Report: An Assessment of Mobile Predator Populations along Shallow and Mesophotic Depth Gradients in the Hawaiian Archipelago

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Summary

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The following Report, entitled “An Assessment of Mobile Predator Populations along Shallow and Mesophotic Depth Gradients in the Hawaiian Archipelago” is submitted as an output from Project 381: Improving assessments of Hawaii priority reef fish species and apex predators using remote video-survey imagery. This serves as a partial requirement for the FY15 reporting for “Hawaii priority species depth distributions & MHI/-NWHI comparisons of roving predator densities”.

Abstract

Large-bodied coral reef roving predators (sharks, jacks, snappers) are largely considered to be depleted around human population centers. In the Hawaiian Archipelago, supporting evidence is primarily derived from underwater visual censuses in shallow waters (≤ 30 m). However, while many roving predators are present or potentially more abundant in deeper strata (30 – 100 m+), distributional information remains sparse. To partially fill that knowledge gap, we conducted surveys in the remote Northwestern Hawaiian Islands (NWHI) and populated Main Hawaiian Islands (MHI) from 2012 – 2014 using baited remote underwater stereo-video. Surveys between 0 – 100 m found considerable roving predator community dissimilarities between regions, marked conspicuous changes in species abundances with increasing depth, and largely corroborated patterns documented during shallow water underwater visual censuses, with up to an order of magnitude more jacks and five times more sharks sampled in the NWHI compared to the MHI. Additionally, several species were significantly more abundant and larger in mesophotic versus shallow depths, which remains particularly suggestive of deep-water refugia effects in the MHI. Stereo-video extends the depth range of current roving predator surveys in a robust manner than was previously available, and appears to be well-suited for large-scale roving predator work in the Hawaiian Archipelago.

Introduction

Large-bodied, coral reef roving predators (e.g. sharks, jacks, and snappers) are generally believed to be depleted across much of their ranges, particularly close to human population centers [1-7]. Similarly, reduced numbers of sharks and large-bodied teleosts reflect comparable patterns in the heavily populated main Hawaiian Islands (MHI), with reef shark abundances estimated at 3 – 10% of natural baseline levels [7] and populations of several jacks (e.g. *Caranx ignobilis* and *Caranx melampygus*) thought to be depleted as a result of fishing pressure over the past several decades [8-11]. This serves as a stark contrast to abundant roving predator groups found in the remote, difficult to access, and largely unpopulated (i.e. relatively lightly fished) Northwestern Hawaiian Islands (NWHI) [1,12].

The primary source of Hawaiian Archipelago large-bodied, shark, jack, and snapper abundance data comes from underwater visual censuses on open-circuit scuba in 30 meters or less [1,12,13]. However, these groups are also known to inhabit considerably deeper strata, where information on predator movements and habitat use remains understudied [14,15]. For example, tiger sharks (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) have been documented to depths greater than 200 m [16-20]. Other predators commonly

observed during shallow water dive surveys in the NWHI, including the giant trevally (*Caranx ignobilis*) and the bluefin trevally (*Caranx melampygus*), have been found in waters to at least 188 m and 230 m respectively [9,21,22]. Given the documented evidence for higher roving predator abundance and/or biomass estimates in deeper waters around high-density human populations [23], sparsely populated or remote areas [24,25], and the noted rarity or absence of several reef-associated shark species (e.g. sandbar sharks, *Carcharhinus plumbeus* and *Galeocerdo cuvier*) during diver surveys [26], it's feasible that open-circuit underwater visual censuses may be missing the bulk of their populations if surveys remain constrained to less than 30 m. Therefore, this represents a clear need to support the expansion of research into deeper coral reef habitats in order to augment our understanding of roving predator distributions in the Hawaiian Archipelago.

Baited remote underwater stereo-video systems (stereo-BRUVs; herein denoted as BRUVS) represent one alternative sampling tool to assess the relative abundance and size frequencies of roving predator populations. BRUVS can be deployed over a wide range of habitats and depth strata [27], and can be used to generate highly accurate and precise length and abundance data for sharks, jacks, and other roving predators which are comparable to other survey methods [28-33].

Here, we present results of roving predator BRUVS surveys across the Hawaiian Archipelago covering depths down to 100 m, which is greater than 3 times deeper than previous surveys. Research objectives included the: a.) evaluation of overall roving predator assemblage structure between the MHI and NWHI b.) comparison of relative abundances and distributions of major species contributing to those assemblages across shallow and mesophotic depth strata; and c.) assessment of mesophotic habitats as potential depth refugia for those predator species considered rare in shallower habitats that can be readily surveyed by divers.

Methods

Study Area

The Hawaiian Archipelago (Hawaii, USA), consisting of 18 islands and atolls stretching across a 2400 km SE-NW gradient, is one of the most isolated archipelagoes in the world. The archipelago includes the Main Hawaiian Islands (MHI), which are geographically-young, high-islands subjected to heavy population and fishing pressures [1], and the older largely-unpopulated NWHI composed primarily of sandy islets, atoll systems, and submerged shoals. In 2005 the State of Hawaii established the NWHI Marine Refuge which closed all NWHI state waters to fishing. Protection was further enhanced by the establishment of the

Papahānaumokuākea Marine National Monument in 2007. Because of their management status and their remoteness, access is almost entirely limited to research and management groups and traditional Native Hawaiian practitioners.

