Linking Ecological Conditions to Size-Distributions of Abyssal Scavengers Across the Eastern and Central Pacific Ocean

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I certify that I have read this thesis and that, in my opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

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ABSTRACT

Spanning across the Pacific Ocean is a community of abyssal scavengers, constantly foraging for carcasses that sink to the deep-ocean floor. Baited-camera deployments enable *in situ* observations of this poorly understood community, but few studies have been able to evaluate scavenger sizes. Stereo-video camera footage from across the Clarion-Clipperton Zone (CCZ) and Hawaiʻi was analyzed to obtain length measurements of the widespread macrourid fishes, *Coryphaenoides armatus/yaquinae*, and compare size-frequency distributions across the Eastern and Central Pacific and to variation in environmental parameters. There was a distinct difference in fish size between the east and west CCZ, with larger individuals in regions near bathymetric highs and with higher surface productivity, corresponding to increased food availability. Observations off the coast of Hawaiʻi showed the mean size of rattails was two-fold larger in the winter compared to summer, indicating a strong seasonal pattern in the scavenger community, potentially influenced by the carcasses of migratory species such as tuna. Across the entire study region, areas of higher productivity and bathymetric highs featured larger fish, while polymetallic nodule cover, slope, temperature, and particulate organic carbon (POC) flux were not significantly related to fish size. Determining the relationships between *C. armatus/yaquinae* size and ecological factors can inform management strategies involved in monitoring anthropogenic impacts and safeguarding the resiliency of deep-sea communities.

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ABBREVIATIONS

APEI- area of particular environmental interest

AP- abyssal plain

H- abyssal hill

S- seamount

BPI- bathymetric position index

CCZ- Clarion Clipperton Zone

GLM- generalized linear model

EQPAC- Equatorial Pacific Project

ISA- International Seabed Authority

PAFL- pre-anal fin length

POC- particulate organic carbon

CHAPTER 1 INTRODUCTION

Background

The abyssal zone is the most expansive geological feature on Earth, comprising 65.4% of the ocean floor (Watling et al., 2013). In the absence of sunlight, immense levels of pressure, and low temperature, life in this extreme environment is fueled by the energy supplied in the form of detritus that sinks from the upper ocean. In addition to the flux of finer detrital particles, larger food-fall events occur when the carcasses of large organisms reach the seafloor, delivering energy and nutrients to an otherwise food-poor habitat, and supporting a community of abyssal scavengers (Dayton and Hessler, 1972; Higgs et al., 2014; Stockton and DeLaca, 1982; Smith, 1985). Rattail fishes, *Coryphaenoides* spp., are the most prevalent demersal fish observed at abyssal depths, occupying the top trophic level of the abyssal plains (Drazen et al., 2008).

It is only since the 1960's that photographic observations of these inaccessible ecosystems have been possible, as the logistical and financial demands of deep-sea exploration make robust sampling and studying a challenging endeavor (Isaacs, 1969; Priede and Bagley, 2002). To study scavenging communities, baited-camera deployments are performed, simulating food fall events to attract and capture specimens on camera in their natural surroundings. While advancements in this approach have been made and decades of research conducted, scavenger populations remain largely under-sampled, and the abyssal realm vastly unexplored.

Previous baited camera observations of *Coryphaenoides* spp. have examined a variety of scavenger community traits such as swimming behavior, relative abundance, diversity, and a few studies have measured size distributions. Studying how fish size changes under different ecological conditions can bring insight into the life history, structuring of the community, and responses to environmental changes. *Coryphaenoides* spp. size serves as a proxy for age and by extension reproductive potential (Stein and Pearcy, 1982). Changes in size can also result in shifts in the ecological role of fish, because diets transition from smaller to larger prey as fish size increases (Drazen et al., 2009, 2008). Size distribution studies, combined with research techniques that directly study egg abundance, gut contents, and fish age, work together to depict the life history of these fishes (Stein and Pearcy, 1982; Drazen et al., 2008; Gerringer et al., 2018). It is therefore possible to look at size changes in a deep-sea fish community as an indicator of anthropogenic pressures such as fishing (Godbold et al., 2013; Mindel et al., 2018).

Studies of fish body size have been used to investigate the occurrence of "bigger-deeper" patterns. Baited camera work has a revealed a bigger-deeper trend for *Coryphaenoides* spp. in several studies (Priede et al., 1994, Merrett, 1992; Collins, 2005). This is postulated to result from a larger size is being needed to swim further distances in search less frequent, large food-falls at greater depths. However, this trend was not witnessed by Drazen and Yeh (2011) or Gerringer et al (2018), and instead bigger rattails have been seen at shallower depths near abyssal hills where food-availability is increased (Durden et al., 2015; Leitner et al., 2017). Such discrepancies suggest a variety of influential factors are at play, and further studies are needed to clarify which conditions are driving rattail size distributions.

Rattails consume large food parcels that sink from above and assimilate the carbon and nutrients stored in the bodies of large carcasses, effectively sequestering carbon (Mariani et al., 2020). Defecation and sloppy feeding makes some of these nutrients accessible to lower trophic levels, which are transported across ocean basins by these highly mobile species (Moreno and Haffa, 2014; Stockton and DeLaca, 1982; Smith, 1985). A seasonal migration of *Coryphaenoides* spp. has been suggested on large scales, possibly across ocean basins, following the changes in overlying primary productivity that correspond to increased food availability (Armstrong et al., 1991; Milligan et al., 2020; Priede et al., 2003). Thus, the size distributions of scavenging fish are likely to be influenced by both spatial and temporal heterogeneity of food supply (Leitner et al., 2017).

Deep-sea mining in the Clarion Clipperton Zone

The Clarion Clipperton Zone (CCZ) spans from south of Hawaiʻi to the margins of Central America and is located within two biogeographic regions that follow a productivity gradient from the oligotrophic Northern Central Pacific to the eutrophic Eastern Tropical Pacific (Sutton, 2005; Watling et al., 2013; Wedding et al., 2015). The vast area of the CCZ features a variety of deep-sea communities and geological formations such as abyssal hills and seamounts.

The CCZ is also home to a vast quantity of polymetallic nodules scattered across the sea-floor (Kuhn et al., 2017; Wedding et al., 2015). These small concretions contain metals used in electronic devices and the batteries that can contribute to a cleaner energy grid. Interest in the extraction of polymetallic nodules and the associated research of ecological impacts began in the 1970s and continues today with mining companies worldwide holding exploratory claims across the CCZ, seeking to fulfill future demands for valuable metals (Wedding et al., 2015).

Mining operations are expected to have negative impacts on deep-sea communities in nodule-covered regions of the CCZ, based on both experimental and modeled scenarios (Drazen et al., 2019; Jones et al., 2017; Miljutin et al., 2011; Smith et al., 2020). Direct disturbances to the sea-floor are estimated to affect 300–600 km^2 per year and sediment plume re-deposition reaching over scales of 10–100 km away from mining sites (Oebius et al., 2001; Wedding et al., 2013). Recovery of benthic communities will range from years to centuries depending on the functional group, while permanent habitat loss will occur for the organisms that live on the nodules which take millions of years to form (Jones et al., 2017; Smith et al., 2020). Benthic prey support higher trophic levels including scavengers such as *C. armatus/yaquinae* (Drazen et al., 2009), so the widespread, long-term, and irreversible impacts of deep-sea mining will extend beyond the benthic communities.

Regulation of deep-sea mining is controlled by the International Seabed Authority (ISA), an international organization of 127 countries created by the United Nations, that oversees the mineral exploitation of the deep-sea floor outside national jurisdiction. The

ISA is responsible for negotiating deep-sea mining claims with public and private stakeholders worldwide, while also maintaining a “duty to ensure the effective protection of the marine environment from harmful effects that may arise from deep-seabed related activities” (https://www.isa.org.jm/). As part of this mandate, their guidelines for environmental research include the study of demersal scavengers and fishes, recognizing they are important to deep-sea ecosystems.

The goal of this study is to examine size-frequency distributions of the ubiquitous macrourid species complex *Coryphaenoides yaquinae/armatus* across the CCZ to Hawai‘i and investigate the influence of oceanographic conditions and habitat heterogeneity on fish size. This approach will enable a better understanding of baseline conditions in the CCZ prior to mining activities. Furthermore, this study evaluates seasonal changes in fish size-frequency distributions at Station ALOHA (Karl and Lukas,1996). Linking size-frequency distributions with seasonal oceanographic conditions can provide insights into the environmental drivers of rattail population dynamics across the North Pacific.

