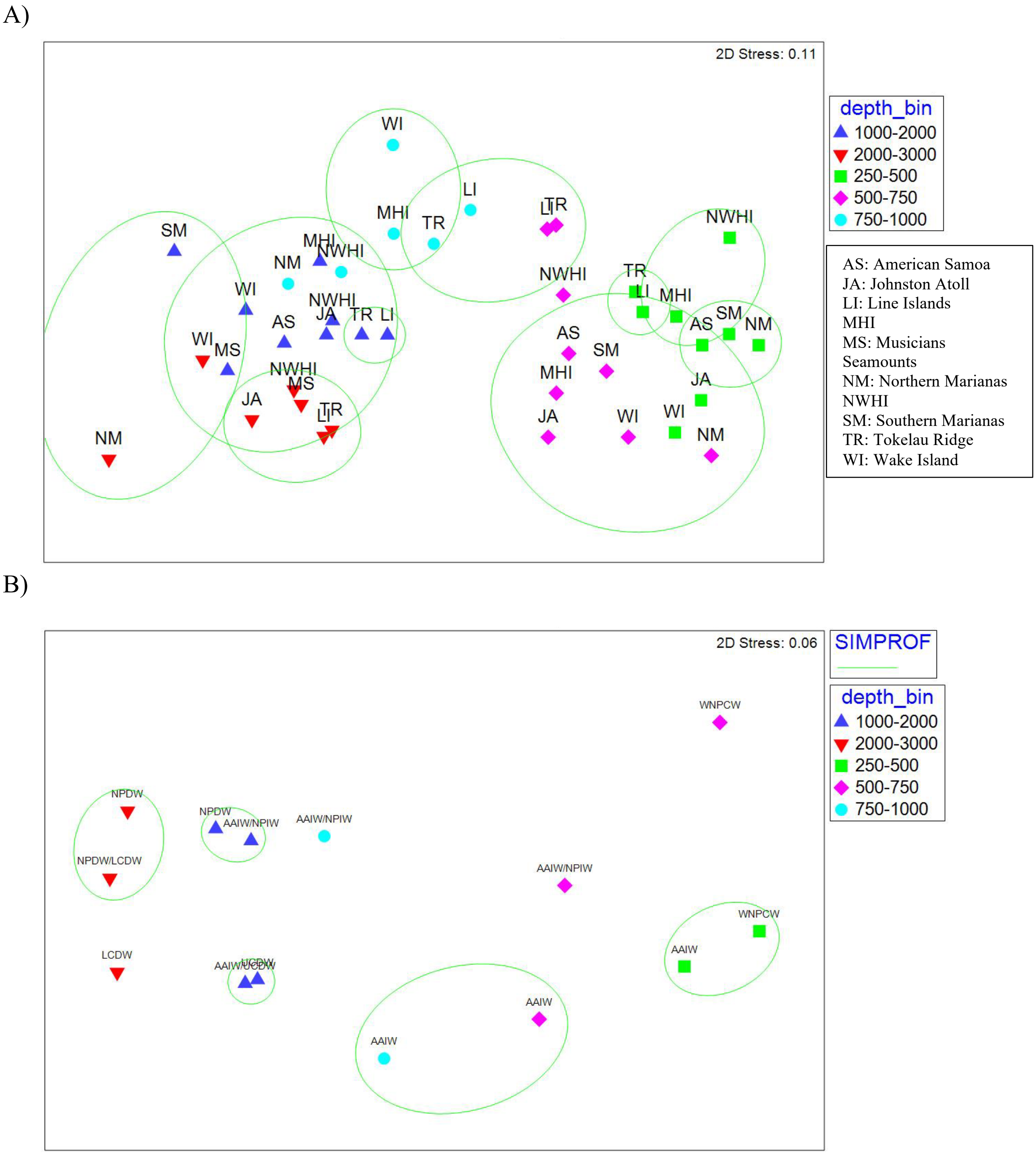


Figure 5) NMDS ordination based on Bray Curtis similarities calculated on square-root transformed and wisconsin double standardized averaged abundances. Combined factors of A) region and depth bin (stress =0.11) and B) water mass and depth bin (stress = 0.06). Symbols are color coded by depth bin (m) and

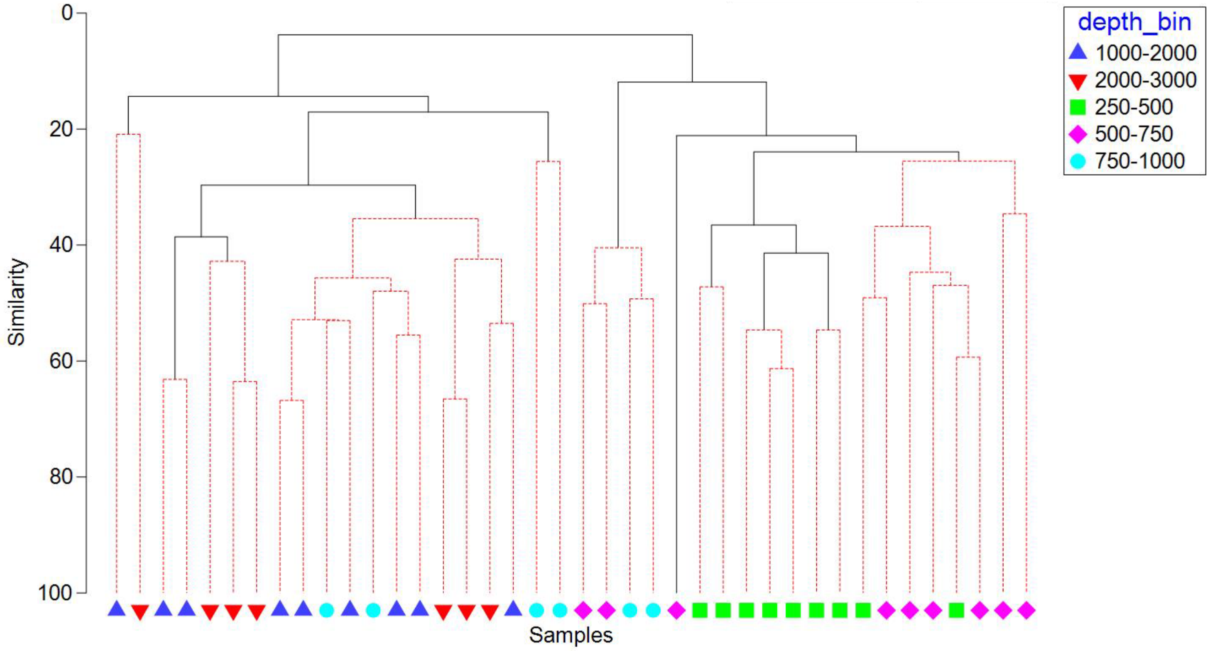
water mass are labeled (Table 2). Green ovals correspond to similar groups determined by the SIMPROF analysis (SIMPROF, $P<0.05$).

The differences in community composition covaried significantly with geographic distance in upper bathyal (250-500 m), intermediate (500-750, 750-1000 m) and deep (1000-2000, 2000-3000 m) depth strata (Mantel statistic: 250-500 m: 0.17, $P = <0.001$, 500-750 m: 0.27, $P = <0.001$, 750-1000 m: 0.23, $P = <0.001$, 1000-2000 m: 0.19, $P= 0.001$, 2000-3000 m: 0.13, $P =0.001$). The 250-500 m depth zone had the most regions that were statistically different and had a few regions that were different from one another despite being in relatively close geographic proximity. For instance, American Samoa was different from Tokelau Ridge just to its north and Johnston Atoll was different from the MHI and NWHI despite Johnston Atoll being less than 1000 km from the MHI and NWHI. Between 500-750 m, the number of regions that were different compared to the upper bathyal (250-500 m) was nearly cut in half. However, there were still differences between regions that were relatively close. American Samoa was still different from the Tokelau Ridge and Johnston Atoll was different from the NWHI. The intermediate 750-1000 m depth bin has limitations for interpretation due to gaps in sampling; however, the MHI were different from the Line Islands and Tokelau Ridge. The deeper depth bins (1000-3000 m) had the least number of different regions. However, the statistical power available for samples from 2000-3000 m is hampered by no samples available in American Samoa and the MHI. Despite this limitation, Johnston Atoll was different from the NWHI in the 2000-3000 m depth bin but not in the 1000-2000 m.

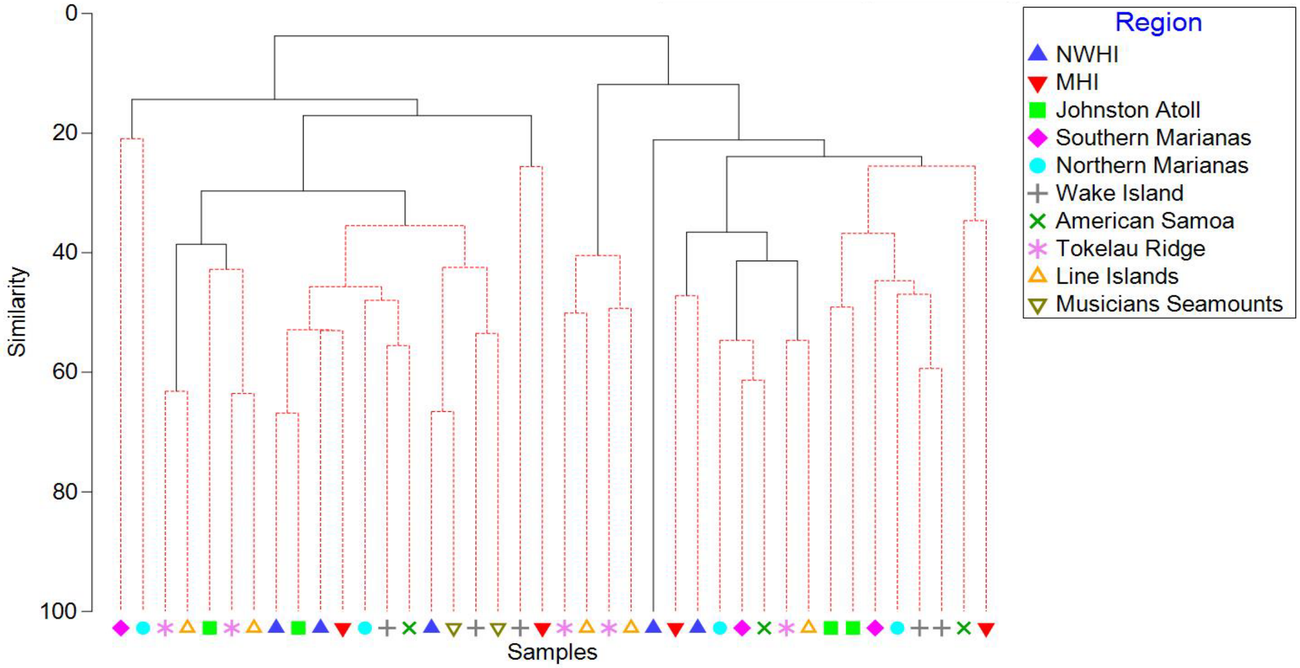
3.3 Community Structure

There were 24 communities and four outliers identified (MHI: P4-231: 250-500, LI: P5-653: 250-500, MHI: P5-772: 250-500, LI: NA110-H1762: 250-500) which were not due to a small number of fishes or low number of genera represented in each sample (range 127 to 715 fishes/ outlier sample and a minimum of 10 genera, SIMPROF $P<0.05$). The communities generally consisted of upper bathyal, intermediate, and deep samples clustered together with a few exceptions. When combining factors of region and depth bin and water mass and depth bin, a clearer picture of community structure resulted (Figure 5). Structuring by depth was more apparent than structure by region or water mass. In the cluster analyses combining average region and depth bin (Figure 6 A & B), there were two main assemblages structured by depth at ~17% similarity which further branched into 10 assemblages (one outlier) ranging in similarity between 17% and 63%. The two main communities separated out 250-750 m samples from 1000 - 3000 m with some intermixing of the 750 - 1000 m depth bin. No overall clear communities seemed to occur by region, however, within a depth strata, samples from the Tokelau Ridge, Line Islands and MHI frequently clustered together. In the cluster analysis combining average water mass and depth bin (Figure 6 C&D), there were also two main assemblages clustered by depth bin at ~15%. However, there were more outliers compared to the cluster analyses looking at average region and depth bin. The groups further divided into five assemblages (four outliers). The depth structuring of the two major communities followed the depth pattern of region and depth. When coding by water mass, communities matched mostly that of the depth structuring with water masses occurring in the upper and intermediate boundary layer on the right (i.e., WNPCW, AAIW) and those occurring in the deep layer on the left (i.e., CDW, NPDW).