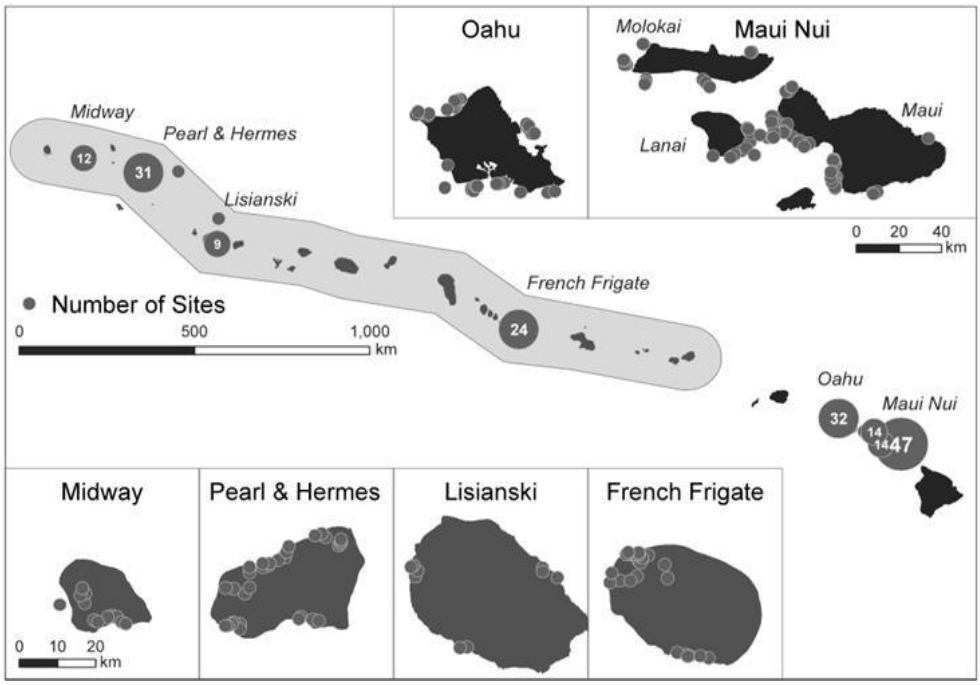

Figure 1. Map indicating stereo-BRUVs sampling locations across the Hawaiian Archipelago.

Survey Operations and Site Selection

Four of the MHI (Oahu, Maui, Molokai, Lanai) were sampled during two NOAA research expeditions in September and October 2012, with additional Oahu shore-based small boat sampling efforts completed in November 2013. Subsequent deployments in the NWHI were conducted during two NOAA research expeditions in May and September 2014 (Figure 1). During each sampling effort, sites were selected in 'mesophotic' (30 – 100 m) and 'shallow water' (0 – 30 m) forereef and fringing reef habitats. Shallow water sites were randomly selected from locations previously surveyed by SCUBA divers conducting routine monitoring operations for reef fish and roving predators [34,35], with there being at least an hour between the completion of diver surveys and deployment of baited camera stations. Mesophotic survey sites were randomly selected from a pool of 500 x 500 m grid cells generated from bathymetric and habitat maps constrained within a 100 m contour line, and stratified into three predetermined depth bins (30 – 53 m, 53 – 76 m, 76 – 100 m). Because the goal was to compare among hard-bottom habitats, grid cells containing backscatter values > 35% derived unconsolidated sediment were excluded from the site pool. However, at some locations (esp.

the MHI), bottom type information was not available or was inaccurate, leading to sampling of unconsolidated sediment (sand flats).

All BRUVS surveys were completed between 0800 – 1600, with soak times of at least 60 minutes, and all sampling sites separated by at least 500 meters. A total of 107 baited sites in the MHI (1 Niihau site excluded) and 78 sites in the NWHI were sampled. Outputs from efforts by region and depth strata are listed in Table 1.

Table 1. Summary of sampling effort in the Hawaiian Archipelago, detailing the number of sites per region, depth strata, and habitat type.

Location	Depth (m)	Hard-bottom	Soft-bottom	Total Sites
Main Hawaiian Islands	0-30	38	2	40
	30-53	24	5	29
	53-100	10	28	38
	Total	72	35	107
Northwestern Hawaiian Islands	0-30	27	-	27
	30-53	19	3	22
	53-100	23	6	29
	Total	69	9	78

Stereo-video collection and data processing

The BRUVS design used in this study followed the design of Harvey *et al.* [36-38], and were constructed from a pair of high definition Sony handheld video cameras with a wide-angle lens adaptor, held in waterproof housing (BRAND) and mounted on a base bar 0.7 m apart, and inwardly converged at 8^{o}. Prior to and following each research mission, each BRUVS was calibrated using CAL^{TM} software (www.seagis.com.au) according to protocols described elsewhere [37-40]. The oily fish Japanese sanma (*Cololabis saira*) was used as bait, which was pulped and loaded into 800g wire-mesh baskets attached 1.2 m from the stereo-cameras prior to deployments.

Following completion of BRUVS deployments, all video footage was converted from MT2S to AVI format using the program Xilisoft^{TM}, followed by the annotation of stereo-video imagery with EventMeasure^{TM} videographic software (www.seagis.com.au) [39]. Species were identified to their lowest possible taxonomic level, with relative abundance recorded as *MaxN* measures. *MaxN*, defined as "the maximum number of fish belonging to each species present in the field of view of the cameras at one time" [41-46] is a conservative abundance measure that avoids repeated counts of the same targets. Length-based measurements were derived by making nose- to-tail fork length measurements (FL) in EventMeasure at the time of *MaxN*. To

ensure the accuracy and precision of measurements, and for consistency with established BRUVS protocols, *MaxN* and length measurements were limited to targets within 7 m of the stereo-cameras [47]. All *MaxN* and fork-length data were compiled and cataloged according to the National Fisheries Information System (FIS) Information Portal practices [48].

Deployments were excluded from analysis when the field of view was $\geq$ 30% obstructed – i.e. if BRUVS had flipped and were facing straight down or straight up, if they were blocked by upright substrate, or when visibility dropped below 7 m, which occurred for a number of MHI sites in < 6 m depth.

Target groups

Analysis of BRUVS surveys was focused on high-level roving predators - all shark species, large-bodied non-planktivorous jack species (*Carangidae*), the great barracuda (*Sphyraena barracuda*), and the green jobfish (*Aprion virescens*).