CHAPTER 2 METHODOLOGY

Data collection was performed across five different research expeditions across the North Pacific, in which various deployments were performed within sites often defined in terms of their respective mining claim, or stratum (Table 1). In the Eastern CCZ (ECCZ), deployments took place in the Ocean Mineral Singapore (OMS stratum) mining claim-area and the UKSRL (UK Seabed Resources, LTD; the UK1 stratum) from Feb-Mar, 2015 aboard the research vessel (R/V) *Thompson*, and a single deployment in the Areas of Particular Environmental Interest (APEI) 6. Deployments also were performed in the Western CCZ (WCCZ) region south of Hawai‘i from Aug-Sept, 2015 aboard the R/V Kilo Moana (EQPAC1 & EQPAC2) as reported in Leitner et al. (2017). Additional deployments in the WCCZ took place aboard R/V *Kilo Moana* from May-Jun, 2018 (KM1808, APEIs 1, 4, and 7). The most recent deployments took place outside the CCZ, north of Hawai‘i at Station ALOHA aboard the R/V *Kilo Moana* in July 2019 (KM1914) and Jan 2020 (KM2002).

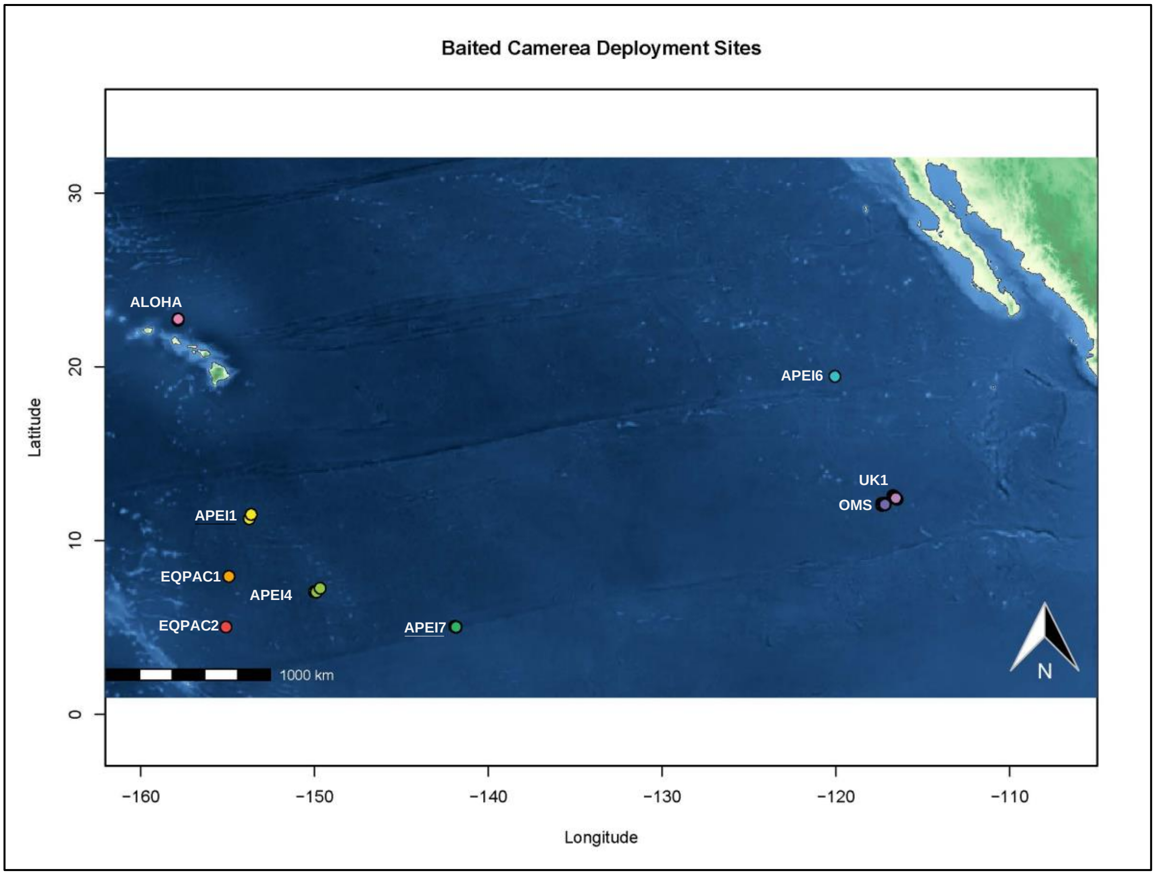

Figure 1. DeepCam deployment locations across the CCZ and Hawai‘i labeled with corresponding the stratum

Table 1. Deployment information. Cruise identifier and associated deployment number, where applicable, the Stratum refers to the 30 x 30 km box around each point used for including Station ALOHA (ALOHA), Equatorial Pacific Project (EQPAC) 1&2, Areas of Particular Environmental Interest (APEIs) including Abyssal Plains (AP), Seamounts (S), and Hills (H). Launch date refers to the baited camera deployment date.

Cruise - Deployment	Stratum	Launch Date	Depth (m)	Latitude	Longitude
KM2002	ALOHA	1/19/2020	4728	22.68	-157.87
KM1914	ALOHA	7/21/2019	4728	22.46	-157.51
KM1515 EQPAC CA02	EQPAC1	9/5/2015	4170	5.02	-155.10
KM1515 EQPAC CA01	EQPAC2	8/24/2015	5231	7.93	-154.93
KM1808 DC09	APEI1 AP	6/9/2018	5236	11.25	-153.76
KM1808 DC11	APEI1 S	6/12/2018	4218	11.50	-153.65
KM1808 DC05	APEI4 AP	6/1/2018	5216	7.05	-150.01
KM1808 DC06	APEI4 AP	6/2/2018	5004	7.03	-149.90
KM1808 DC08	APEI4 S	6/5/2018	3497	7.25	-149.68
KM1808 DC02	APEI7 AP	5/24/2018	4860	5.05	-141.93
KM1808 DC01	APEI7 AP	5/22/2018	4878	5.02	-141.86

TN319 CA13	APEI6 AP	3/20/2015	4065	19.45	-120.06
TN319 CA03	OMS AP	2/24/2015	4178	12.12	-117.36
TN319 CA12	OMS AP	3/15/2015	4093	12.03	-117.35
TN319 CA10	OMS AP	3/11/2015	4095	12.14	-117.25
TN319 CA11	OMS AP	3/13/2015	4090	12.05	-117.22
TN319 CA04	OMS AP	2/26/2015	4078	12.07	-117.18
TN319 CA02	UK1 AP	2/22/2015	4201	12.57	-116.71
TN319 CA08	UK1 AP	3/7/2015	4178	12.45	-116.65
TN319 CA06	UK1 AP	3/3/2015	4209	12.51	-116.62
TN319 CA09	UK1 H	3/9/2015	3555	12.44	-116.55
TN319 CA01	UK1 AP	2/18/2015	4137	12.38	-116.49

Fish lengths were measured using the video-lander system, DeepCam (Figure 2). This system was deployed autonomously to the seafloor, where a sequence of video clips tracked the appearance and behavior of bait-attending species. Across all deployments, a standard ~1kg Pacific mackerel (*Scomber japonicus*) was affixed to a pole with a net protecting the bait to allow for extended feeding times and to attract more individuals. Two stereo-configured and geometrically calibrated HD cameras were positioned in underwater housings attached to the lander frame. With the bait pole attached in between the cameras and recording images from two different angles, this system enables high precision length measurements. The cameras are synchronized with a lighting system to provide a 1.86 m^2 half-elliptical field of view, which allows for direct observation of activities and measurements of all fish so long as they are in the field of view of both cameras. Video footage was taken in a sequence of 2 minutes of recording with the lights on, followed by 8 minutes with the system turned off. This was designed to maximize battery life enabling deployments of 24 hours, as well as to reduce the potential effects of light disturbance on bait-attending fauna. For a more detailed description of the DeepCam system, see Leitner et al. (2017).