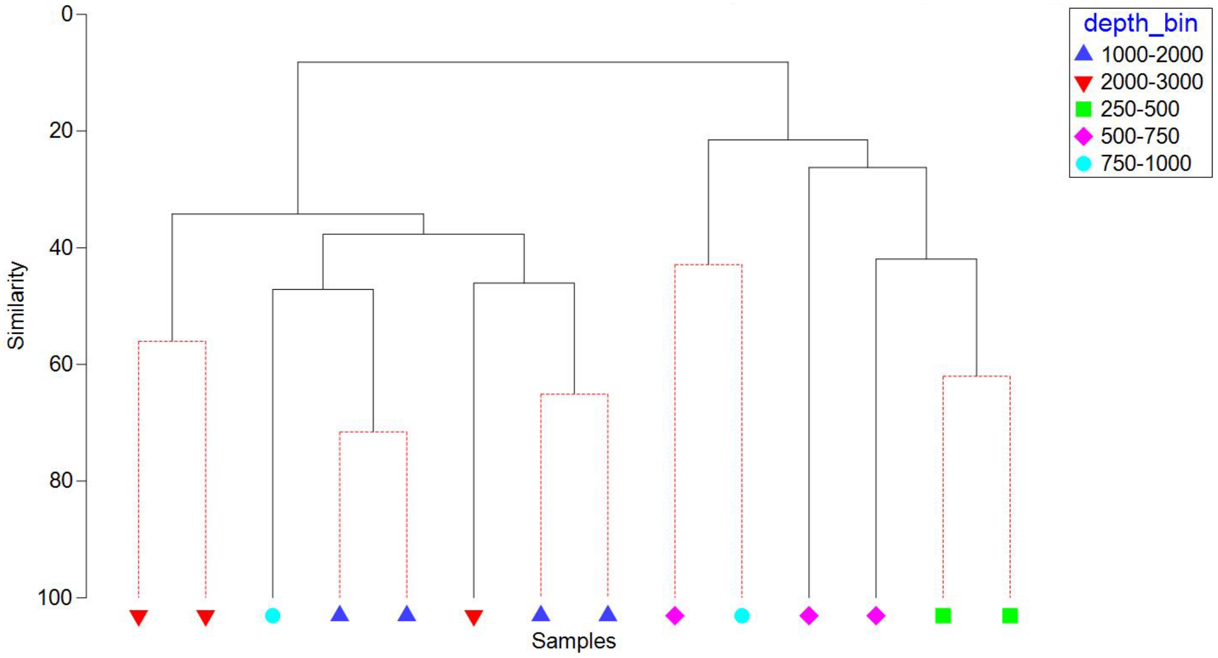
A)


0
20
40
60
80
100
Similarity
Samples
depth_bin
1000-2000
2000-3000
250-500
500-750
750-1000

B)


0
20
40
60
80
100
Similarity
Samples
Region
NWHI
MHI
Johnston Atoll
Southern Marianas
Northern Marianas
Wake Island
American Samoa
Tokelau Ridge
Line Islands
Musicians Seamounts

C)



D)

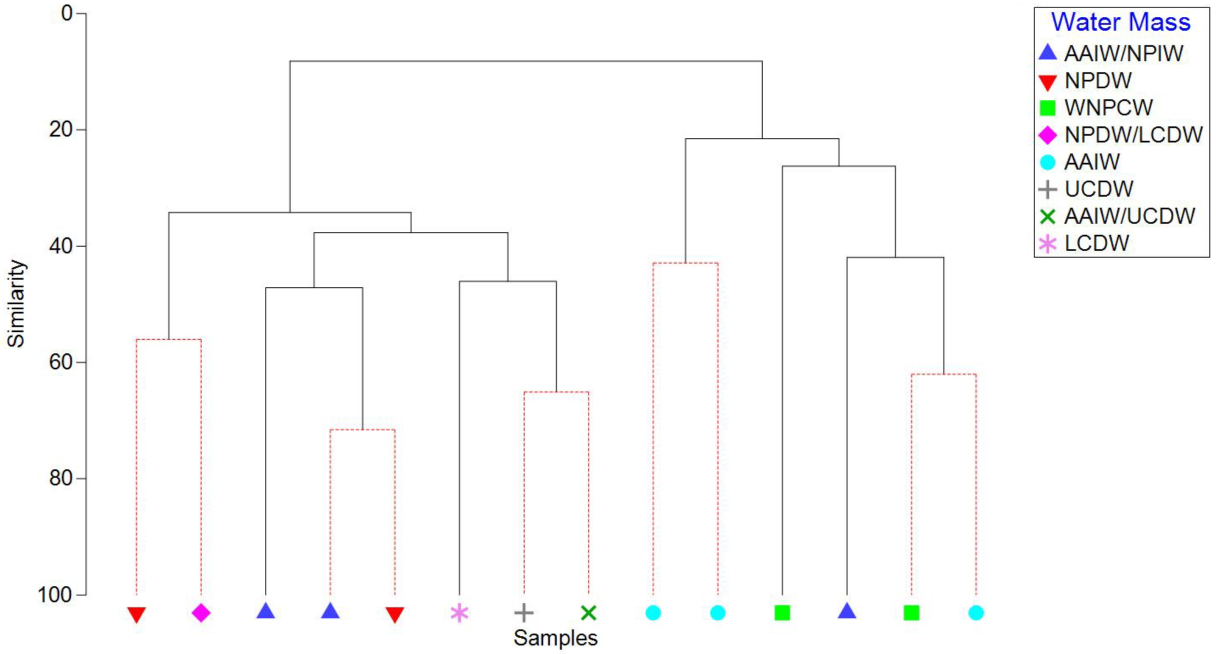


Figure 6) Dendrogram produced by hierarchical clustering and group average linking of Bray-Curtis similarities. Black lines denote significantly different clusters (SIMPROF, $p<0.05$). A and B denote

average of region and depth bin coded by A) depth bin and B) region. C and D represent the average of water mass and depth bin coded by C) depth bin and D) water mass. Symbols correspond to similar groups determined by the SIMPROF analyses. Based on Bray Curtis similarities of square root transformed and wisconsin standardized data.

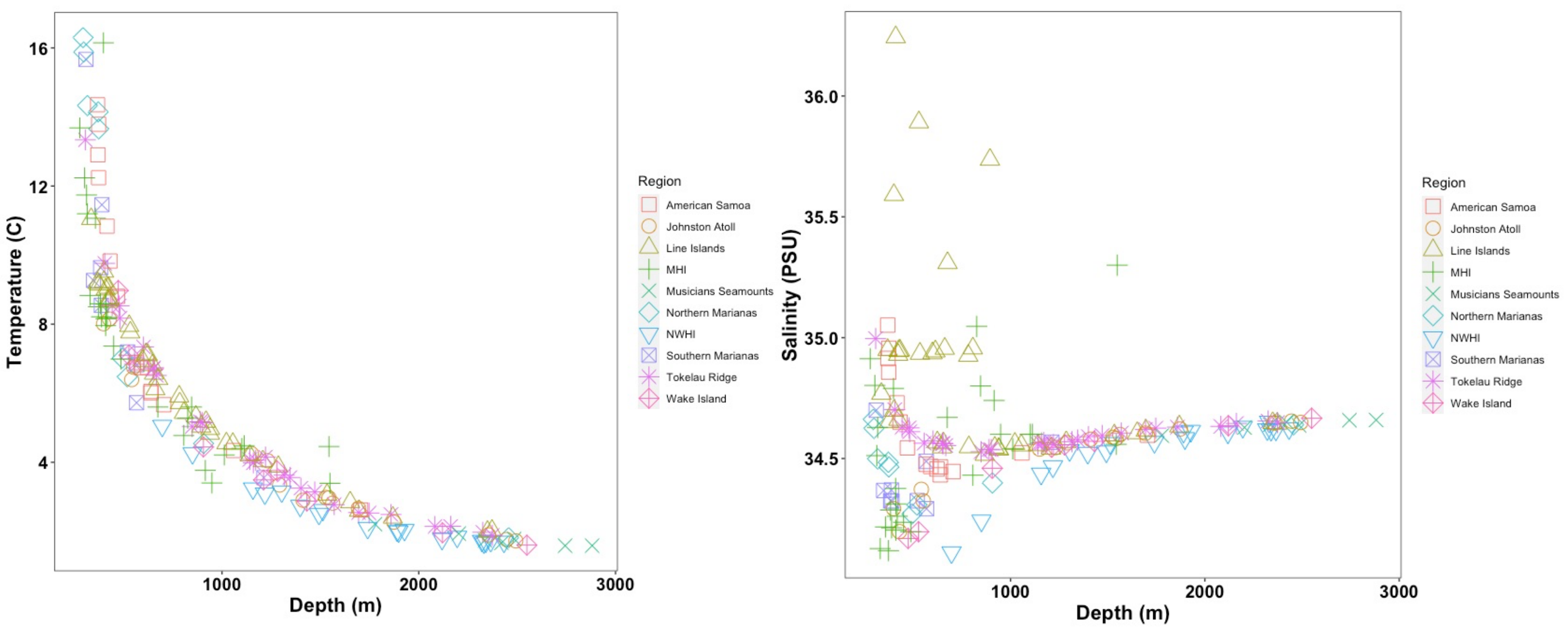
In general, there were more upper bathyal communities compared to deep ones and a wider range in depths of assemblages in the upper bathyal regions compared to the deep (Table 5). Group average similarities ranged from 16% to 81%. The group that occurred in the most regions was group d (750-1000 m) which included samples from Johnston Atoll, Line Islands, Northern Marianas, Northwest Hawaiian Islands and Tokelau Ridge (21% similarity). The group with the highest similarity was group n (250-750 m) at 81% similarity which just included the Main Hawaiian Islands. Group s (250-500 m) at 16% just included American Samoa and had the least similar communities of all the groups. The large range in group average similarity may indicate limitations in the sample effort and or low spatial resolution. There were four assemblages that encompassed wide depth ranges between 250 and 1000 m and 13 assemblages that occurred between 250 and 750 m. There were only three assemblages that occurred strictly between 1000 and 3000 m. There were six assemblages in the upper bathyal and intermediate depths that occurred in only one region. These included the 250-500 m Line Island assemblage which were dominated by *Chrionema* (14.7% contribution), 250-500 m MHI assemblage (*Owstonia*, 31% contribution), 250-750 m MHI assemblage (*Chascanopsetta*, 22% contribution), 250-500 m Northern Marianas assemblage (*Plectranthias*, 23% contribution), 250-500 m American Samoa assemblage (*Etelis*, 70% contribution), and 500-750 m American Samoa assemblage (*Phenacoscorpius*, 90% contribution).