Environmental variables

Depth data was obtained from UWATEC dive gauges attached to the stereo-camera base bar. Habitat type was visually-classified based on video footage into one of 9 categories: aggregate reef, spur and groove, pavement, rock/boulder, reef rubble, aggregate patch reef, sand with scattered coral/rock, or sand [35]. Habitat complexity was visually estimated on a five-point scale: 1= flat, no vertical relief; 2= low and sparse relief; 3= low but widespread relief; 4=moderately complex; and 5= very complex with numerous fissures and caves [35,49]. Finally, cover of hard coral, soft coral, macroalgae, turf algae, crustose coralline algae, and sand was visually-estimated from video imagery.

Data Analysis

Experimental Design

Roving predator abundance and fork length-based measurements were examined according to two *a priori* factors for this study: Region (MHI and NWHI: two levels, fixed) and depth strata (shallow water (0-30 m); upper mesophotic (30 – 53 m); lower mesophotic (53 – 100 m); three levels, fixed), with the decision to combine 53 – 76 m and 76 – 100 m abundance estimates *post-hoc* as a result of the reduced number of MHI hard-bottom mesophotic sites. A third *post-hoc*, two-level fixed factor was added (Habitat; hard-bottom, unconsolidated sediment), as coral reef roving predators were commonly sighted along both substrate types which precluded

the exclusion of BRUVS surveys that sampled sand flats. Finally, length data was pooled into two comparative depth strata (0 – 30 m; 30 – 100 m) as a result of small sample sizes.

Statistical analyses

Multivariate roving predator assemblage analysis was conducted on a zero-adjusted Bray-Curtis (B-C) [50] dissimilarity matrix using square root transformed relative abundance data using PRIMER v7 with the PERMANOVA+ add on software [51,52]. Segregated regional and depth-inferred differences between roving predator population aggregates were first obtained through the bootstrapping function [53,54], and visualized as a metric multidimensional scaling (mMDS) [55] ordination with bootstrap regions set to 95% confidence intervals (plotted as ellipses (CE)), a Kruskal stress formula set to 1, and minimum stress assigned to 0.01. A successive mMDS assemblage ordination was calculated from distanced-dissimilarities between group centroids (region x depth x habitat) in order to visualize potential effect sizes and their interactions. Linkages between group centroids were overlaid from a Hierarchical Cluster Analysis [56], with the original dissimilarities (distances between individual centroids) compared against cophenetic dissimilarity (distance between centroid clusters). Akin to a suitability index, a cophenetic correlation of $r > 0.8$ can be interpreted as a strong representation of the original centroid dataset [57].

A shade plot/heat map [58] was constructed to further delineate abundance distributions across regions and depth strata, with sites ordered along the x-axis according to region and increasing depth. The y-axis was constructed according to roving predator groups, which were first standardized, transformed into a distance-based resemblance matrix using Whittaker's Index of Association, and plotted via Hierarchical Cluster analysis [56] using group average clustering and a Type III similarity profile (SIMPROF) analysis [59] with 9999 permutations.

Variation in assemblage structure between regions, depth strata, and habitat types were tested using a Permutational Multivariate Analysis of Variance (PERMANOVA) as this is a robust test examining correlations within potential heterogeneous variances [60]. A random, mixed three-way design PERMANOVA with 9999 permutations, constructed using Type III sum of squares (SS) was carried out. If factor effects or their interactions were significant, additional PERMANOVA pair-wise comparisons were conducted to investigate levels of significance, with Monte Carlo p-values used for cases with fewer than 30 unique permutations [51]. Because PERMANOVA can remain sensitive to differences in multivariate dispersions, tests for dispersion homogeneity within groups (permutation of dispersions, PERMDISP), with 9999 permutations, were conducted in concert with PERMANOVA to further assess the variability of sampling regions against different depth and habitat strata.

A Similarity Percentages, Species Contributions (SIMPER) test [61,62] was used to identify the predominant species similarities/dissimilarities within and between regional and depth strata factors, along with the percentage of species which explained similarities/dissimilarities. For species that provided significant contributions to those identified in the SIMPER tests, additional univariate PERMDISP and PERMANOVAs using Euclidean dstance measures were conducted on square root transformed relative abundance data. For univariate non-parametric analyses of *Seriola* species, *Seriola dumerili* and *Seriola rivoliana* abundance totals were pooled together (pooling herein denoted as "*Seriola sp*$^{+}$") along with individuals marked "*Seriola sp"* that couldn't be differentiated between the two. *Seriola rivoliana*, which had distinctly different characteristics than other members of the *Seriola* genus, were rarely encountered and were excluded from pooling.

Length-based estimates

Differences in length distributions for those species identified in SIMPER output were first compared between respective regions using untransformed raw length data (no zeros) across model factors and the non-parametric Kolmogorov-Smirnov test [63], with subsequent PERMANOVA pair-wise test combinations between regions and depth strata (Region: MHI, NWHI; Depth: Shallow [0 – 30 m], Mesophotic [pooled 30 – 100 m strata]). Average fork-length estimates (mm) were obtained for several species, including *Aprion virescens*, *Caranx melampygus*, *Caranx ignobilis*, *Carcharhinus galapagensis*, and *Triaenodon obesus*. All other species were measured, but excluded from analysis due to insufficient fork-length sampling pools (Table 4).

Habitat Characterization

In order to gauge the ecological relationships between shallow water and upper and lower mesophotic zones between regions, a Principal Component Analysis (PCA) [64,65] was performed on normalized environmental variables. Additional inferences on underlying environmental relationships between regions and depth strata were visualized through bootstrapping from the original sampling pool. Bootstraps were plotted as a metric multidimensional scaling (mMDS) ordination, with bootstrap regions set to 95% confidence interval ellipses (CEs), a Kruskal stress formula set to 1, and minimum stress assigned to 0.01. Finally, linkages between the normalized, Euclidean-distance based environmental matrix and the roving predator abundance matrix were explored using the DISTLM function in PERMANOVA+ [51], with the most parsimonious model constructed using a modified Akaike's

Information Criterion (AICc) and *BEST* procedure, and further examined using a distance-based redundancy analysis (dbRDA).