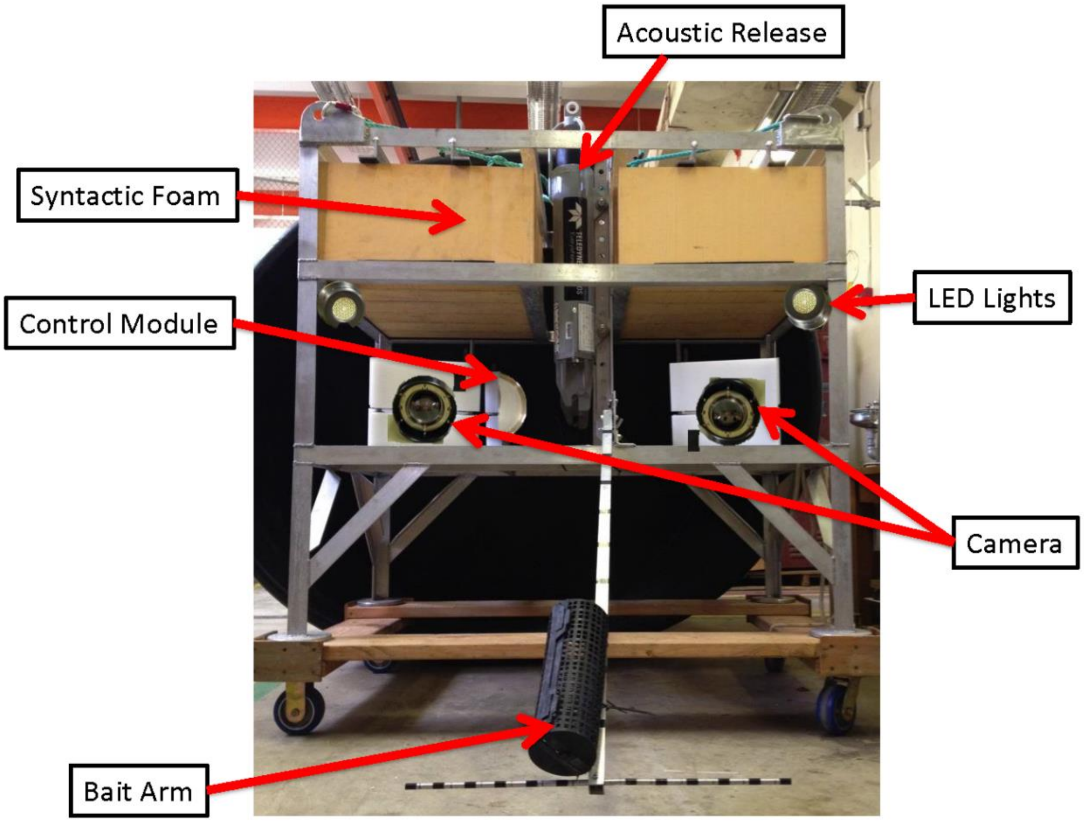

Figure 2. DeepCam baited camera system

The two macrourid species inhabiting the abyssal plains across the Pacific are *C. armatus* and *C. yaquinae* and they are nearly indistinguishable on camera (Wilson and Waples, 1983). Jamieson et al. (2011) suggested identifying the two based on the reflectivity of the fish scales while looking at downward-facing baited camera images. They found *C. armatus* was lighter and *C. yaquinae* darker in coloration. The Jamieson et al. approach was not possible in this study because the orientation of the DeepCam camera system was not facing downward (Figure 3), so fish were observed at various distances which is also a determinant of how bright the fish appear.

Baited camera footage from various dive sites was analyzed to measure lengths of *Coryphaenoides* spp. using the software Event Measure (https://www.seagis.com.au/). The pre-anal fin length (PAFL) of *Coryphaenoides* spp. was measured as a size indicator. This is a commonly used metric in captured macrourid specimens (since many of their tail tips are damaged (Drazen et al., 2008; Yeh & Drazen, 2011)) as well as in baited camera work by Leitner et al. (2017). From the viewpoint of the cameras, this section of the body is less distorted by the movements of fish and thus more reliable than measuring total length.

Each fish that swam in direct view of both cameras was measured a minimum of three times and a minimum of 5 video frames apart (frame rate was 30 frames per second), but often separated by minutes when a clear view of the fish was in the frame. Each measurement was taken by placing a pair of points on the fish's snout and point of anal-fin insertion on both left and right video frames (Fig.3). Measurements had to meet strict precision parameters to be accepted (RMS>10 mm, precision to length ratio <5%, precision <10 mm). Fish may swim in and then out of the field of view and then back in again. The potential for repeated measurements on the same individuals was reduced by carefully identifying and tracking fish with distinguishable characteristics (damaged fins, parasites, scarring, etc.). While many individuals had no identifiable features, each measurement was contingent on the randomness of ideal positioning, unobstructed by other fish, sediment plumes, the bait, and bait-arm, so it is unlikely that one fish was positioned perfectly throughout a deployment.

Figure 3. Example of a single PAFL measurement in the geometrically-calibrated left and right video still

In two deployments, DC01 and EQPAC1, nearly every fish that entered and exited the frame was measured, resulting in nearly 200 measurements per deployment, far exceeding the number of fish measurements made in other deployments and certainly resulting in multiple measurements of the same fish. To address the issues of pseudo-replication and disproportionate sample sizes, duplicate values (to the millimeter) were removed, and a subsample was randomly taken with the number of measurements matching the average number of individuals measured in other abyssal plain deployments.

Length data from deployments that took place in the same stratum and research cruise were combined to provide more robust sample sizes for size comparisons between broader study regions. Station ALOHA: KM1914 and KM2002 occurred during separate times of the year, so they were treated as separate groups.

The potential influence of habitat variables on *Coryphaenoides* spp. size was investigated in terms of the topographic and environmental predictors at each deployment (Table 2).

BPI is a metric that measures the difference in elevation between the specified location and surrounding area to determine if the location is a local high or low. BPI was set with an inner range of 2.5km, between bathymetric grid cells with an outer radius of 5 km, reflecting the general diameter of the abyssal hills found in the CCZ (Leitner et al., 2017). Nodule cover on the seafloor provides a substrate and protection for benthic taxa, increasing epifaunal cover (Amon et al. 2016; Vanreusel et al. 2016) and likely providing prey for larger megafauna such as *Coryphaenoides* spp. (shown by Leitner et al. 2017). The temperatures experienced by these fish have been demonstrated to play a role in predicting the presence of macrourids by Linley et al. (2017), as well as correlating with the mean size of *C. armatus/yaquinae* (Leitner et al., 2017). Chlorophyll-a concentration is a proxy for phytoplankton biomass and hence for food production in surface waters, indicating the amount of pigment that is used to absorb light energy and fix carbon, thus indicating the general productivity of a region. Meanwhile, seafloor slope has been shown to influence fish abundance and size through increased POC flux caused by funneling of nutrients to benthic communities (Collins et al., 2005; Durden et al., 2015). Seafloor POC flux measures how much organic carbon (almost all from phytoplankton) sinks to depth and seafloor, where it provides food for the benthic fauna (Smith et al., 2006), which compose a part of the *C. armatus/yaquina*e diet (Drazen et al., 2008).

Table 2. Environmental factors of interest

Data	**Source**	**Usage**
Depth (m)	Acoustic Doppler Current Profiler (ADCP) (Aquadopp 6000, Nortek AS, Norway)	A sensor measuring temperature, current, and depth was attached to DeepCam but was lost during DC09
CCZ bottom-water temperature	ADCP	as above
Station ALOHA bottom-water temperature (°C)	Aloha Cabled Observatory (ACO) at Station ALOHA	Mean bottom temperature of the day corresponding to the two Station ALOHA deployments
Average chlorophyll-a (mg m^{-3}) from the previous month	AQUA MODIS satellite data (http://coastwatch.pfeg.noaa.gov/erddap/index.html)	Surface phytoplankton biomass values for the month prior to each deployment at a 30 x 30 km grid size around deployment coordinates
Lutz annual mean POC flux at the seafloor (mg m^{-2} day^{-1}) over the interval 1997-2004	Estimated using the Lutz et al. (2007) calculation	Particulate organic matter flux at the seafloor, calculated based on the seasonal primary production and depth in a region.
Percent nodule cover	image color extractor (http://www.coolphptools.com/color_extract)	Spectral analysis of the camera field of view calculates the proportion of nodule coverage based on the dark vs light pixels of study site images
Bathymetric Position Index (BPI)	Benthic terrain modeler (BTM) (https://coast.noaa.gov/digitalcoast/tools/btm.html) ArcGIS 10.0 and special analysis extension (Wright et al., 2012).	Bathymetric data input into ArcGIS with the BTM program to classify benthic environments
Slope (°)	as above	as above

Statistical Analysis

Length data from two seamount deployments were excluded from statistical tests due to low sample sizes of four individuals at the APEI1 seamount and one individual at the APEI4 seamount. The program R Studio was used to explore the relationship of environmental parameters to differences in the size distributions of *Coryphaenoides* spp. across the study region (R Studio Team, 2020).