Table 5) List of genera that contribute most (70%; SIMPER) to similarity within the 24 fish communities identified by hierarchical analysis.

Depth	Group	Sim%	Region	Genera	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
250-500	o	39.29	LI, MHI, NWHI	*Grammicolepis*	0.15	15.16	2.83	38.57	38.57
				Hollardia	0.12	7.65	1.07	19.47	58.04
				Randallichthys	0.13	7.56	1.15	19.24	77.29
250-500	r	62.71	LI	*Chrionema*	0.11	9.21	5.45	14.68	14.68
				Hoplostethus	0.09	8.28	5.1	13.2	27.88
				Grammicolepis	0.09	7.81	5.43	12.45	40.33
				Setarches	0.1	7.57	2.74	12.07	52.4
				Synagrops	0.09	6.53	2.02	10.41	62.81
				Coelorinchus	0.06	5.66	18.21	9.02	71.83
250-500	u	36.15	LI, SM	*Synchiropus*	0.13	10.39	SD=0!	28.75	28.75
				Myroconger	0.08	7.35	SD=0!	20.33	49.08
				Plectranthias	0.08	4.37	SD=0!	12.08	61.16
				Hoplostethus	0.04	4.24	SD=0!	11.74	72.89
250-500	p	39.5	MHI	*Owstonia*	0.13	12.4	7.21	31.38	31.38
				Hollardia	0.08	8.29	12.5	20.97	52.35
				Lophiodes	0.07	5.44	3.53	13.78	66.13
				Epigonus	0.06	4.41	1.16	11.17	77.3
250-750	n	81.13	MHI	*Chascanopsetta*	0.17	18.05	SD=0!	22.25	22.25
				Malacocephalus	0.16	17.42	SD=0!	21.47	43.73
				Hymenocephalus	0.15	15.09	SD=0!	18.6	62.32
				Satyrichthys	0.16	14.74	SD=0!	18.17	80.49
250-500	w	47.4	NM, SM	*Hoplostethus*	0.14	14.77	6.27	31.16	31.16
				Plectranthias	0.14	13.66	2.56	28.81	59.97
				Antigonia	0.06	4.74	2.32	10	69.98
				Pontinus	0.05	3.9	1.08	8.22	78.2
250-500	t	37.02	NM	*Plectranthias*	0.08	8.52	SD=0!	23.02	23.02
				Pristilepis	0.11	7.38	SD=0!	19.94	42.96
				Gymnothorax	0.07	7.25	SD=0!	19.58	62.54
				Odontanthias	0.06	4.76	SD=0!	12.85	75.39
				Synaphobranchus	0.05	2.36	0.48	7.61	76.44
250-500	x	28.17	AS, SM	*Chlorophthalmus*	0.07	5.36	1.56	19.03	19.03
				Plectranthias	0.11	5.02	1.82	17.81	36.84
				Odontanthias	0.06	4.4	2.13	15.64	52.47
				Etelis	0.06	2.87	0.58	10.18	62.65
				Parascombrops	0.06	2.27	0.58	8.04	70.69
250-500	s	16.14	AS	*Etelis*	0.15	11.24	SD=0!	69.63	69.63
				Epigonus	0.04	2.57	SD=0!	15.93	85.56
250-750	k	23.31	AS, JA, MHI, NM, NWHI, SM, WI	*Beryx*	0.15	9.48	0.69	40.67	40.67
				Chlorophthalmus	0.14	7.7	0.57	33.05	73.72
250-500	y	24.77	AS, MHI, NM, TR	*Pontinus*	0.07	5.99	3.32	24.18	24.18
				Chrionema	0.06	3.61	2.16	14.58	38.76
				Symphysanodon	0.06	3.11	0.83	12.56	51.31
				Antigonia	0.06	3.02	0.78	12.2	63.51
				Etelis	0.06	2.37	0.56	9.58	73.1
250-750	j	18.55	AS, JA, MHI, TR	*Chlorophthalmus*	0.07	4.95	1.35	26.68	26.68
				Cyttomimus	0.06	3.88	0.91	20.92	47.6
				Hymenocephalus	0.08	3.17	0.54	17.1	64.7
				Plesiobatis	0.11	1.84	0.22	9.94	74.64
250-750	l	23.01	LI, MHI, NWHI, TR	*Chaunax*	0.09	5.33	0.8	23.17	23.17
				Squalus	0.08	4.61	0.62	20.05	43.22
				Hollardia	0.05	3.43	0.89	14.89	58.11
				Polymixia	0.04	2.17	0.83	9.42	67.53
				Laemonema	0.03	1	0.42	4.34	71.87
250-1000	ab	24.55	AS, LI, MHI	*Bathycongrus*	0.21	14.57	0.8	59.35	59.35
				Synagrops	0.2	7.93	0.41	32.32	91.67
250-1000	aa	21.87	LI, SM, TR, WI	*Coelorinchus*	0.12	7.13	0.9	32.61	32.61
				Hoplostethus	0.08	4.42	0.76	20.21	52.82
				Neocyttus	0.05	3.4	1.09	15.55	68.37
				Bathycongrus	0.04	1.04	0.35	4.74	73.11
500-750	z	26.51	AS	*Phenacoscorpius*	0.25	23.99	SD=0!	90.48	90.48
500-750	e	30.96	MHI, NWHI	*Ectreposebastes*	0.25	15.46	0.86	49.93	49.93
				Neoscopelus	0.12	7.99	0.9	25.79	75.72
500-1000		31.98	MHI, NWHI	*Nettastoma*	0.16	18.23	15.1	57.01	57.01
				Synaphobranchus	0.11	7.29	0.58	22.8	79.81
750-2000	i	45.7	JA, MHI, NWHI, TR	*Synaphobranchus*	0.39	38.48	1.78	84.21	84.21
750-2000	d	20.66	JA, LI, NM, NWHI, TR	*Diplacanthopoma*	0.09	4.37	0.63	21.13	21.13
				Coryphaenoides	0.07	4.24	0.91	20.53	41.66
				Nezumia	0.04	2.27	0.56	10.99	52.66
				Bassozetus	0.04	1.6	0.42	7.75	60.4
				Halosaurus	0.04	0.99	0.33	4.77	65.17
				Lepidion	0.04	0.93	0.27	4.5	69.68
				Spectrunculus	0.03	0.71	0.23	3.42	73.09
750-2000	h	34.5	MHI, NWHI	*Aldrovandia*	0.14	11.06	1.59	32.07	32.07
				Synaphobranchus	0.07	5.75	1.08	16.65	48.72
				Nettastoma	0.12	5.57	0.74	16.15	64.87
				Apristurus	0.09	4.87	0.64	14.1	78.98
1000-2000	g	30.26	JA, NWHI, TR, WI	*Synaphobranchus*	0.12	10.07	3.17	33.28	33.28
				Venefica	0.19	9.96	0.62	32.92	66.2
				Monomitopus	0.11	3.47	0.32	11.47	77.67
1000-3000	b	24.83	JA, LI, MS, NM, TR	*Bassozetus*	0.23	15.78	1.56	63.55	63.55
				Acanthonus	0.09	3.15	0.34	12.68	76.23
1000-3000	c	30.96	AS, JA, MS, NWHI, SM, WI	*Kumba*	0.22	17.6	1.24	56.84	56.84
				Ilyophis	0.09	3.71	0.42	11.99	68.83

3.4 Relationship between community composition and environmental variables

Environmental variables changed with depth and patterns varied between regions (Figure 7). Temperature shows a steep decline with depth in all regions as expected. Salinity values are relatively constant for most of the regions (34.1-36.2 PSU). However, the Line Islands was the only region that had salinity slightly above 35.5 PSU. DO concentrations ranged from 0.57 to 6.45 mg/L, with the lowest DO concentration between 250-500 m in the Line Islands (*EV Nautilus* Dive, NA110- H1763). POC fluxes at the seafloor ranged from 1.19 to 9.2 mg C/m^2/day and decrease with depth. The Line Islands had the highest POC flux values for all depth bins (5D).


A)

B)

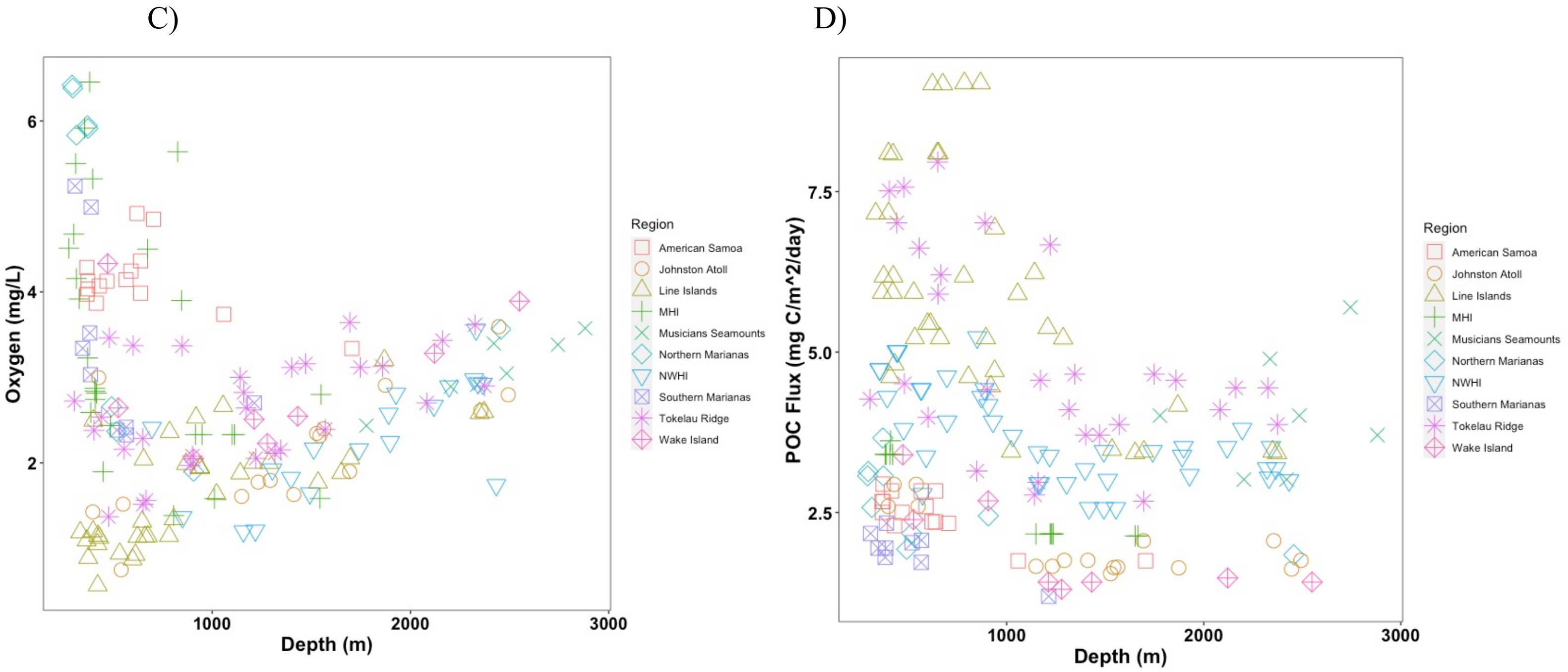


Figure 7) Environmental variables by region for each sample by depth (m). A) Average temperature (°C), B) Average salinity, C) Average DO (mg/L) by mean depth, D) average seafloor POC flux values for samples (mg C/m^2/day).