Results

Roving Predator Assemblage Description

A total of 198 individual roving predators were recorded over 107 BRUVS samples in the MHI (mean and SE: 1.85 ± 0.27 SE), while 425 roving predators were recorded over 78 BRUVS sites in the NWHI (5.45 ± 0.84, Table 2). The snapper *Aprion virescens* was the most common roving predator species overall, comprising a large proportion of the pooled roving predator community in each region (22% MHI, 19% NWHI). However, as a collective group, *Carangidae* comprised 65% of all roving predators belonging to ten species in the MHI (1.22 ± 0.19 SE, Table 2), with *Caranx melampygus* dominating shallow water abundances (51%) and *Carangoides orthogrammus* remaining prevalent in mesophotic depths (27%). Similarly, eight species of *Carangidae* accounted for 61% of all observations in the NWHI (3.33 ± 0.70 SE), with *Caranx ignobilis* dominating shallow waters (40%), and *Seriola sp*† comprising the major group (28%) in mesophotic habitats. Finally, sharks formed 12% and 20% of MHI and NWHI roving predator abundances respectively (Table 2, Figure 2). In total, 22 sharks belonging to 4 species were recorded in the MHI (0.21 ± 0.05 SE), with sandbar sharks (*Carcharhinus plumbeus*) encompassing the majority of all shark sightings (59%) and another 23% of sightings belonging to tiger sharks (*Galeocerdo cuvier*). In contrast, 85 sharks belonging to 5 species were recorded in the NWHI (1.09 ± 0.14 SE), with Galapagos (*Carcharhinus galapagensis*; 56%) and whitetip reef sharks (*Triaenodon obesus*; 30%) comprising the majority. Neither species were sampled by BRUVS in the MHI.

Roving predator assemblages differed between regions ($p < 0.001$) and depth strata ($p < 0.001$, Table 3), with overlaps noted between shallow water and upper mesophotic zones within each respective region and separation of lower mesophotic zones (Figure 3A). When assessing the unbalanced sampling of hard-bottom vs. unconsolidated sediment sites, assemblage patterns largely aligned as previously described (Figure 3B) with outliers (MHI: n=2, 0 – 30 m and NWHI: n=3, 30 – 53 m) attributed to small sample size for those strata. Interactive effects were disproportionately driven by intra- and inter-regional differences highlighted in successive pair-wise tests (Supplementary Material, Table A). Finally, the prominent species identified in SIMPER and the shade plot (Figure 4) largely drove assemblage differences between regions and depth strata. These included *Aprion virescens*, *Caranx melampygus*, *Carangoides*

Table 2. Average abundance (mean *MaxN*), standard error (SE), and NWHI:MHI abundance ratios for roving predator species sampled in the Hawaiian Archipelago. * *Seriola sp.* that could not be differentiated between *Seriola dumerili* and *Seriola rivoliana*. †pooled totals of *Seriola dumerili*, *Seriola rivoliana*, and unidentified *Seriola sp*.

Species	Common Name	Main Hawaiian Islands (MHI)					Northwestern Hawaiian Islands (NWHI)					Abundance Ratio
		n	Mean *MaxN*	% Drops	Min. depth (m)	Max.depth (m)	n	Mean *MaxN*	% Drops	Min. depth (m)	Max.depth (m)	NWHI:MHI
Barracuda (*Sphyraenidae*)												
Sphyraena barracuda	Great barracuda	2	0.02±0.01	1.9	30.2	53.9	-	-	-	-	-	-
Snappers (*Lutjanidae*)												
Aprion virescens	Green jobfish	43	0.41±0.11	26.2	13.4	94.8	80	1.03±0.16	73.1	2.7	100.0	2.51
Jacks (*Carangidae*)												
Main species												
Carangoides orthogrammus	Island jack	40	0.37±0.13	15.9	17.1	96.6	15	0.19±0.08	9.0	5.5	50.3	0.51
Caranx melampygus	Bluefin trevally	46	0.43±0.09	26.2	3.0	46.6	43	0.55±0.14	34.6	2.7	50.3	1.28
Caranx ignobilis	Giant trevally	9	0.08±0.03	7.5	30.8	80.8	67	0.86±0.29	28.2	2.7	50.3	10.75
Pseudocaranx cheilio	Thick-lipped jack	-	-	-	-	-	37	0.47±0.31	10.3	40.5	100.0	-
Seriola dumerili	Greater amberjack	6	0.06±0.03	4.7	42.7	92.0	55	0.71±0.39	14.1	23.5	93.3	11.83
Seriola rivoliana	Almaco jack	6	0.06±0.03	2.8	21.3	92.0	27	0.35±0.17	16.7	24.7	100.0	5.83
Unidentified *Seriola sp.**		-	-	-	-	-	7	0.09±0.04	7.7	60.4	-	-
Subtotal *Seriola sp.†*		12	0.12±0.05	6.5	21.3	92.0	89	1.13±0.42	29.5	23.5	100.0	9.42
Other species												
Alectis ciliaris	Threadfin jack	5	0.05±0.02	0.9	58.5	-	-	-	-	-	-	-
Carangoides ferdau	Barred jack	4	0.04±0.03	1.9	14.3	30.5	1	0.01±0.01	1.3	37.8	-	0.25
Elagatis bipinnulata	Rainbow runner	1	0.01±0.01	0.9	14.9	-	-	-	-	-	-	-
Gnathanodon speciosus	Yellow trevally	2	0.02±0.01	1.9	14.3	42.4	-	-	-	-	-	-
Scomberoides lysan	Queenfish	3	0.03±0.02	2.8	3.05	30.5	-	-	-	-	-	-
Seriola lalandi	Yellowtail amberjack	-	-	-	-	-	5	0.06±0.03	2.6	65.5	85.3	-
Unidentified Carangidae		9	0.08±0.04	4.7	4.6	96.6	3	0.04±0.03	2.6	43.6	55.8	0.50
Subtotal *Other species*		24	0.22±0.05	11.2	4.6	96.6	9	0.12±0.06	6.4	37.8	85.3	0.55
Subtotal all jacks		131	1.22±0.19	48.6	4.6	96.6	260	3.33±0.7	70.5	2.7	100.0	2.73
Sharks (*Carcharhinidae*)												
Main species												
Carcharhinus galapagensis	Galapagos shark	-	-	-	-	-	48	0.62±0.15	30.8	6.1	81.1	-
Carcharhinus plumbeus	Sandbar shark	13	0.12±0.05	8.4	54.9	95.1	7	0.09±0.03	9.0	55.8	93.3	0.75
Triaenodon obesus	Whitetip reef shark	-	-	-	-	-	26	0.14±0.05	25.6	5.8	61.6	-
Other species												
Galeocerdo cuvier	Tiger shark	5	0.05±0.02	4.7	4.6	55.8	1	0.01±0.01	1.3	86.6	-	0.20
Carcharhinus amblyrhynchos	Grey reef shark	2	0.02±0.01	1.9	24.1	68.3	1	0.01±0.01	1.3	73.2	-	0.50
Carcharhinus melanopterus	Blacktip reef shark	1	0.01±0.01	0.9	14.9	-	-	-	-	-	-	-
Unidentified shark		1	0.01±0.01	0.9	57.0	-	2	0.03±0.02	2.6	38.1	73.2	3.00
Subtotal *Other species*		9	0.08±0.03	7.5	4.6	68.3	4	0.05±0.03	3.8	38.1	73.2	0.63
Subtotal all sharks		22	0.21±0.05	15.9	4.6	95.1	85	1.09±0.17	55.1	5.8	93.3	5.19
Total mobile predators		198	1.85±0.27	67.3			425	5.45±0.84	85.1			2.95