A Kruskal-Wallace nonparametric comparison test was performed to determine statistical significance between median lengths across different strata, followed by a Bonferroni-corrected, Conover-Iman post hoc test using the *conover.test* package in R (Dinno, 2017). The Conover-Iman test was performed to make pairwise comparisons between median lengths in each stratum, with the null hypothesis that there is an equal probability of a randomly selected fish being larger than an individual in a different stratum. The null hypothesis was rejected when $p < 0.05$.

The relationships between environmental parameters and fish length were categorized by deployment rather than large-scale stratum due to habitat differences within each stratum. This was particularly important while looking at geological variables such as percent nodule cover, which ranged from 0 – 78% within the UK1 abyssal plain (AP) deployment (Table 3). A generalized linear model (GLM) was constructed to evaluate the relationship of these conditions to fish size.

The R package *car* was used to check the variance inflation factor (VIF) for the environmental predictors to confirm that collinearity was not present (Fox and Weisberg, 2019). Initial predictors consisted of BPI, slope, monthly sea-surface chlorophyll a, seafloor POC flux, bottom-water temperature, and percent nodule cover. For each model scenario, deviance residuals were examined for outliers, constant variance, distribution patterns, and shape assumptions of the predictors versus the residuals.

To explore the roles of food supply and topography in relation to size, the environmental variables with the strongest influence were compared to the average size measured in each deployment: energy availability in terms of chlorophyll, and habitat in terms of BPI. Patterns in average PAFL were analyzed with these key variables as different descriptors of size in terms of standard deviation, mode, and kurtosis, (McClain et al., 2018; Grient and Rogers, 2019). Kurtosis was calculated with the *psych* package (Revelle, 2015). The number of modes in a deployment was estimated based on the hierarchical clustering of Gaussian mixture models using the *mclus*t package in RStudio (Scrucca et al. 2016), and a Poisson generalized linear model (GLM) was conducted to analyze the number of modes in the deployment size distributions with the significant environmental predictors. Figures were made with the R packages *marmap, ggplot2, dplyr, plotly* (Pante and Simon-Bouhet, 2013; Wickham, 2016; Bivand and Lewin-Koh, 2020; Auguie, 2017; Wickham et al. 2018).

CHAPTER 3 RESULTS

Size Distribution Comparisons

Comparisons of length distributions across the study region offer insight into how *C. armatus/yaquinae* populations vary between large-scale and more localized areas in the North Pacific (Figure 4). Fish lengths from camera deployments in the WCCZ plains showed no significant differences between sites (Table 4, $p > 0.05$), which were observed during the summer of 2018 (APEI 1, 4, and 7) and the summer of 2015 (EQPAC1). Meanwhile, the EQPAC2 deployment on an abyssal hill showed significantly larger fish than the APEI 4 plains deployment ($p < 0.05$). Surprisingly, the EQPAC2 hill showed no significant difference from the EQPAC1 plains ($p = 0.42$). Although the mean length (± SD) was higher (21.9 ± 6.34 and 17.4 ± 4.9 cm, respectively), outliers and low sample sizes may have been responsible for the lack of significance between the two deployments (Figure 4; Table 3).

Similar to the WCCZ, the fish lengths in the ECCZ plains were not significantly different between sites ($p > 0.1$) and the abyssal hills at UK1 (UK1 H) showed significantly larger fish compared to the UK1 and OMS1 plains ($p < 0.05$ and $p < 0.0001$). Individuals less than 20 cm were absent from the UK1 H deployment, unlike the other strata in this study (Figure 4). The difference between UK1 H and the APEI6 abyssal plain ($p = 0.06$) did not meet the significance threshold of the Conover Iman test, however the shape of the APEI6 size distribution resembled the other ECCZ deployments, and not UK1 (Figure 4).

A stark contrast between size distributions at Station ALOHA was observed during the summer of 2019 (KM1914) and the winter of 2020 (KM2002) ($p < 0.001$, Conover-Iman), with average PAFL size observed in the summer (12.69 ± 1.68 cm) half recorded in the winter of 2020 (24.45 ±1.50 cm). This corresponded to a change in surface chlorophyll from 0.06 mg m^{-3} in the summer to 0.10 mg m^{-3} in the winter (Table 3). Furthermore, the mean length seen in the winter was not significantly different from mean lengths seen in the ECCZ ($p > 0.1$), while the mean length of KM1914 (summer) was not significantly different from the WCCZ ($p > 0.1$) except for the abyssal hill at EQPAC2 ($p = 0.0023$). Interestingly, mean fish size at KM2002 and UK1 Hill were not statistically different ($p = 0.7$), despite being located on opposite ends of the region, existing in very different habitats (i.e. abyssal plain vs. abyssal hill).

Table 3. Environmental and average size data per DeepCam deployment. Site describes the stratum/location and geomorphology of the deployment (AP = Abyssal Plain, H = Hills, S = Seamount). Ordered by longitude from the west (KM1914) to the east (CA01). See Table 2. for descriptions and units of environmental parameters

Deployment	**Stratum**	**Depth**	**Temp**	**POC**	**Chl**	**Nodule**	**Slope**	**BPI**	**# of Fish**	**PAFL**	**STDEV**
KM2002	ALOHA	4728	1.52	1.37	0.1	0	0.83	-2	14	24.5	5.62
KM1914	ALOHA	4728	1.51	1.37	0.06	0	0.83	-2	17	12.7	6.92
EQPAC2	EQPAC2	4170	1.44	1.7	0.07	0	32.3	252	14	21.9	6.34
EQPAC1	EQPAC1	5231	1.5	1.21	0.07	0	0.26	-403	24	17.4	4.9
DC09	APEI1 AP	5236	*N/A*	1.1	0.06	0.14	0.21	-81	19	18.3	5.38
DC05	APEI4 AP	5216	1.67	1.38	0.12	0.53	2.71	-217	20	17.7	5.95
DC06	APEI4 AP	5004	1.64	1.43	0.12	0.15	0.59	-138	38	16	4.14
DC02	APEI7 AP	4860	1.62	1.85	0.12	0	0.18	-208	38	17	5.09
DC01	APEI7 AP	4878	1.62	1.85	0.12	0	0.41	-235	24	19.3	3.75
CA13	APEI6 AP	4065	1.63	1.46	0.09	0.39	1.96	17	52	25.6	7.14
CA03	OMS AP	4178	1.57	1.66	0.23	0.44	5.17	54	21	24.3	6.94
CA12	OMS AP	4093	1.56	1.67	0.17	0.2	2.87	-24	8	26.9	3.3
CA10	OMS AP	4095	1.56	1.64	0.17	0.32	5.64	36	6	24.1	5.04
CA11	OMS AP	4090	1.56	1.61	0.17	0.46	0.73	44	49	21.5	5.65
CA04	OMS AP	4078	1.56	1.61	0.21	0.51	4.59	24	11	26.3	5.23
CA02	UK1 AP	4201	1.83	1.72	0.19	0	3.15	69	9	27.8	6.96
CA08	UK1 AP	4178	1.58	1.66	0.17	0.23	1.76	214	19	25.2	7.11
CA06	UK1 AP	4209	1.58	1.68	0.17	0.78	2.72	0	39	25.4	5.96
CA09	UK1 H	3555	1.58	1.83	0.18	0.25	6.51	355	54	28.6	2.93
CA01	UK1 AP	4137	1.52	1.68	0.22	0.35	2.42	20	31	25	6.31