There were some significant correlations between community composition at the genus level and the environmental variables of depth, water mass, DO, POC flux, and salinity which together explained a total of 24% of the variation in community composition (Figure 8, constrained proportion = 0.24). This first axis, CAP1, explained ~10% of the constrained variation (proportion explained = 0.09) and was strongly correlated with depth, medium correlated with POC flux, and weakly correlated with concentrations of dissolved oxygen and salinity. POC flux varies in the opposite direction along this axis which was expected as POC flux generally declines with depth. The second axis, CAP2, explained ~4% of the constrained variation (proportion explained = 0.03) and has dissolved oxygen and POC flux occurring in opposite directions and little contribution from depth and salinity. The Line Islands and Tokelau Ridge had the highest POC flux values and lowest concentrations of dissolved oxygen and therefore may be driving this pattern on the CAP 2 axis. There was also a fundamental shift in the structure of the communities that were associated with water mass which is mainly a function of depth and salinity. Generally, deeper water masses (NPIW, NPDW, and CDW) are positioned on the left in accordance with deeper depths and shallower water masses on the right (AAIW and WNPCW). However, water masses in the upper layer (WNPCW) were mainly associated with high concentrations of dissolved oxygen and the AAIW with high POC flux values. Once past the intermediate depths, ~1000 m, environmental variation decreased as expected.

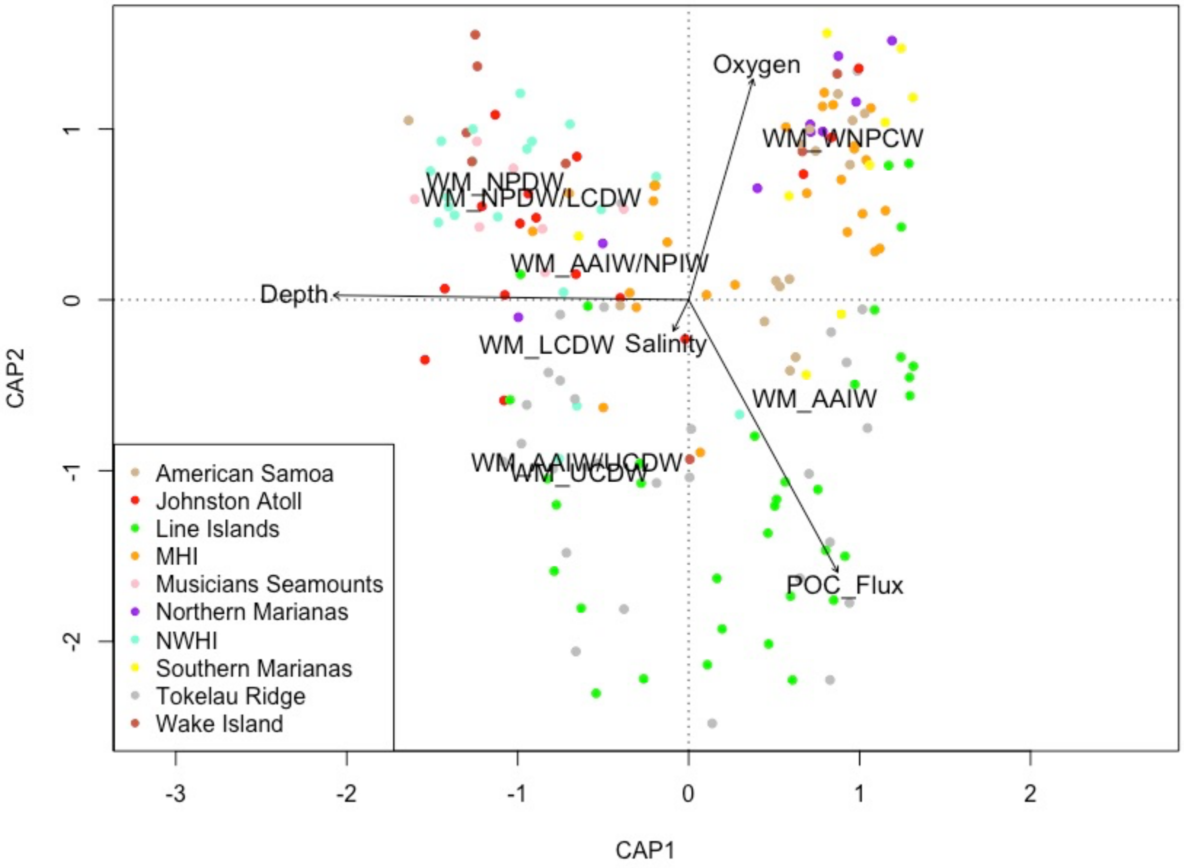


Figure 8) Canonical analysis of principle coordinates (CAP) based on Bray Curtis similarities calculated on wisconsin transformed data (n = 212 samples). CAP1 explains 10% of the total variation while CAP2 explains 4%. Depth is the predictor most strongly correlated with CAP 1 which is the axis that explains

the most variation in community composition and varies from left (deep depths) to right (shallow depths) across all regions. The position of water masses (abbreviated by WM) are indicated by the text. The total constrained variation explained by all axes is 24%. CAP statistics generated by capscale() in R. Colors=regions.

3.5. Total Abundance

Total fish abundances generally decreased with depth across the regions. However, the MHI and Tokelau Ridge had the highest abundances between 750 and 1000 m, which were driven by the high abundance of Epigonidae and Setarchidae, respectively. Total abundance was greatest in the Line Islands between 250-500 m (6.05 fish/m) followed by the Northern Marianas between 250-500 m (4.42 fish/m). Samples with the least average abundances (<0.01) occur mostly in the intermediate to deep depths, however the MHI and Tokelau Ridge had very high abundances between 750-1000 m (Figure 9). Sample sizes for each of the regions and depths are available in Table 1. Changes in fish abundance with depth were significant in all regions (*P*= 0.001) except for the Musicians Seamounts (*P* = 0.9), with 75.1%. of the deviance explained in the model (Figure 10).

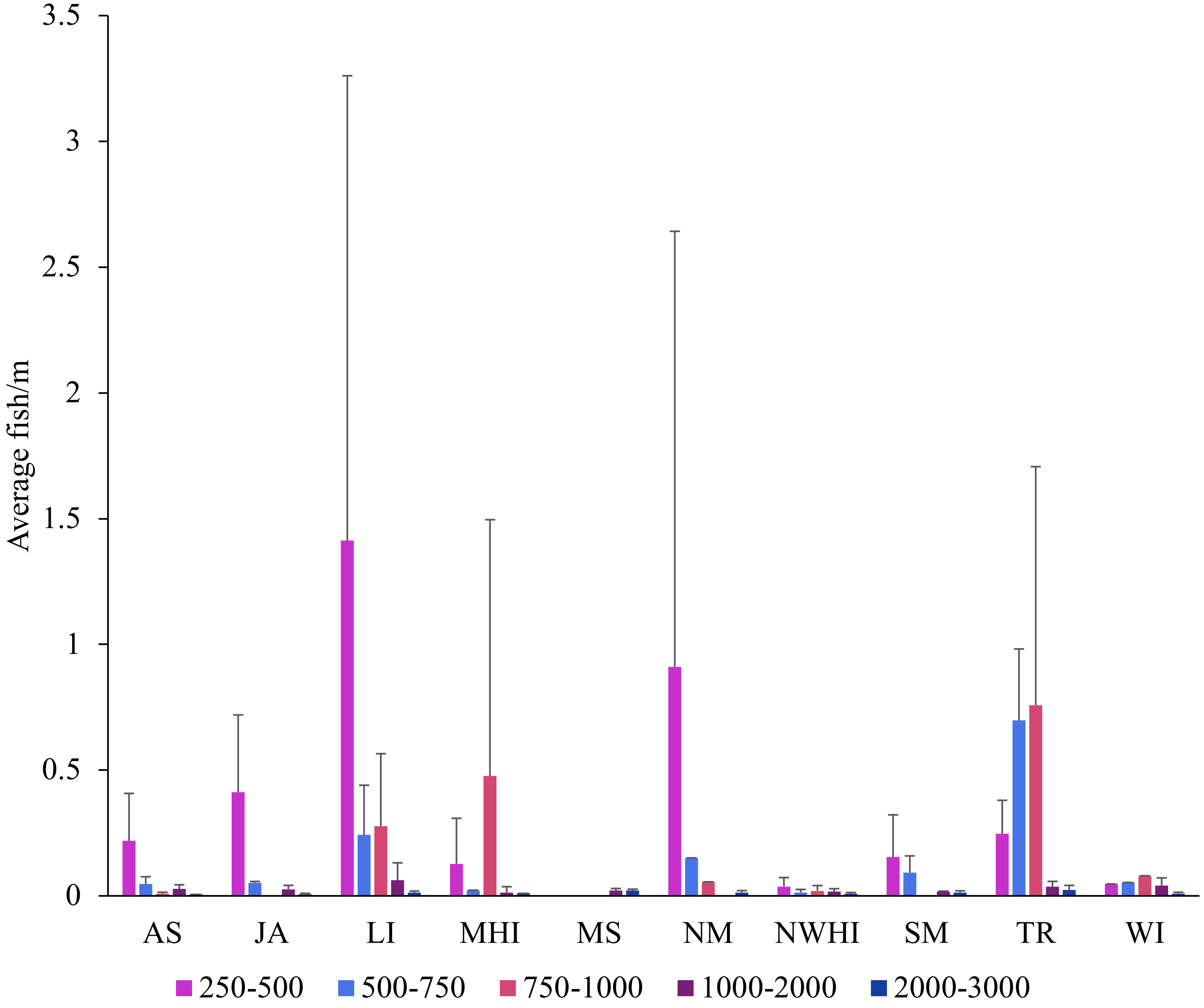


Figure 9) Average abundance (fish/m) throughout sample regions. American Samoa (AS), Line Islands (LI), Johnston Atoll (JA), Main Hawaiian Islands (MHI), Musicians Seamounts (MS), Northern Marianas (NM), Northwest Hawaiian Islands (NWHI), Southern Marianas (SM), Wake Islands (WI), and Tokelau Ridge (TR). Sample sizes are listed in Table 1.