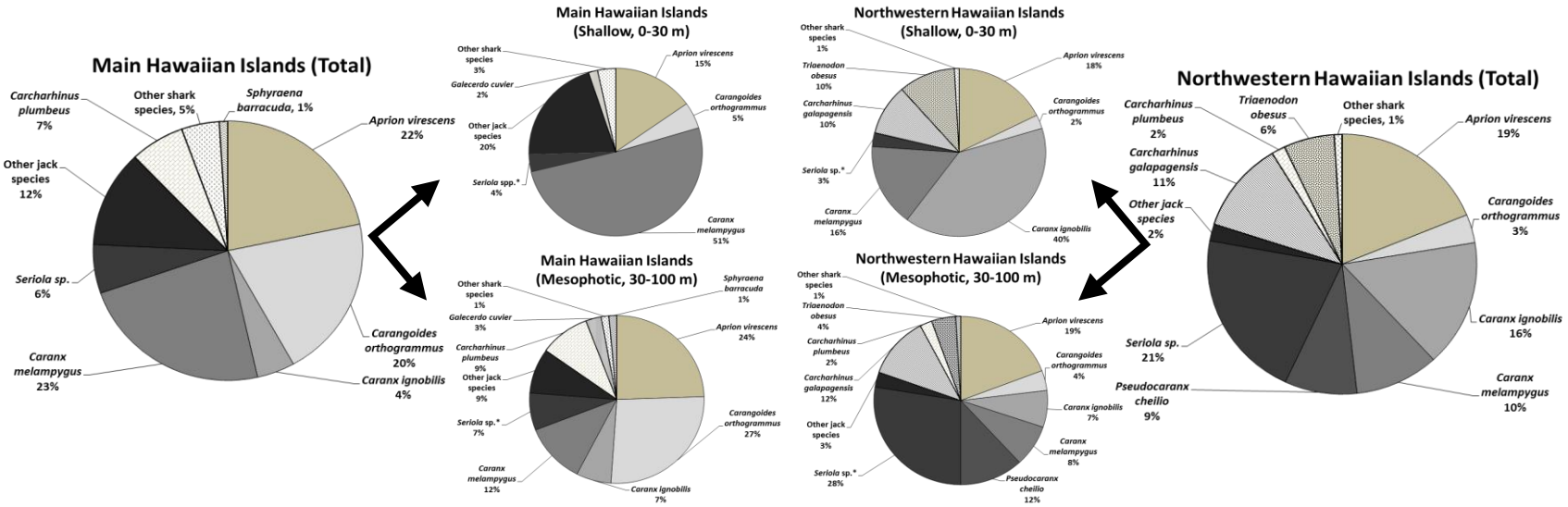

Figure 2. Relative composition of total predator assemblages in the MHI (top left) and NWHI (top right), along with respective shallow and mesophotic components, * Indicates numerical abundance of *Seriola dumerili* and *Seriola rivoliana* pooled.