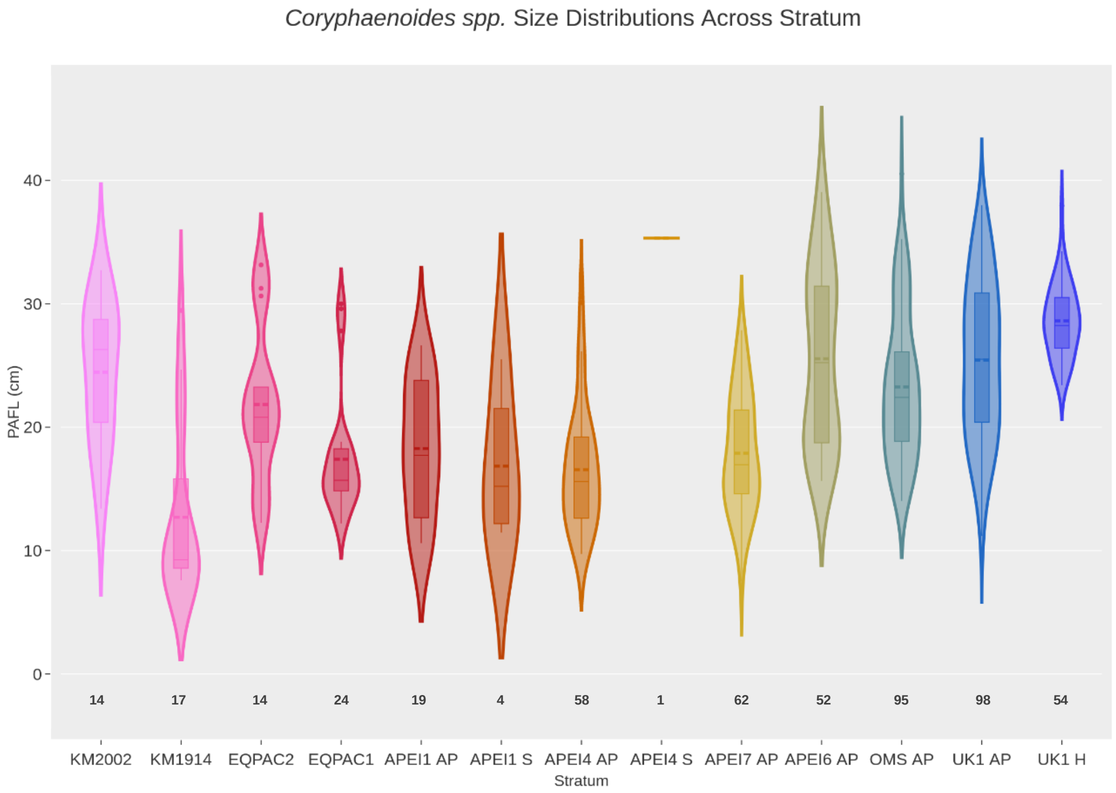

Figure 4. Size distributions of *Coryphaenoides* spp. compared across strata, moving from the west to the east (left to right). Mean PAFL is denoted by the dotted line, median PAFL by the thin line, and the ends of the box are the quartiles. Upper and lower adjacent values are contained within the vertical lines, and outliers shown as dots correspond to the upper/lower quartile ± 1.5 inner-quartile range (IQR) The filled-in shapes correspond to a Kernel Density plot indicating the distribution of size frequencies in each stratum. Numbers above the x-axis denote the number of fish measured in each stratum. APEI4 S and APEI1 S were not included in statistical tests due to low sample sizes.

Table 4. Pairwise comparisons of fish lengths between sites using the Conover-Iman test with a Bonferroni correction. Values in the right corner denote the t-test statistic for rank-sum differences, while those shaded in grey denote the p-value. '*' denotes where p <= 0.05, when the null hypothesis is rejected.

	ALOHA 2002	**ALOHA 1914**	**EQPAC2**	**EQPAC1**	**APEI1 AP**	**APEI4 AP**	**APEI7 AP**	**APEI6 AP**	**OMS AP**	**UK1 AP**	**UK1 H**
ALOHA 2002	—	-5.33	1.29	4.13	3.21	4.99	4.17	-0.37	0.88	-0.48	-2.50
ALOHA 1914	0.0000*	—	-3.97	-1.68	-2.37	-1.58	-2.52	-7.27	-6.35	-7.83	-9.61
EQPAC2	1.00	0.0045*	—	-2.68	-1.82	-3.35	-2.51	1.99	-0.83	-2.19	-4.13
EQPAC1	0.0023*	1.00	0.42	—	0.85	-0.40	0.66	6.08	-4.99	-6.70	-8.72
APEI1 AP	0.08	0.99	1.00	1.00	—	1.35	0.39	-4.63	-3.50	-5.05	-7.05
APEI4 AP	0.0000*	1.00	0.0479*	1.00	1.00	—	-1.39	-8.36	-7.41	-9.79	-11.83
APEI7 AP	0.0020*	0.66	0.68	1.00	1.00	1.00	—	7.14	-6.01	-8.43	-10.65
APEI6 AP	1.00	0.0000*	1.00	0.0000*	0.0003*	0.0000*	0.0000*	—	2.09	-0.15	-3.29
OMS AP	1.00	0.0000*	1.00	0.0000*	0.0280*	0.0000*	0.0000*	1.00	—	-2.69	-5.87
UK1 AP	1.00	0.0000*	1.00	0.0000*	0.0000*	0.0000*	0.0000*	1.00	0.41	—	-3.62
UK1 H	0.70	0.0000*	0.0023*	0.0000*	0.0000*	0.0000*	0.0000*	0.06	0.0000*	0.0178*	—

A comparison of size data between the eastern and western CCZ abyssal plains showed distinct separation in *Coryphaenoides* spp. size structure across the North Pacific (Figure 5; *t*-test, $p < 0.001$). Mean PAFL ± SD was 17.4 ± 4.9 cm in the west and 24.6 ± 6.5 cm to the east. The shape of the distributions shows the ECCZ supports larger fish overall, with a PAFL range of 11.2 to 40.5 cm compared to 7.5 to 30.5 cm in the west (Figure 5).

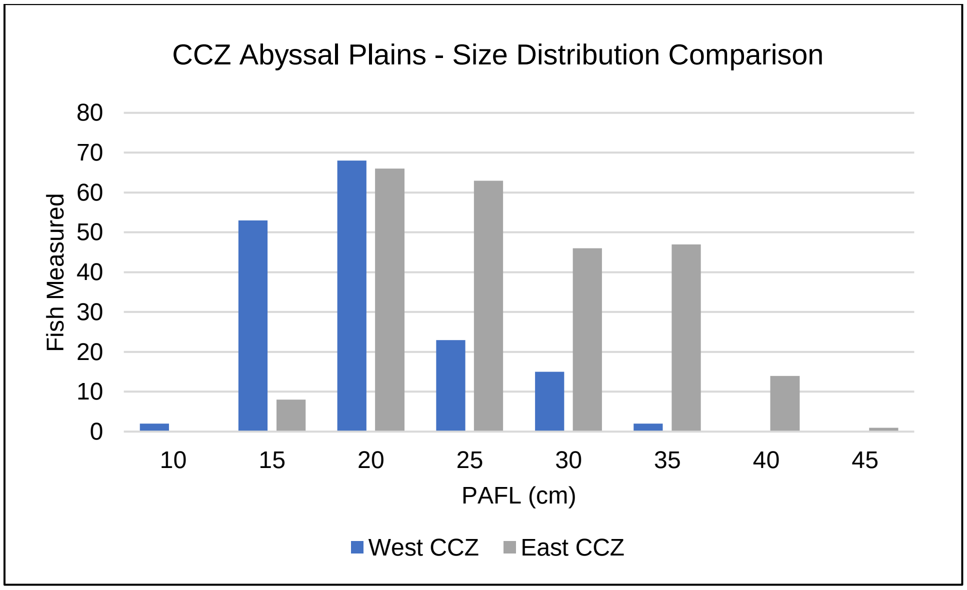

Figure 5. Distribution of size measurements across the CCZ abyssal plains, separated into the western region (EQPAC 1, APEI 1, 4, and 7) and the eastern region (APEI 6, UK1, and OMS1. EQPAC 2 and UK1 H took place on abyssal hills and were excluded from the comparison.