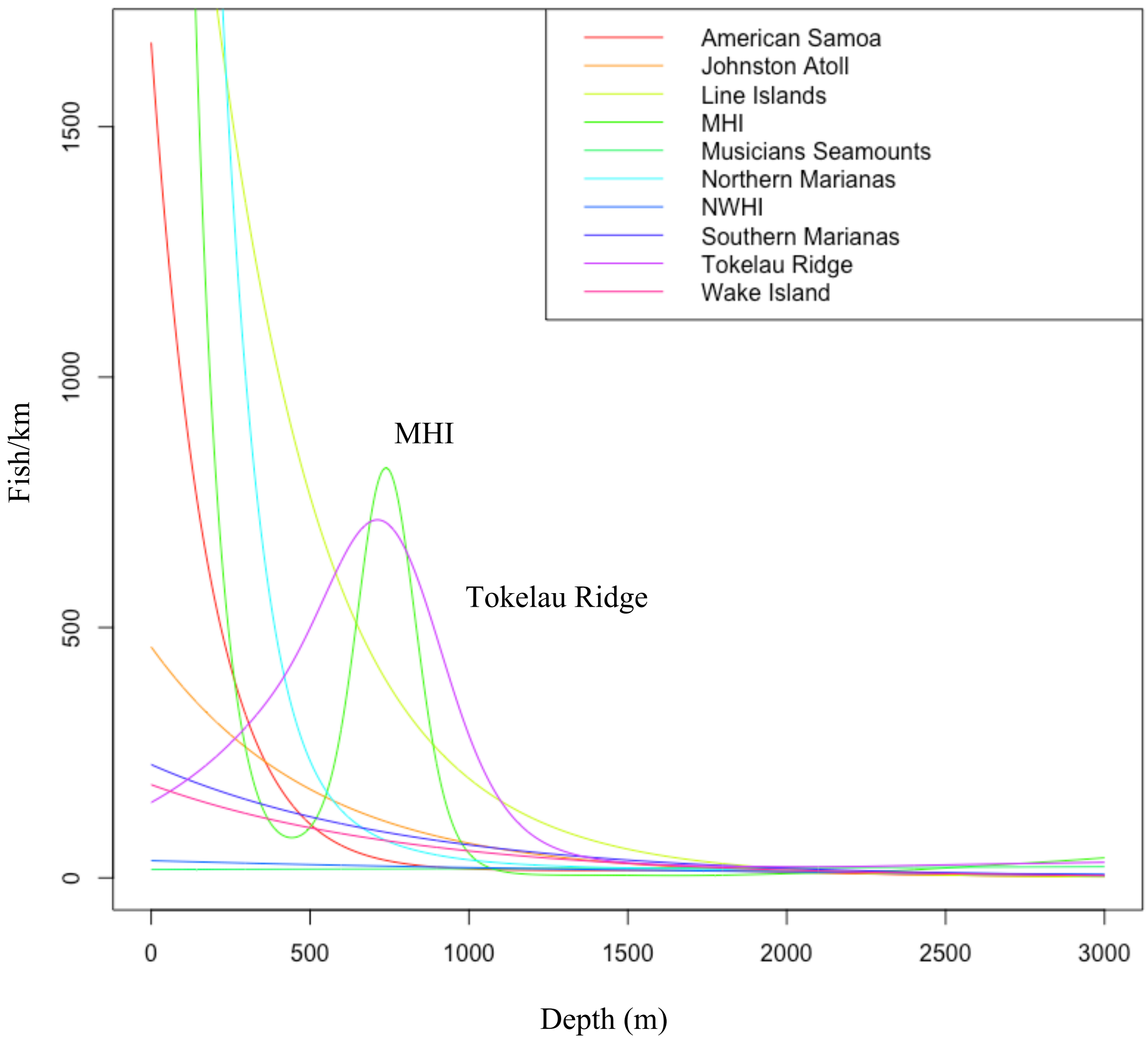


Figure 10) Smoothers in Generalized Additive Model (GAM) for total abundance (fish/km) by depth plotted by all regions. All regions significant (*P*= 0.001) except for the Musicians Seamounts (*P* =0.9)

3.4 Relationship between total abundance and environmental variables

All environmental variables of depth, concentrations of DO, POC flux, and salinity had a significant relationship with fish abundance (fish/km) (*P*=0.001) and explained a little over 50% of the variation in total abundance (deviance explained =73.6%, generalized cross-validation score= 900) (Figure 11A-D). Total abundance was highest at depths of ~250 and ~725 m but then declined at ~1500 m where it remained relatively stable (*P*=0.001). Concentrations of DO were highly significant related to abundance (*P*=0.001) where total abundance appeared highest between DO concentrations of 1.5 and 3.5 mg/L. Abundance increased with salinity; however, confidence intervals at ~34.5 and beyond are very large so this trend could be driven by a few data points with high salinity and high total abundance. Fish abundance values were relatively stable up to ~4 mg C/m^2/day then increased with increasing POC flux. In summary, fish abundances were predicted to be highest at the upper bathyal depths (250-500 m), with concentrations of dissolved oxygen between 1.5-3.5 mg/L, salinity values ~ 34.5, and POC flux values > 4 mg C/m^2/day.

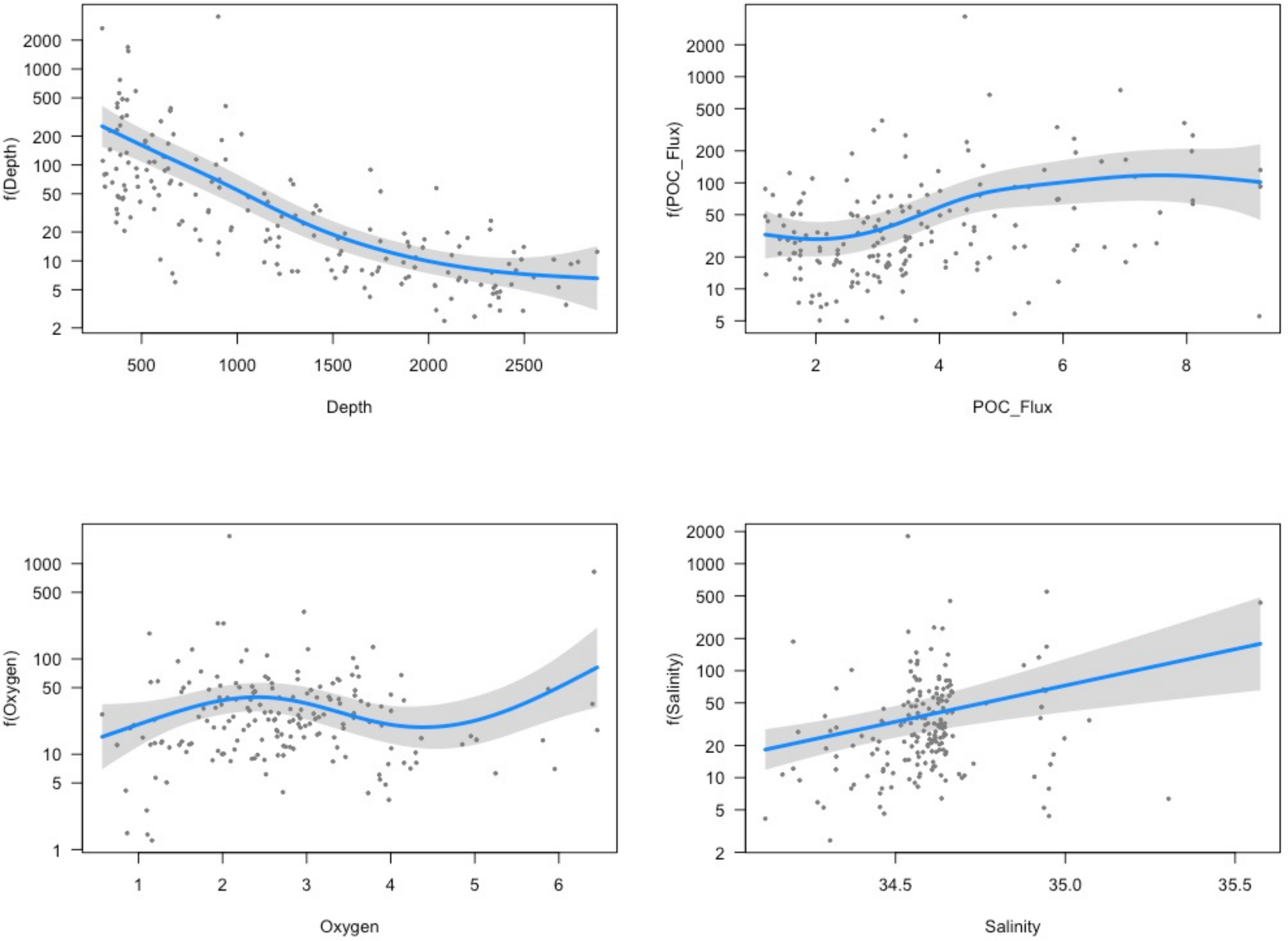


Figure 11) Generalized Additive Models (GAM) for total abundance (fish/km) in relation to A) depth (m), B) POC flux (mg C/m^2/day), C) DO (mg/l), and D) Salinity (PSU) to the seafloor. Back transformed GAM functions with residuals. The spread of the data (y axis maxima) changed between plots because the plots show partial residuals and unexplained variation is added on top of the smoother. The shaded grey bands indicate confidence intervals on the standard deviation scale.

3.6 Diversity

Sampling adequacy was evaluated by fitting accumulation curves. There were not enough samples to generate curves based on region by depth bin, therefore, samples were parsed separately as region and depth. None of the regions and depth bins reached accumulation asymptotes and therefore were not fully sampled (Figure 12). The asymptote of the curves represents the estimated number of genera that would theoretically be found if a large number of samples were collected. However, there are some curves that appear to be closer to an asymptote (sampling adequacy) than others. This is most clear in samples parsed by depth bin. For example, the 250 - 500 m bin appears to be accumulating genera at a faster rate than 1000 - 2000 m whereas the 2000 - 3000 m bin may be closest to an asymptote than the other depth bins (Figure 12B).

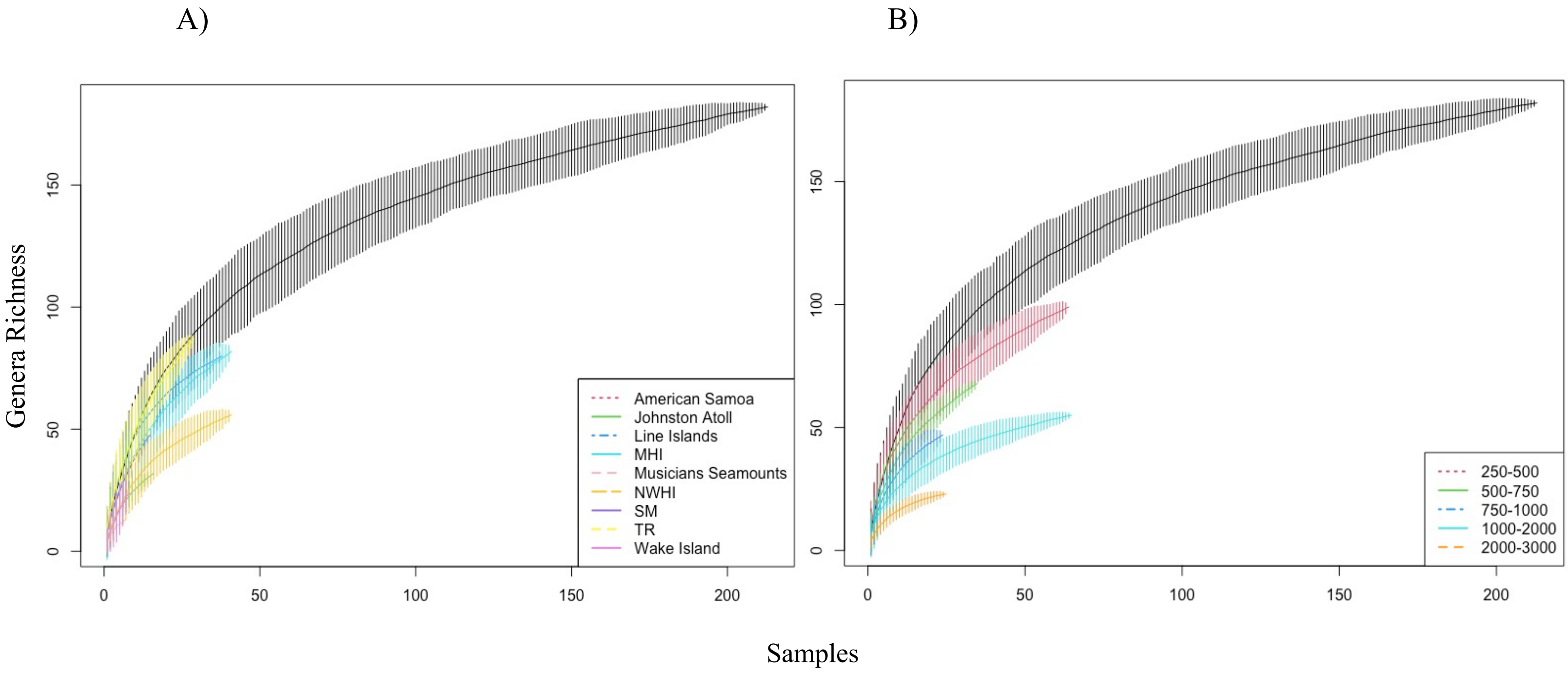


Figure 12) Genera accumulation curves parsed by A) region and B) depth bin for estimating sampling effectiveness. The top curves represent all regions and depths pooled, respectively. Vertical bars represent confidence intervals based on standard deviation.