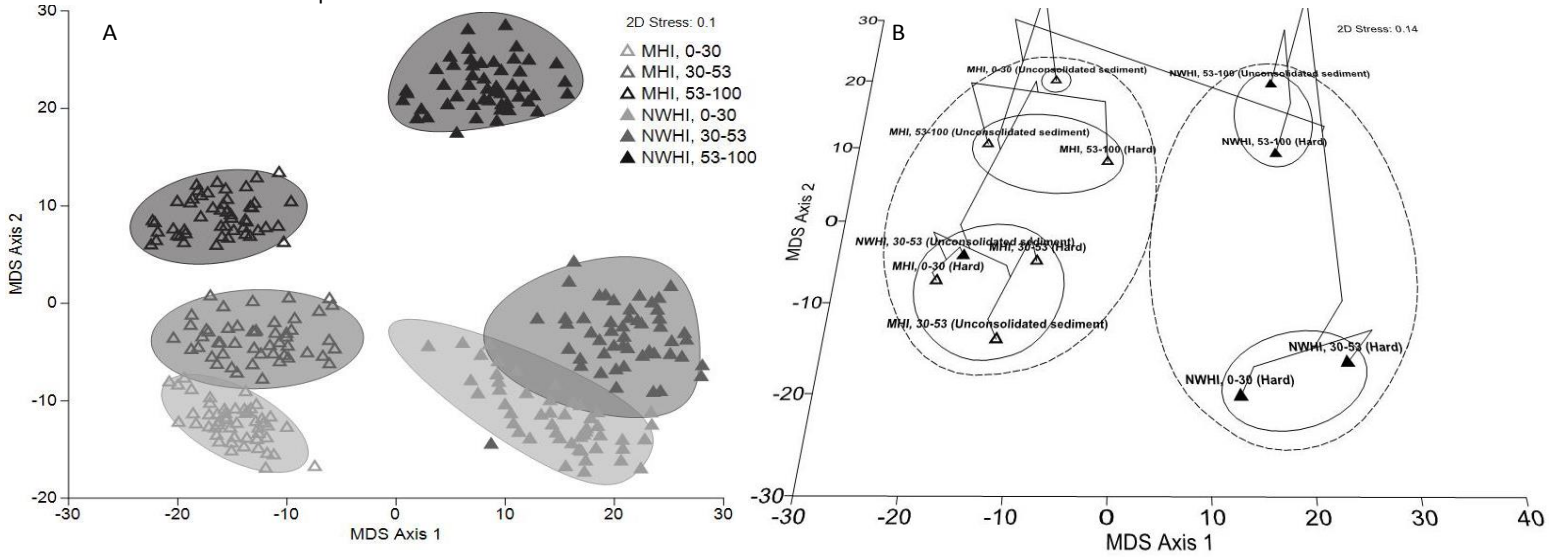

Figure 3A.) Bootstrap resampling plot, 50 bootstraps per group. Square root transformed, zero-adjusted Bray Curtis roving predator abundance data (MaxN) by Region (MHI, NWHI) x Depth Strata (SPC; upper and lower mesophotic), plotted metric multi-dimensional scaling (mMDS). Shaded bootstrap regions, which represent measurements of centroid error: 95% confidence intervals, averages based on m = 10 dimensional metric MDS (rho = 0.985). Open diamonds represent MHI sites, closed diamonds represent NWHI sites. Light grey = shallow (0-30 m), medium grey = upper mesophotic (30-53 m), dark grey = lower mesophotic (53-100 m). B.) Plotted metric multi-dimensional (mMDS) of Region (MHI, NWHI), Depth (MHI, NWHI), and Habitat (Hard-bottom, unconsolidated sediment) group centroids overlaid with a hierarchical cluster analysis dendrogram. Contours from resemblance levels slices at 20 (solid circles) and 35 (dashed circles). Note the absence of NWHI unconsolidated sampling sites between 0 – 30 m. Open diamonds = MHI, closed diamonds = NWHI. Cophenetic correlation = 0.92.