Size in relation to environment

Deployment lengths and environmental predictors were compiled for each site, except for APEI1 where bottom temperature was not measured due to the loss of the ADCP sensor (Table 3). This had a direct effect on models that included temperature because the 19 fish measured in API1 were omitted to allow the function to run, making comparisons between models with different parameters unequal in sample size. A correlation analysis between all variables revealed a positive correlation between BPI and depth, and since BPI offers more insight into topographic heterogeneity, depth was removed from the statistical models. Linear regression analysis between fish size and the six environmental parameters of interest gave insight into which variables would be important in the construction of the GLM (Figure 6). Temperature indicated no relationship with size (Figure 7F, $p > 0.1$) while the response to changes in slope was insignificant and skewed due to the outlier value at EQPAC2 hill, which took place at 32.029 degree slope (Table

3). Based on these findings, temperature and slope were not included in the initial GLM (Table 6).

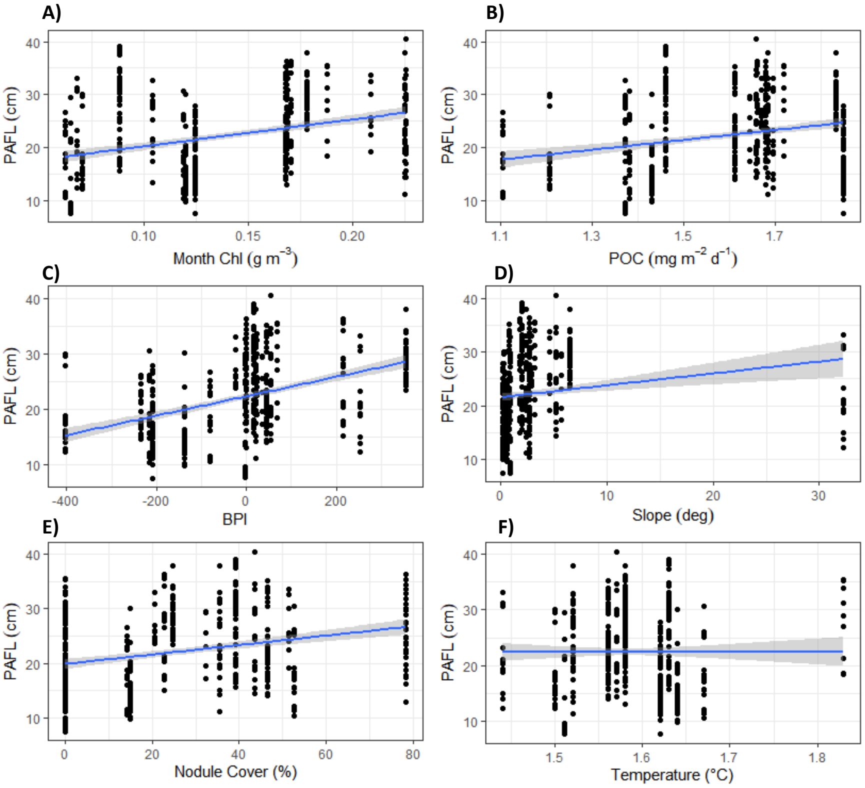

Figure 6. Linear regression models for the starting environmental parameters and the unweighted length measurements. The blue line represents the best fit of the linear regressions and shaded areas represent the 95% confidence interval

Following the exploration of trends in the BPI, slope, monthly chlorophyll, seafloor POC flux, bottom-water temperature, and percent nodule cover (Fig. 6), an optimized general linear model (GLM) was constructed to explain size by removing the environmental predictors that were furthest away from the significance threshold ($p > 0.05$). The optimized GLM for measurements across deployments was Length ~ BPI + MonthChl + Nodule. However, percent nodule cover was a significant factor only when the GLM was performed using every length measurement in each deployment (ANOVA, $p < 0.001$), so deployments with more fish measurements were overrepresented in the model. The significance disappeared entirely when the model was constructed for mean lengths for each deployment ($p = 0.874$). This was largely due to deployment CA06 in the UK1 AP stratum, which featured 78% nodule coverage (Table 3), while average coverage was 24%. Additionally, deployments that showed no visible nodule coverage (KM2002, EQPAC2, and CA02 UK1) were statistically identical to the mean size seen from the CA06 UK1 AP (Table 3; $p > 0.1$). The univariate linear regression for Mean length versus POC flux indicated a significant relationship (Figure 6; $\bar{x}=55.87 \pm 1.961$, $F_{1,18}=13.94$, $p=0.0015$); however, when included in the GLM function, POC flux was not found to be significant, even when chlorophyll was removed from the model ($p > 0.1$).

Iterations of the GLM were run until each environmental predictor in the model had a *p*-value under the threshold of 0.05, omitting variables one at a time based on model outputs (Table 5). The optimized model showed monthly chlorophyll and BPI to be the only significant environmental predictors of mean PAFL ($p < 0.05$; Table 5).

Table 5. Initial GLM (top) and final GLM (bottom) outputs relating environmental parameters to mean PAFL. Signif. codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

GLM function	Slope	STD Error	t-value	Pr(>|t|)
BPI	-2.454e-05	1.065e-05	-2.305	0.03585 *
Chl	-7.714e-02	4.475e-02	-1.724	0.10530
Nodule	-3.246e-05	8.527e-05	-0.381	0.70877
POC	-1.387e-03	1.195e-02	-0.116	0.90911
Chl	0.0115	0.00418	2.764	0.01328 *
BPI	42.532	13.6678	3.112	0.00634 **

The role of these two key predictors was further explored by looking at linear regressions performed with four different body-size descriptors. The slopes of the final GLM showed mean size had a significant positive correlation with BPI, indicating larger fish were found at bathymetric highs (Table 5). The positive relationship was further explored by looking at mean PAFL and BPI alone (Figure 7A; mean 0.0161 ± 0.00476, $F_{1,18} =$ 11.5, $p =$ 0.003, variance = 35.59 %). The other body-size descriptors had no significant correlation (Figure 7; SD 0.0013 ± 0.00168, $F_{1,18} = 0.5885$, $p =$ 0.45, variance = -2.21%; kurtosis -0.0015 ± 1.224, $F_{1,18} = 1.50$, $p =$ 0.2366, variance 2.56%; mode 0.001 ± 1.207, $X^2 =$ 1.46 , $p =$ 0.227).

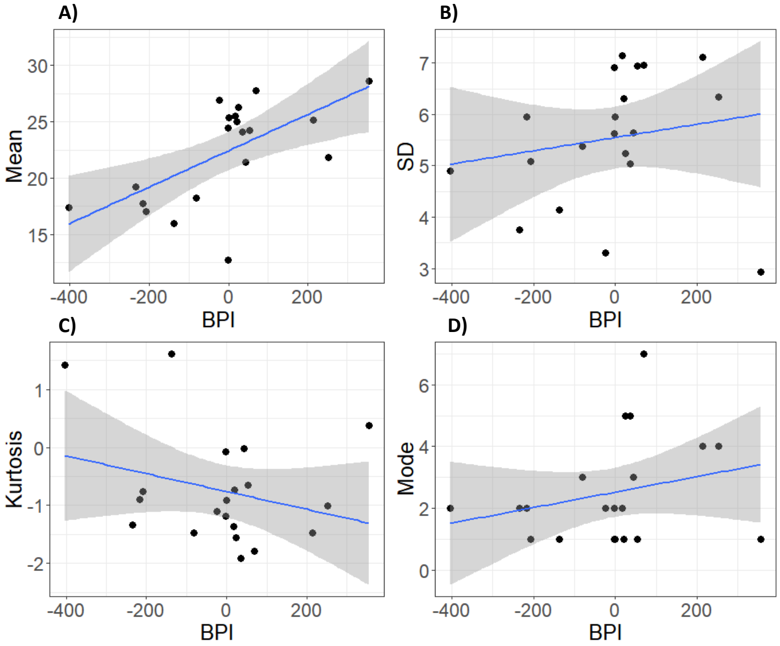

Figure 7. Descriptors of size distributions in relation to broad-scale BPI: (A) mean, (B) standard deviation, (C) kurtosis, and (D) number of modes in the distribution. The blue line represents the best fit of the linear regressions and shaded areas represent the 95% confidence interval

Mean size was found to have a significant correlation with monthly chlorophyll (Table 5, slope), showing larger average fish lengths with higher monthly surface chlorophyll content (Figure 8A; mean 55.87 ± 14.961, $F_{1,18} = 13.95$, $p = 0.001518$, variance 40.53%). The other body-size descriptors had no significant correlation (Figure 8; SD -0.356 ±

5.5934, $F_{1,18} = 0.004$, $p = 0.95$, variance -5.53%; kurtosis -4.007 ± 4.1815, $F_{1,18} = 0.918$, $p = 0.35$, variance, -0.43%, mode 1.641 ± 2.7294, $X^2 = 0.3627$, $p = 0.55$).