Rarefaction curves (Hill, q=0) were used to compare samples at the same sampling intensity (the same number of individuals) to determine whether generic richness differed between regions and depths. Because samples were combined by region and depth bin, respectively, rarefaction represents pooled samples and does not capture between-sample heterogeneity (beta diversity). Extrapolation was included in the curves for reference but not used in comparisons. Rarefaction curves fundamentally are not designed for extrapolation to estimate total richness but were helpful to reference in later diversity results. There were four regions with enough individuals (n = 2500) to compare at the same sampling intensity (the same number of individuals). These regions included the Northern Marianas, Line Islands, MHI and Tokelau Ridge (Figure 13A). Out of these, Tokelau Ridge and MHI had the highest estimated generic richness as these curves are well above the Line Islands and Northern Marianas curves. Results for samples parsed by depth bin indicated that deeper depths were far less sampled than shallower locations (Figure 13B). The only depth bins with enough individuals (n = 2500) to compare at the same sampling intensity were 250-500 m and 500-750 m, which were closely aligned.

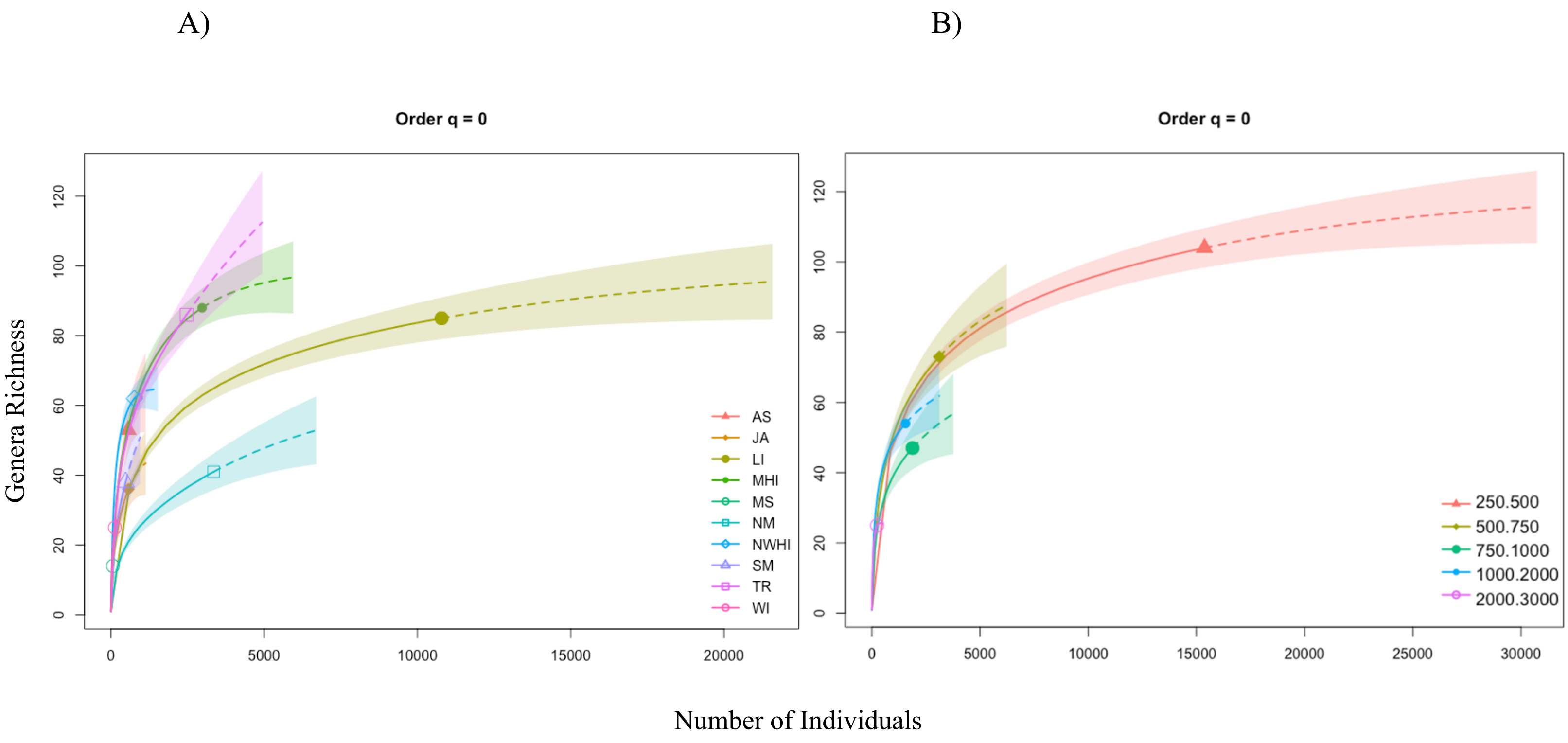


Figure 13) Rarefaction curves, by number of individuals, of genera richness (q=0, with 95% CI) A) across all regions and B) across all depth bins between 250-3000 m. Extrapolations are indicated by dashed lines.

Since the rarefaction curves were based on pooled individuals, all beta diversity (differences in species structure between samples) was lost. Therefore Chao 1 and Chao 2 were used to estimate generic richness based on samples rather than pooled individuals. Chao1 and 2 richness estimators predict higher richness for all regions and depths bins than the rarefaction extrapolation. Even for curves that are near asymptotes (LI and 250-500), Chao 1 and 2 predict higher richness than rarefaction, reflecting the capture of beta diversity. In all Chao 1 and 2 cases, estimates exceed the number of genera collected indicating that there are still genera that remain uncollected. For example, Chao 1 and Chao 2 both estimate over 120 genera in the

Northern Marianas, whereas only ~40 genera were collected, indicating that many genera are yet to be sampled in this region (Figure 14 A & B). Similarly, Chao 1 and Chao 2 both estimate ~140 genera in 250-500 m, whereas only ~100 genera were collected, indicating that this depth bin is estimated to have the highest regional richness with many genera yet to be collected (Figure 14 C & D). There were six regions with enough samples (n = 10) to compare estimated generic richness at the same sampling intensity. These regions included Johnston Atoll, NWHI, American Samoa, MHI, Line Islands, and Northern Marianas (Figure 13A). Out of these, the Northern Marianas, followed by the Line Islands and MHI had the highest estimated generic richness (Figure 14B). However, Chao 2 estimated the MHI to have the second highest generic richness. Results of Chao1 and 2 by depth bin indicated that there were enough samples to compare all depth bins at n = 10. Estimated generic richness generally was highest in the shallower depth bins and decreased with depth. However, estimates of richness in the 500-750 m and 750-1000 m depth bins were more closely aligned in Chao 1 compared to Chao 2 (Figure 14 C & D).

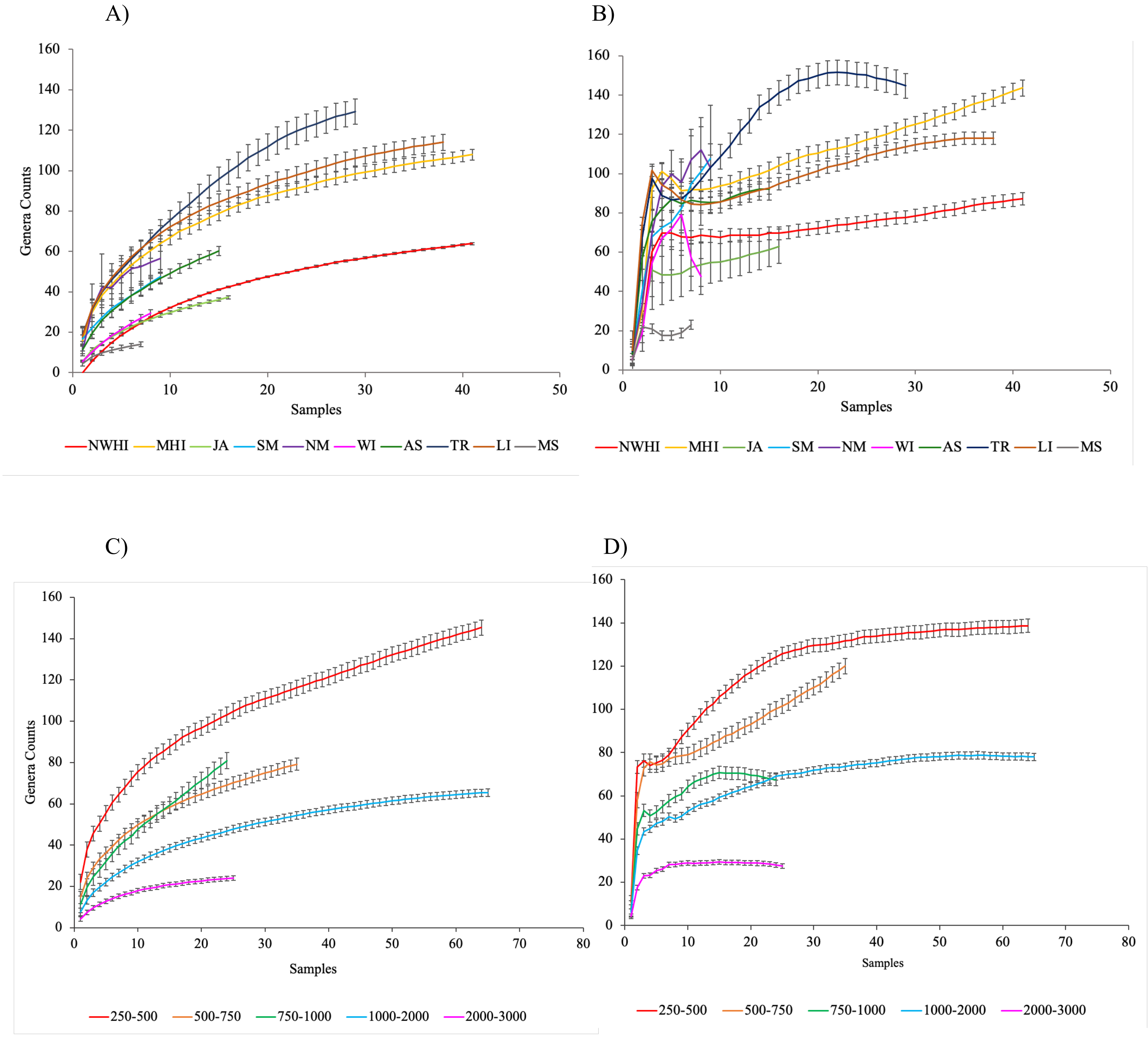
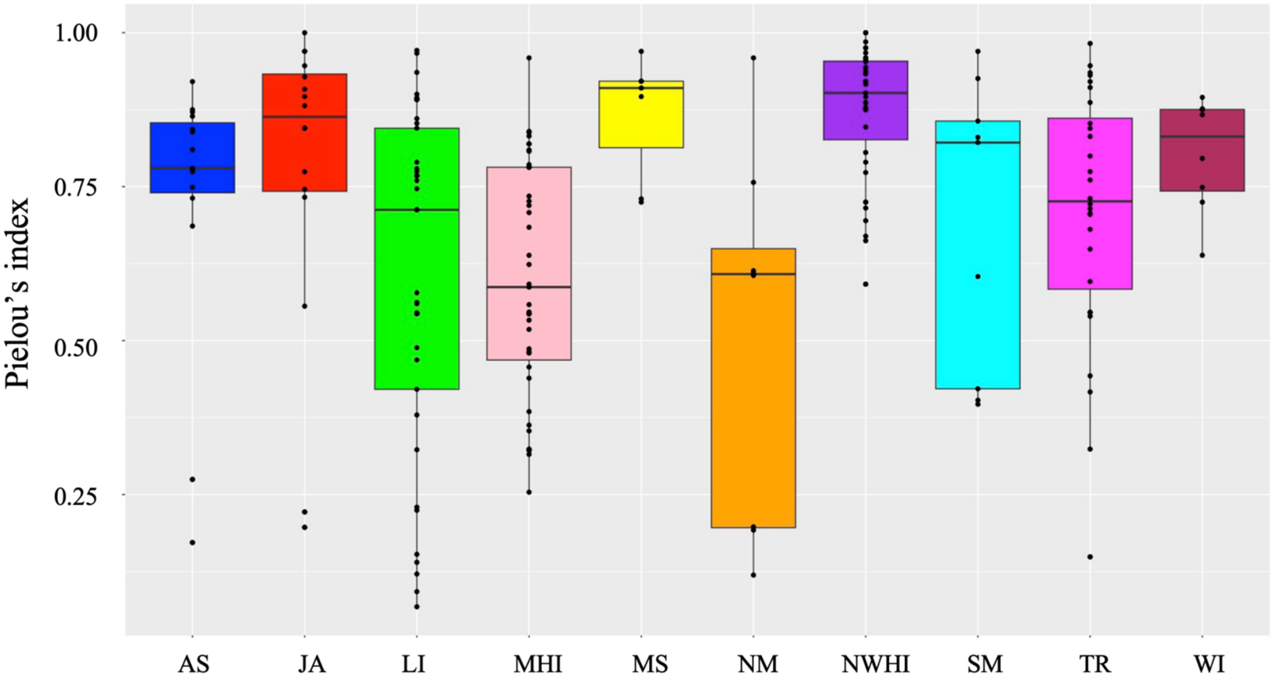