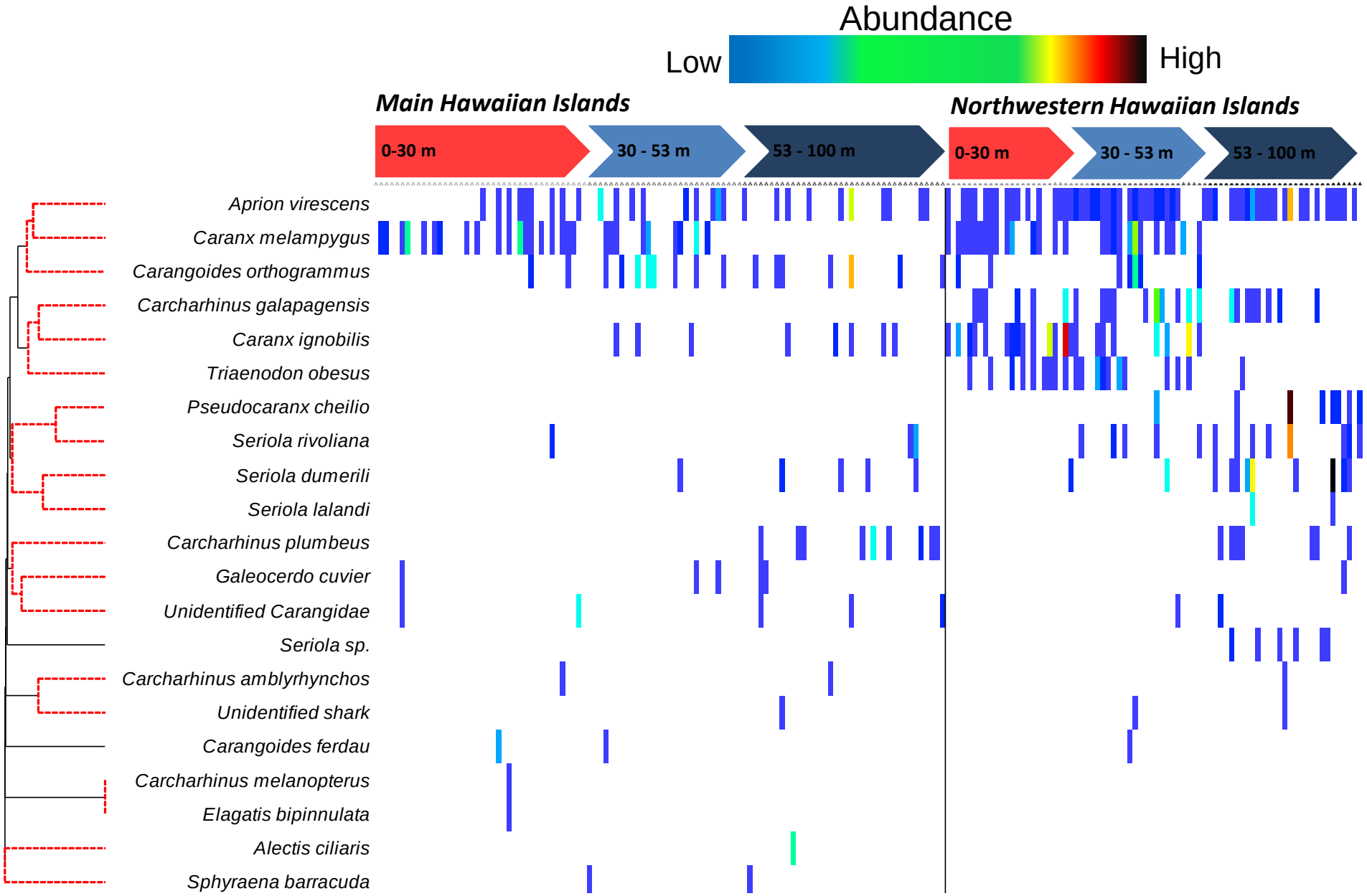

Figure 4. Shade plot showing regional (MHI, NWHI) and depth distributions of all roving predator species. Raw species relative abundance values (*MaxN*: color ramped blocks) were square root transformed to down-weight more abundant species. Y-axis (roving predator resemblance): position of standardized MaxN predator values, ranked by Whittaker's Index of Association transformation and Group Average Hierarchical Cluster analysis (Type III SIMPROF, with permutation between sites). Red dotted lines: groups of coherent species. b.) X-axis (site resemblance): Sites grouped according to region (MHI: open diamond; NWHI: closed diamond) and depth strata (shallow: red, mesophotic; blue), and aligned from left to right by increasing depth. Square root transformed, relative species abundances (MaxN) plotted by ramped spectrum from blue (low) to red (high).

orthogrammus, *Caranx ignobilis*, *Triaenodon obesus*, *Carcharhinus galapagensis, Pseudocaranx cheilio*, *Seriola dumerili, Seriola rivoliana*, and *Carcharhinus plumbeus*.

Roving Predator Abundances: Univariate analysis

Aprion virescens were homogeneously dispersed ($p > 0.05$) across all depth and habitat strata (Tables 3 – 4; Figure 5, top left), recording significant regional differences ($p < 0.001$; 2.5 times greater abundance in the NWHI versus MHI) irrespective of depth strata or inclusion/exclusion of habitat as a pooled covariate. In contrast, *Caranx melampygus* recorded no differences with any tested factor when accounting for its absence beyond 53 m across the archipelago. Habitat served to obfuscate the 3-factor design ($p > 0.45$) for *Carangoides orthogrammus*. When constrained to 53 m or less, depth was significant in the MHI ($p < 0.01$) as a result of a 6 – 15 fold increase in abundance between 0 – 30 m hard-bottom and all substrates between 30 – 53 m (Supplementary Material Table A).

Caranx ignobilis and *Seriola sp*† (both $p < 0.001$) were an order of magnitude more abundant in the NWHI (Table 2). In particular, only small numbers of *Caranx ignobolis* were encountered between 30 – 100 m (upper and lower mesophotic zones) in the MHI (Tables 3 – 4, Supplementary Material Table A, and Figure 5 middle left) in contrast with estimates recorded between 0 – 53 m in the NWHI. When accounting for dispersion heterogeneity driven by depth absences and habitat obfuscation, pair-wise tests retained regional dissimilarities between counts compared between 30 – 53 m (Supplementary Materials, Table A). In contrast, *Seriola sp*† recorded between 3 – 8 (MHI) and 21 – 22 (NWHI) times higher abundances in 53 – 100 m versus 0 – 30 m (Tables 3 – 4, Figure 5 center). Following the inclusion of pooled habitats, retests for region and depth remained significant (both $p < 0.001$), interactive, and heterogeneously dispersed, primarily due to the 6 – 13 fold abundance increase between 53 – 100 m in the NWHI ($p < 0.001$), and asymmetric, intra-regional differences in shallow versus mesophotic strata. Lastly, *Pseudocaranx cheilio* were completely absent in shallow waters and often observed schooling with *Seriola sp*† in mesophotic depths (Tables 3 – 4), although no differences were detected between mesophotic zones (Supplementary Materials, Table A).

The most commonly encountered shark in the MHI - *Carcharhinus plumbeus* - recorded low numbers in the lower mesophotic zone (Figure 5, bottom left), with nearly 4 times the number of sightings occurring on unconsolidated sediment versus hard-bottom substrate with a similar (albeit less prevalent) pattern noted for the NWHI (Table 4). Regional abundances were homogenous and non-significant when pooled habitats were compared between regions ($p > 0.05$, Supplementary Materials, Table A). Finally, the two species of shark only recorded in the NWHI - *Carcharhinus galapagensis* and *Triaenodon obesus* - similarly recorded peak

Table 3**.** PERMANOVA tests of pooled roving predator abundance (all species), *Aprion virescens*, *Caranx melampygus*, and *Carangoides orthogrammus* between region (Re), depth (De), and habitat strata (Ha). PERMANOVA tests of *Caranx ignobilis, Carcharhinus plumbeus,* and *Seriola sp*** are presented for region x depth strata, following preliminary three-factor tests, and for *Carcharhinus galapagensis* and *Triaenodon obesus* between depth and habitat strata in the NWHI. Figures in bold indicate significant results. Total number of permutations per cell exceed 9700 except for the univariate factor test (depth) for *Triaenodon obesus*.

All Roving Predators (Pooled)					*Aprion virescens*			*Caranx melampygus*			*Carangoides orthogrammus*		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Re	1	8792.3	7.4288	**0.0001**	3.8974	11.803	**0.0004**	0.02812	0.098861	0.7538	0.3993	1.5871	0.2125
De	2	4637.8	3.9186	**0.0001**	0.16104	0.4877	0.5934	2.5871	9.0951	**0.0013**	1.3098	5.206	**0.0053**
Ha	1	1944.4	1.6429	0.1496	0.004282	0.012968	0.905	0.52007	1.8284	0.1765	-	-	-
RexDe	2	2298.2	1.9418	**0.0333**	0.15957	0.48325	0.6142	0.24641	0.8663	0.4208	0.35809	1.4233	0.2437
RexHa	1	1288.8	1.089	0.3755	0.026249	0.079494	0.7679	0.1228	0.43171	0.5026	-	-	-
DexHa	2	1740.6	1.4707	0.1481	0.56074	1.6982	0.1685	0.38141	1.3409	0.2476	-	-	-
RexDexHa**	1	3202.1	2.7056	**0.0189**	0.86488	2.6192	0.0996	0.1228	0.43171	0.4995	-	-	-
Res	174	1183.5			0.3302			0.28445			0.2516		