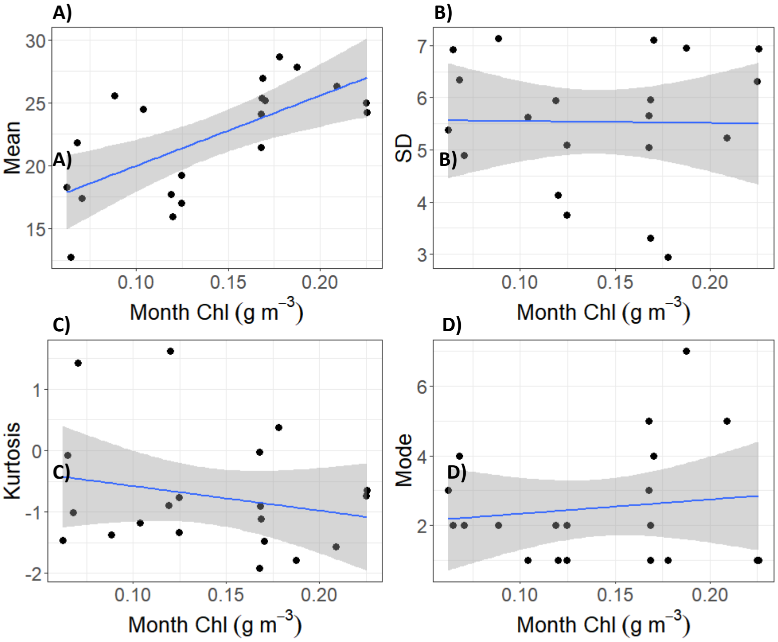

Figure 8. Descriptors of size distributions with monthly chlorophyll: (A) mean, (B) standard deviation, (C) kurtosis, and (D) the number of modes in the distribution. The blue line represents the best fit of the linear regressions and shaded areas represent the 95% interval

Differentiating between *C. armatus* and *C. yaquinae* was not possible in this baited-camera work. However, captured voucher specimens from baited-trap data can give some information as to the composition of these two scavengers (Table 6). While overall sample sizes were very small across the study region, *C. yaquinae* was captured across the CCZ and off Hawai‘i, whereas *C. armatus* was only found in the ECCZ.

Table 6. *Coryphaenoides* spp. specimens collected from baited trap deployments in the CCZ and Hawai‘i, including deployments from an earlier cruise at UK1

Cruise	**Region**	**Date**	***C. armatus***	***C. yaquinae***
AB01 UK1	East CCZ	10/7 -10/22/2013	3	8
AB02 UK1	East CCZ	02/18 - 03/16/2015	2	20
KM1808	West CCZ	05/21- 05/25/2018	0	3
KM1914	Hawai‘i	1/2/2019	0	2
KM2002	Hawai‘i	7/21/2020	0	2

CHAPTER 4 DISCUSSION

Spatial and topographic influences on size distributions

There is a declining productivity gradient from the east to the west in the CCZ and out to Hawai‘i, as one moves from the productive continental margins to the oligotrophic Central North Pacific, which coincides with the decrease in the observed size of C. *armatus/yaquinae* across the study region. Surface chlorophyll is an indicator of primary production, which influences the flux of phytodetritus and carrion to the base of the abyssal food web. Average of chl-a was assessed for the month before deployments, and it was interesting to find that this concurrent value of surface water processes related to *C. armatus/yaquinae* mean size.

Seafloor POC flux is directly correlated to surface productivity and inversely correlated with water depth, and an increase in sinking organic particles directly increases the biomass and abundance of benthic fauna (Gage and Tyler, 1991; Lutz et al., 2002; Smith et al., 1997). Further, this was an annual average value for the interval 1997-2004, indicative of longer-term food supply than chl-a. Thus, it was somewhat surprising that seafloor POC flux did not have a stronger influence on *C. armatus/yaquinae* size. The POC values in this study were not directly measured and depended on the Lutz (2007) annually based calculation of flux at depth, which may fail to capture the precision required to identify trends in POC flux at time scales relevant to the fishes. Alternatively, the time interval modeled (1997-2004) may have had different fluxes than the years of baited camera deployments (2015 -2020). However, Drazen (2002) found that carbon export did not influence the nutritional condition of *C. armatus, yaquinae*, and *acrolepis* over seasonal timescales. The migratory nature of these mobile scavengers and the dietary importance of carrion from the upper ocean may decouple *C. armatus/yaquinae* from the benthic food web that is supported by seafloor POC flux (Collins et al., 2005; Drazen et al., 2009, 2008; Drazen, 2002; Smith et al., 1997). Rather, *C. armatus/yaquinae* have been shown to be more connected to epipelagic nekton as a food resource (Drazen et al., 2008,2012). So, the relationship between monthly chlorophyll and scavenger size may be evident if monthly chlorophyll is a better predictor of carrion supply to the seafloor than annual average POC flux.

Abyssal hills are known to feature increased megafaunal biomass, driven by the horizontal transport of food particles in enhanced currents (Durden et al., 2015). Thus, fish in proximity to topographic highs likely experience the ecological benefits, e.g., enhanced prey availability, of these geological features, which is likely why larger individuals are seen in areas with a higher BPI (Durden et al., 2015; Leitner et al., 2017).

The descriptors indicating the relationship between size, surface chlorophyll, and BPI suggest a shift in the sizes of fish in response to food supply. The larger fish present under conditions of higher food supply - higher chla and/or BPI - suggests that ecological thresholds exist at which fish of the minimum and maximum size groups are better equipped to thrive. Larger scavengers can swim faster and further between meals, though requiring more energy from infrequent food-falls, while the smaller, slower fish may be unable to compete, and rely more on small benthic prey (Collins et al., 2005; Drazen et al., 2008). Camera footage from throughout the study showed larger fish taking over the bait while smaller individuals were pushed away, suggesting that size-based competition could explain the prevalence of larger fish in prime feeding regions (also reported in Leitner et al., 2017).

Contrary to the findings of Leitner et al (2017), nodule cover and temperature were found to have no significant relationship to fish size in this study. Our data includes that of Leitner et al (2017) with the addition of data from the WCCZ and Hawaiʻi. Nodules have been demonstrated to be important in macrofaunal abundance in the CCZ and may provide benthic prey for opportunistic predators such as *C. armatus/yaquinae*, resulting in larger individuals due to competition over preferred habitats (Amon et al., 2016; Leitner et al., 2017). This study included sites in very large areas with no nodule coverage, and the absence of the nodule-abundance-versus-size relationship suggests that nodule abundance is more relevant at a smaller regional scale where there is less variation in food supply from the surface.

Temporal changes in fish size at Station ALOHA

Only two deployments were performed at Station Aloha in this study; however, this limited data suggests *C. armatus/yaquinae* mean size may vary seasonally off Hawaii, perhaps related to changes in food supply. *C. armatus* and *C. yaquinae* have slow growth rates (Gerringer et al. 2018) and travel long distances with slow swimming speeds of ~0.1 m/s (Priede and Bagley, 2000). Based on the *C. yaquinae* growth rate equation from Gerringer et al. (2018), it would take around five years for the winter fish to reach the lengths observed in the summer. Therefore, recruitment and mortality can be ruled out as explanations for the observed size change.

Chlorophyll values at Sta. ALOHA were higher during the winter when primary production is low. This is reflective of the process of photoacclimation, in which chlorophyll concentration in phytoplankton increases under reduced-light conditions (i.e. winter), while less chlorophyll is required for photosynthesis during the high-radiation conditions of summer when primary production is highest, and when producers may also be deeper out of range from satellite measurement (Geider, 1987). Satellites capture the light reflected by chlorophyll, so in the oligotrophic waters around Sta. ALOHA, satellite-based chlorophyll content is *inversely* proportional to the abundance of phytoplankton (White et al., 2015). The presence of larger fish in the less productive winter months suggests that the relationship between primary production and rattail size is not universal, and variations exist for different reasons at a local scale. Furthermore, different indicators of productivity would be more appropriate when assessing changes in size over temporal scales.