Figure 14) Genera richness estimators: Chao 1, Chao 2 plot by A) region: Chao1, B) region: Chao2, C) depth bin: Chao1, D) depth bin: Chao2 for estimating sampling effectiveness. 95% confidence intervals are displayed on all curves.

The Line Islands, MHI, and Northern Marianas, and Tokelau Ridge had the lowest generic evenness (Pielou), with median index values under 0.75. The regions with the highest evenness were the Musicians Seamounts and the NWHI (Figure 15A). When separating the data by depth bin, it becomes apparent that overall, evenness increased with depth. Although 750- 1000 m has the lowest evenness value, 250-750 m are not far off, and the 2000-3000 m depth bin has the highest evenness value (Figure 15B).

A)



B)

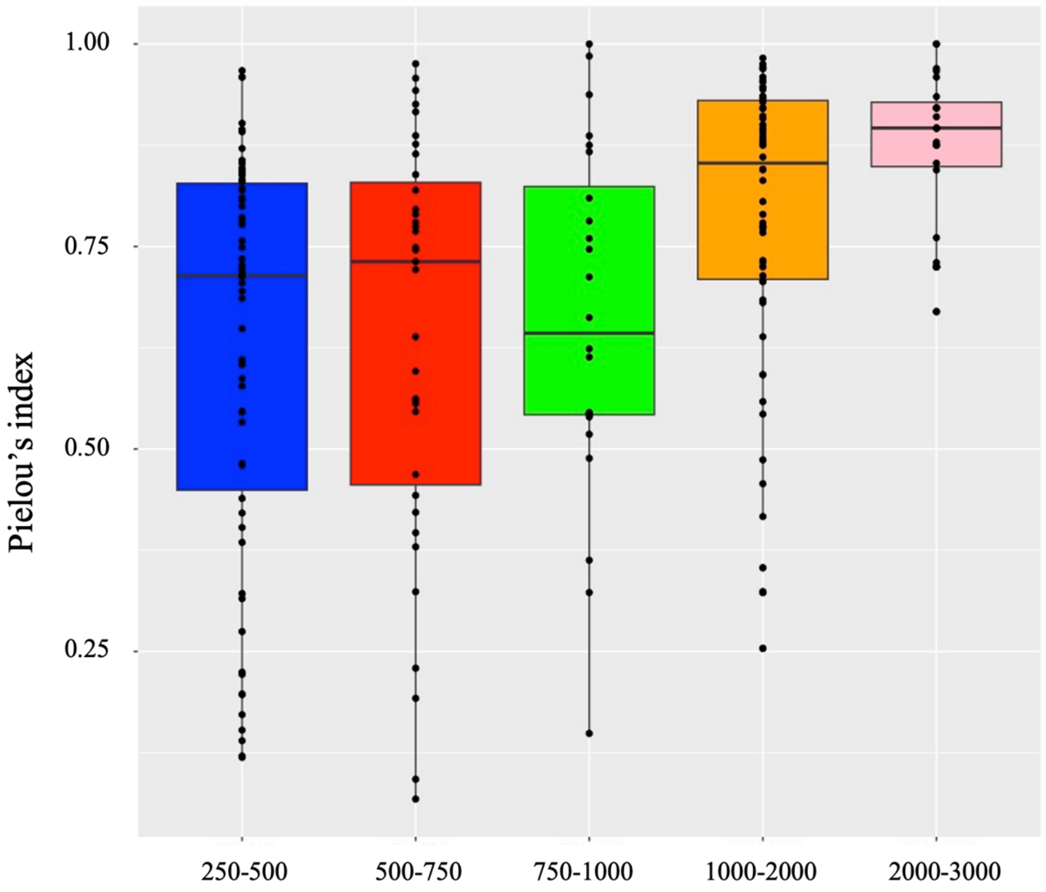


Figure 15) Boxplot of evenness values (Pielou's J) for the genera observed parsed by A) regions and B) depth bins. Five summary statistics are displayed (median, two hinges, two whiskers, and all outlying points).

4) Discussion

Estimates of community composition, abundance, and diversity can be influenced by the tool used to sample and the level of sampling effort (Paller et al., 1995). The observation of demersal fish communities by ROVs and submersibles has allowed for an improved estimation of community variability in the deep sea (Mercado et al., 2019). Modern-day deep-sea exploration has received growing efforts over the last decade (Tyler et al., 2016) and has demonstrated that the deep-sea possesses enormous biodiversity, often on par with the biodiversity observed on coral reefs and in tropical rainforests (McClain and Schlacher, 2015). The video collected during these expeditions is extremely rare and valuable and although future collections are needed to confirm some identifications, the imagery collected has provided information useful for addressing relevant ecological questions (Quattrini et al., 2017). This data enables us to evaluate benthic fish communities in the central Pacific, which is a crucial first step and further, adds to our current understanding of the variability of deep-sea fishes across multiple regions in the central Pacific.

4.1) Patterns in community structure

Comparisons of demersal fishes between regions in the central Pacific indicate that depth (and its correlates, temperature, and pressure) may play the most influential role in structuring communities. This was expected as depth zonation of demersal fishes is a common phenomenon in the deep-sea globally (Carney, 2005). The reduction of light, temperature, dissolved oxygen, and food supply along with increasing pressure has been found to strongly influence the spatial distribution of species along with their functions and morphologies (Gallo and Levin, 2016). Despite some limited sampling at intermediate depths, communities became more similar with increasing depth and there was more group structuring in the shallow upper bathyal depths compared to deeper depths. Deep-sea fishes are also known to have wider distributions (resulting in increased similarities in assemblages) than shallower fishes due to the increase in homogeneity and stabilization of environmental variables (Menezes et al., 2006, Clark et al., 2010). Depth zonation of demersal fishes is a common phenomenon in the deep sea and has been observed in other studies in the Pacific Ocean within the Hawaiian archipelago and northern Gulf of Mexico (Yeh and Drazen, 2009, De Leo et al., 2012, Powell and Haedrich, 2003).

Regional separation was also apparent between communities suggesting that there are significant regional differences in the composition of demersal fauna across archipelagos in the central Pacific. The MHI and NWHI had an upper bathyal community (250-750 m) that was different from all other regions (Figure 5A). Shallow reef studies show that the MHI are characterized by a large number of endemic species (30% of inshore fishes) due to its geographic isolation (Hourigan and Reese, 1987). Here we show that Hawaii`s isolation may be causing its distinct shallow fish community. The genera that may be contributing to these differences in the upper bathyal zone are *Owstonia*, a bandfish genus that is found in the deep waters of the Indian and Pacific Ocean (Smith-Vaniz and Johnson, 2016) and *Chascanopsetta*, a lefteye flounder that has a tropical distribution from the Western Atlantic to the Western Pacific (Hensley, 1986). Although we were unable to identify the majority of fishes beyond genera in the present analysis, our patterns could derive from patterns of endemic species similar to shallow reef environments. The Line Islands and Tokelau Ridge had an upper bathyal and intermediate community (250-1000 m) that was different from all other regions (Figure 5A) which align with studies that have found that neighboring regions harbor more similar fish communities (Clark et al., 2010). Also, these regions are within the equatorial upwelling zone, which is an area that experiences high productivity due to the dynamic seasonal changes in sea surface temperature (SST) and water column thermal and oxygen structure. Cold SST that is prevalent in equatorial waters during ENSO events like La Niña and shoaling of the thermocline and oxycline from enhanced upwelling may be creating a physiological barrier in these regions (Carlisle et al., 2017). The

Line Islands and Tokelau Ridge had some of the lowest concentrations of dissolved oxygen and highest POC flux values, suggesting that these regions may be a biogeographic zone of faunal change. The center of the South Pacific provinces as described in Watling et al., (2013) are within oligotrophic central gyres and are characterized by extremely low POC flux. Conversely, the Equatorial Pacific province underlies high productivity related to equatorial upwelling and is characterized by moderately high POC flux. Faunal studies conducted across the postulated transition zone of the Equatorial and North Central Pacific provinces have observed significant changes in the diversity of mesopelagic fishes (Clarke 1987; Barnett 1984) as well as macrofaunal polychaetes and sediment dwelling foraminiferans matching food availability at abyssal depths (Smith et al., 2008). Therefore, it's possible that a similar transition zone may be occurring across the Equatorial and South Pacific contributing to the changes observed in the demersal fish community.

Community structure was also found to correspond with the vertical stratification of water masses. Depth zonation patterns matching water mass distribution have been observed for deep-sea fishes in the Atlantic (Koslow 1993, Bergstad et al., 2012, Quattrini et al., 2015), off the Azores, Cape Verde and Madeira (Menezes et al., 2006, 2009, 2015), and in Australia (Williams et al., 2001). AAIW was also found to be associated broadly with communities across all depth zones. The widespread distribution of AAIW may be offering adult deep-sea fishes a mechanism for long-distance dispersal by remaining in a preferred water mass (Clark et al., 2010).

4.2) Relationship between community composition and environmental gradients

Oxygen played a role in structuring central Pacific fish communities with the presence of low-oxygen zones from 250-1000 m in some regions. Persistent OMZs are likely to be important boundaries to species distributions and are hypothesized to be barriers to gene flow within populations in the deep sea (Rogers, 2000). Regional variation in the thickness and intensity of OMZs can be attributed to the differences in oceanographic currents, productivity, and aerobic respiration in the water column (Stramma and Visbeck, 2009). In the Hawaiian archipelago, there is a relatively weak OMZ between depths of 600 and 700 m with minimum oxygen concentrations of 0.84 mg/L at ~650 m (Yeh and Drazen, 2009, De Leo et al., 2012). Reduced fish abundances have been found there (De Leo et al., 2012). In the present study, the lowest concentration (minimum DO value) of dissolved oxygen for the regions investigated in the Hawaiian archipelago were 1.16 mg/L in the NWHI, 1.38 mg/L in the MHI, and 2.32 mg/L in the Musicians Seamounts. Outside of the Hawaiian archipelago, the regions with the lowest concentrations of dissolved oxygen were the Line Islands (minimum DO value of 0.56 mg/L), Johnston Atoll (minimum value of 0.75 mg/L), and Tokelau Ridge (minimum value of 1.3 mg/L). Although dissolved oxygen in these regions is higher than the threshold considered for oxygen minimum zones around the globe (0.7 mg/L, Gibson, 2003), and more characteristic of an oxygen minimum layer characterized as hypoxic (dissolved oxygen (DO < 2 mg/L) (Jaker et al., 2020)), the low oxygen could be acting as a physiological barrier to genera.

Part of the variance in the community structure of demersal fishes in the central Pacific can be attributed to POC flux, a proxy for food availability. Generally, POC flux decreases with depth and the distance from shore, the source of coastal nutrients, and vascular plant and macroalgae material. However, depth-related decrease in POC flux becomes more complicated with more complex bathymetry and where OMZs intersect continental margins and seamounts (De Leo et al., 2014, Levin et al., 2001). Both indirect and direct changes in food quantity and quality in deep-sea communities can alter food web structure, abundance, and diversity; therefore, it's not surprising that POC flux values had a significant influence on community composition across all regions. Deep-sea habitats generally have low biomass due to the low food availability, and reproduction and growth of fishes are all reduced with increasing depth which is likely related to both food supply and temperature (Levin et al., 2001). POC flux was highest in the Line Islands and Tokelau Ridge for all depths which also had some of the lowest oxygen levels. It's likely that the low-oxygen environments in these OMZs are influencing material cycling in the region and the transfer of organic matter to deep waters (Ma et al., 2021).

Care is needed when interpreting the overall importance of environmental variables in governing community composition. The first two axes in the CAP analysis combined accounted for ~14% of the variation, indicating that there are other predictors that explain the variation not included in the present study. Small-scale habitat variability was found to contribute to the spatial variation of deep-sea fish communities among different slopes of the same seamount in the NWHI (Mejia-Mercado et al., 2022). Other abiotic factors such as mesoscale oceanography, light intensity, and hydrostatic pressure along with biotic factors such as competition, food web linkages, and parasitism may be contributing to the unexplained variation (Levin et al., 2001).

4.3) Relationship between total abundance and environmental gradients

Overall, total abundance was found to decrease with depth which is in alignment with the decrease in food input available for organisms inhabiting deeper depths and the physiological adaptations fishes have acquired for dealing with low food quantity and quality at depth (Johnson et al., 2007). An exponential decrease in fish abundance with depth has also been observed in oligotrophic areas of the Atlantic (Merrett et al., 1991). However, there were two exceptions to this general pattern in the MHI and Tokelau Ridge where there was a high abundance of fishes at ~750 m. This was driven primarily by two genera, *Epigonus* and *Setarches.* In a 2015 dive conducted during CAPSTONE (D2-EX1504L4-01), which took place just south of O`ahu (MHI), there was a high abundance of *Epigonus*. Similarly, in a 2017 dive conducted during CAPSTONE (D2-EX1703-08) which also took place on an island flank near Howland Island (Tokelau Ridge), there were a high abundance of *Setarches*. It's possible that these high abundances were driven by the enhancement of phytoplankton in near-island ecosystems known as the Island Mass Effect (IME). Although much yet remains unknown about the exact mechanisms causing this phenomenon, the increase in phytoplankton biomass in close proximities to island ecosystems has been documented for over half a century. Across the central and western Pacific, islands and atolls exposed to elevated levels of nearshore phytoplankton support higher fish biomass. However, IME strength can vary depending on the geomorphic type, bathymetric slope, and local human-derived nutrient input (Gove et al., 2016).

The relationship between total abundance and all environmental predictors (depth, concentrations of dissolved oxygen, POC flux, and salinity) were significant. Total abundance was predicted to be highest at upper bathyal depths between 250-500 m which is in accordance with the strong depth zonation patterns in fish communities that are linked with both biotic (competition, predation, and nutritional resource availability) and abiotic variables (substrate, temperature, light) that vary with depth (Scott et al., 2022). Total abundance increased with higher POC flux values which were generally highest in shallower water as expected. However, it's important to note that seafloor POC flux values were averaged across varying water column characteristics (i.e., seamounts, atolls, islands), therefore there may be regional differences that are unable to be captured by the POC flux model. Further, organic matter may be underestimated, especially from human-derived runoff near islands (Gove et al., 2016). In addition to the positive relationship with POC flux, total abundance was found to be highest between dissolved oxygen values of 1.5 to 3.5 mg/L, however, sampling was limited where values were >4 mg/L. Many studies have found a general decrease in demersal fish density, biomass, or CPUE with decreasing oxygen levels, however, the effect is nonlinear and there are greater reductions below certain oxygen thresholds which are region-specific and influenced by depth, temperature, and the demersal fauna inhabiting them (Gallo and Levin, 2016). In Hawai`i, where OMZ conditions are weak, there is a reduction in demersal fish abundances where oxygen conditions are lowest. However, in other regions such as the Indian margin, fish densities increased within the lower boundary of the OMZ and were almost twice as high compared to the OMZ core (Gallo and Levin, 2016). The regions with the lowest DO and highest values of benthic POC flux (Line Islands and Tokelau Ridge) also had some of the highest average fish abundance values. Since there are limitations in the POC flux model's ability to capture regional habitat variation, this relationship (and potential correlation with POC flux) is hard to disentangle. Total abundance was highest at salinity values ~34.6, however, the dynamic range of salinity is very small (34.1-36.2), therefore this pattern may not be ecologically relevant.

4.4) Diversity Patterns

Although none of the regions were sampled adequately for a comprehensive comparison of diversity patterns, there were a few major trends that can be explored. Overall, genera richness was found to decrease with depth and evenness increase with depth. Trends in richness may be explained by the kinetic energy hypothesis which states that warmer temperatures in the shallow upper bathyal zone may support a higher diversity of ophiuroids (Woolley et al., 2016). The decrease in richness with depth may also be explained by the more-individuals hypothesis which theorizes that higher energy availability promotes a higher number of individuals in a community allowing more species to persist (Storch et al., 2018). Bottom-water oxygen availability could also be contributing to this phenomenon because the Line Islands, Tokelau Ridge, and MHI had some of the lowest oxygen concentrations and the highest richness. Habitat diversity may be added in these regions due to the weak, yet thick OMZ that is not present in the other regions. OMZs have been found to provide hypoxia-tolerant species refuge from non-tolerant species leading to changes in community composition (Gallo and Levin, 2016). However, the high richness in these regions may also be due to the disproportionate sampling that was conducted in the shallow upper bathyal depths, which is especially relevant for the MHI and Tokelau Ridge. The trend in evenness increasing with depth may be explained by fish species in deeper habitats being more uniformly abundant due to a reduced input of energy (Zintzen et al., 2012). Also, it is easier to estimate evenness when there are more samples, so the greater sampling effort in the shallow upper bathyal depths may be contributing to this trend.

4.5) New genera sightings for the central Pacific

The present study includes the first published central Pacific observations of *Neocyttus*, a genus of oreos which resembles a species that was described from the western Indian ocean, *Ostichthys* *acanthorhinus* (Greenfield et al., 2017). The first record of *Neocyttus* in the central Pacific occurred during a 2005 HURL submersible dive. There were also new observations of *Halosaurus* in the central Pacific. In both cases, physical specimens were not collected to confirm the sightings despite compelling videographic evidence. These potentially new records emphasize the importance of exploration and the need for detailed follow-up studies in the central Pacific, especially at intermediate depths of 750 – 1000 m and past 3000 m.

4.6) Management Implications

Although this study was data limited, it provides the first insight into the demersal fish fauna inhabiting the central Pacific. It also has direct management implications as it demonstrates that there is clear regional variation in the demersal fish communities. Our results demonstrate that existing Marine National Monuments are complementary components of the regional diversity and harbor unique communities which highlights the need to maintain this broad network of protection. Nonetheless, there is still much to learn about the deep-sea and as our understanding of these habitats improves, many more threats to these environments are recognized. Therefore, the effectiveness of the Monuments will depend on the spatial distribution and depths of human-caused disturbances such as climate change, deep-sea mining, and fishing. For instance, there has already been an increase in the frequency of extreme El Niño and La Niña events which could lead to more physiological barriers and decreases in habitat availability (Carlisle et al., 2016). To get a better understanding of how these systems will be influenced by anthropogenic effects, we first need to get a complete characterization of the communities inhabiting the regions and gain greater clarity of the boundaries and gradients of faunal change.

4.7) Future Considerations

Due to the sample resolution and study design, we did not investigate the relationships between community structure and smaller scale habitat structure such as biogenic coral mounds, boulder fields, and larger seafloor features such as cold seeps, seamount summits, and submarine canyons. However, all of these have been found to influence deep-sea fish community structure (Auster et al., 1995, Auster, 2005, Quattrini and Ross, 2006, Ross and Quattrini, 2007, Milligan et al., 2016, Leitner et al., 2021). The present study provides a first look at these communities at a broader regional scale, but it is important to note that further studies should investigate community structure at a finer scale to fully understand the ecological patterns.

4.8) Conclusions

The potential of continental margins to be sources of habitat heterogeneity (over various spatial scales) (De Leo et al., 2014), and the increase of anthropogenic activity in the deep sea (Glover and Smith, 2003) require a better understanding of the processes that shape demersal fish communities. The present study provides the first insight into the demersal fish fauna inhabiting the central Pacific. Depth was found to be important for structuring communities which become more similar with depth. Fish communities of the Hawaiian archipelago and the Equatorial regions (Line Islands and Tokelau Ridge) were unique and are likely influenced by the presence of an OMZ with high fish abundance likely caused by regionally high food availability (seafloor POC flux). The present analysis was made possible by significant exploratory survey results. Future studies should use the present work to inform sampling designs and increase sampling effort (especially at depths of 750 – 1000 m) to more systematically advance our knowledge of the variables (and at what scales) driving the community structure of fishes in the central Pacific.

Additionally, studies need to collect specimens and identify taxa to the species level for greater insights into biogeographic patterns.

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