The larger fish seen in the winter coincide with the annual migration through Hawaiian waters of the three most abundant tuna species in Hawai‘i: *Thunnus obesus*, *T. albacares,* and *Katsuwonus pelamis* (bigeye, yellowfin, and skipjack) (Gilman et al., 2012). The migration of tuna may increase the frequency of large food-falls in the region due to natural mortality (Stockton and DeLaca, 1982). The Hawaiian longline fleet that targets the tuna serves as the sixth largest commercially fishery in the United States (NOAA, 2016). The deployments at Sta. ALOHA were located within the central-western fishery region, which experiences a high proportion of the longline fishing effort, especially during winter with the arrival of tuna (Gilman et al., 2012; Woodworth-Jefcoats et al., 2018). Longline vessels also create surges in carrion supply via bycatch, by concentrating fish from surrounding waters and discarding unwanted catch, which is then consumed by benthic scavengers (Catchpole et al., 2006; Kaiser and Hiddink, 2007).

Therefore, the rattail migration to Hawaiʻi may be following the arrival of pelagic fish and/or fishery discards, rather than responding to changes in local surface primary production or changes in seafloor small POC flux. Similar to our results, offshore of California (Station M, 4100 m), Drazen et al., 2012 observed an increase in *C. armatus/yaquinae* abundance and a 6-fold increase in biomass associated with the seasonal migration of Pacific hake (*Merluccius productus)*. Hake serve as the target species for humans and rattails alike, and the hake migration is the target of the largest commercial fishery off the west coast of the United States (Methot and Dorn, 1995).

The larger winter fish at Sta. ALOHA were observed feeding directly on the simulated carrion (mackerel), which is in the same family as tuna (Scombridae). Meanwhile, the smaller summer rattails fed mostly on the small amphipods attracted to the bait, despite the abundance of food from the bait in front of them and the absence of competition from larger rattails. Stomach content and stable-isotope analyses support this observation, with differences between *Coryphaenoides spp.* that vary with age/size, with carrion composing a larger proportion of the rattail diet in larger fish (Drazen et al., 2008).

The seasonal trend of *C.armatus/yaquinae* observed here, with larger fish observed in the winter and smaller individuals in the summer, is the opposite of the findings by Priede et al. (2003). They performed baited camera deployments ~600 miles to the north of Sta. ALOHA in the Central North Pacific (Station CNP; 5800m depth), and found smaller fishes in the autumn of 1985 (11.44 ± 0.56 cm) and larger fishes in the summer of 1987 (17.46 ± 0.65 cm) (converted from total length to PAFL using Fishbase.org). Compared to the current study, the Priede et al. findings may coincide with a migratory shift in pelagic fishes that differs latitudinally from Sta. ALOHA. For example, the Sta. CNP rattails could have been feeding on *Thunnus alalunga* (albacore) which arrive in the summer rather than the three tuna species mentioned previously that migrate through Hawaiian waters in winter (Curran, 1996). Alternatively, the Hawaiian longline fishery in the last twenty years has expanded with a five-fold increase in fishing effort, to the point where the rate of bycatch exceeds that of the target species (Woodworth-Jefcoats et al., 2018). With a substantial distance and time separating the sampling from Priede et al (2003) and this study, additional deployments are necessary to determine if the observed differences are due to low sampling effort in the current study, a latitudinal community shift, or ecological changes due to natural and/or anthropogenic factors over the last several decades.

Temporal differences in CCZ sampling

Given the potential for seasonal differences in the mean size of *C. armatus/yaquinae* from Sta. Aloha it is worthwhile to evaluate if temporal variation may have confounded spatial comparisons in the CCZ. The ECCZ was sampled in the winter, while the WCCZ was sampled in the spring (KM1808) and summer (EQPAC1&2). Larger individuals were seen in the winter at both Station ALOHA and in ECCZ, but without knowing the size of fish in the ECCZ summer and WCCZ winter, it is not possible to determine the full extent to which broad-scale temporal versus spatial conditions are important. While deep-sea scavengers have exhibited seasonal foraging patterns related to abundance (Priede et al., 2003, 1994), interannual patterns such as El Niño–Southern Oscillation (ENSO) are also known to affect life at abyssal depths, delivering higher/lower POC flux to benthic communities (Smith et al., 2006, 2008). The nutritional condition of *C. armatus* has also been observed to be potentially driven by interannual cycles tied to a semelparous reproductive cycles or broad-scale climate events (Drazen, 2002). Climate cycles could have influenced the data from the EQPAC cruises in the WCCZ, which occurred in August-September of 2015 during a strong El Niño. However, sampling during different stages of these climate patterns and different times of the year is necessary to understand how mobile megafauna respond to these natural cycles.

Two species of Coryphaenoides spp.

The study region features two species of rattails that have distinct characteristics, which are worth discussing in the context of this study. *C. armatus* has been shown to occupy continental rise regions to depths of 4300m whereas *C. yaquinae* dominates the Pacific ocean central basin at greater depths (Wilson and Waples, 1983). The limited baited-trap collections supported this pattern, with *C. armatus* present in the ECCZ and absent in the few WCCZ and Hawai‘i specimens. The two species are virtually indistinguishable in appearance but have different geographical ranges, diets, growth rates, and longevity

(Wilson and Waples, 1983; Drazen et al., 2008; Gerringer et al., 2018). The two macrourid species could not be differentiated in this study so the species-specific characteristics could be responsible for the size distribution differences seen here. For example, in areas where the two species overlap, such as offshore of California, *C. armatus* is generally larger than *C. yaquinae* (Drazen, 2007; Gerringer et al., 2018). Therefore, the observed ECCZ community could be composed of more large *C. armatus* and smaller *C. yaquinae*, which transitions to a community with fewer large *C. armatus* and more small *C. yaquinae* towards the WCCZ (Wilson and Waples, 1983). Additionally, *Coryphaenoides armatus* are sexually dimorphic (Stein and Pearcy, 1982), with females growing larger and generally inhabiting greater depths than males (Gerringer et al., 2018; Merrett, 1992). While smaller individuals in this study could be either species or sex, the largest individuals were likely older *C. armatus* females (Stein and Pearcy, 1982). Therefore, the size distributions observed in this study could be attributed to a niche separation between the two groups, observable in terms of size, which shifts based on environmental conditions that favor one species over the other.

CHAPTER 5 CONCLUSION

The size of *Coryphaenoides armatus*/*yaquinae* observed in this study varied spatially across the CCZ and possibly seasonally off Hawaii, apparently influenced by topographic highs and food supply driven by the primary production of the region. The two distinct size patterns in the east and west deployments seem to follow the productivity gradient that decreases from the eastern to the western CCZ. Observations at Station ALOHA in the summer and winter suggest a temporally dynamic scavenger community in Hawaiʻi, with a two-fold size increase between the summer and winter that may also be related to the carrion supply from pelagic migratory species. An increase in the spatial scale and frequency of baited camera work is needed to differentiate the spatial and temporal influences of food availability on size, and how this may vary in different parts of the ocean. If there is a coupling of *C. armatus/yaquinae* populations to the movement of pelagic migratory species, deep-sea mining regulations that mitigate the disruption of midwater communities (Drazen et al., 2020) will be necessary to prevent harmful repercussions to the abyssal scavenger community.

Fish size distributions are used in environmental management to track anthropogenic impacts on marine ecosystems. ISA guidelines recommend the deployment of baited cameras to study demersal fish and scavengers in regions that would be affected by mining activities (ISA, 2020). The current study shows that demersal fish, specifically rattails, vary by length/age spatially and potentially temporally. Given the complex dynamics of the *Coryphaenoides spp.* population, and expanded usage of baited cameras will be vital in separating mining impacts from natural variations. The findings of this study reveal the need for a better understanding of how *C. armatus/yaquinae* move and congregate throughout space and time, which is vital for establishing ecological baselines and conservation measures in preparation for deep-sea mining in the CCZ and beyond.

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