Caranx ignobilis					*Carcharhinus plumbeus*			*Seriola sp.†*		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
Re	1	5.7601	20.21	**0.0001**	0.005267	0.060992	0.8088	3863.6	19.597	**0.0001**
De	2	1.9644	6.8924	**0.0017**	1.3877	16.071	**0.0001**	2751.8	13.958	**0.0001**
RexDe	2	3.8234	13.415	**0.0001**	0.005578	0.064598	0.9381	1247	6.3253	**0.0014**
Res	179	0.28501			0.086348			197.15		

Pseudocaranx cheilio					*Carcharhins galapagensis*			*Triaenodon obesus*		
Source	df	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)	MS	Pseudo-F	P(perm)
De	2	1.3364	3.2205	**0.0468**	0.3151	0.71497	0.4901	1.4012	5.7816	**0.0046**
Ha	1	0.25834	0.62255	0.3612	0.43735	0.99237	0.3353	-	-	-
DexHa**	1	0.55416	1.3354	0.194	1.4101	3.1995	0.0755	-	-	-
Res	73	0.41497			0.44072			0.24235	(Note Res df = 66)	

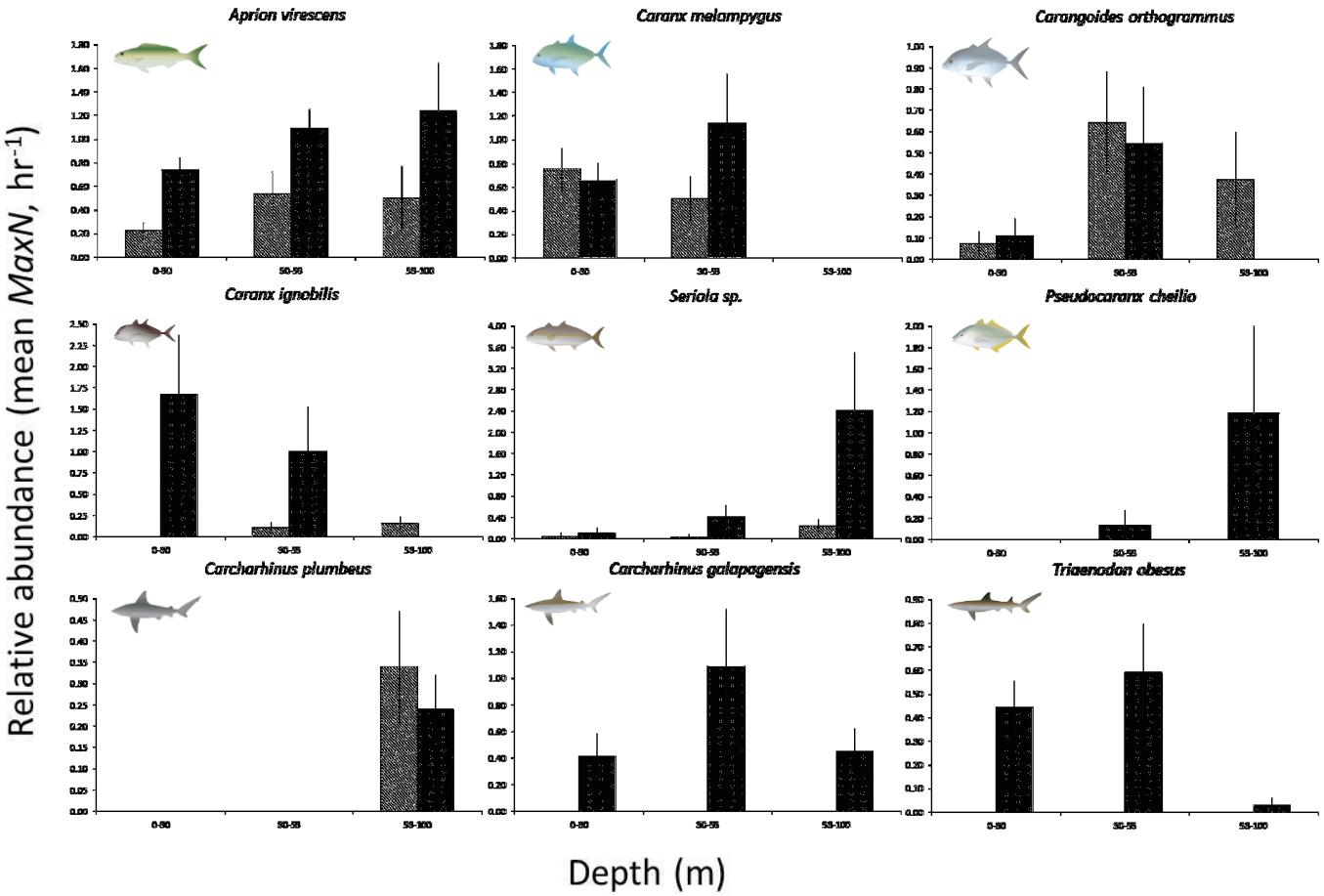

Figure 5. Mean relative abundance (Mean MaxN ±SE) of roving predator species identified in SIMPER analyses across regions and depth strata (habitats pooled). Depth is ordered in increasing intervals, with all habitats pooled. Light grey = MHI, dark grey = NWHI. Note the differences in scales along the y-axis.

abundances between 30 – 53 m, were present in 0 – 30 m, and uncommon in 53 – 100 m. Despite peak *Carcharhinus galapagensis* abundances in the upper mesophotic zone (Table 3 and Figure 5, bottom center), no significant depth differences were detected even when habitat was pooled as a covariate. Similarly, *Triaenodon obesus* was most frequently encountered in the upper mesophotic zone (Figure 5, lower right), with depth remaining significant ($p < 0.01$, Table 4); However, subsequent PERMDISP comparisons of abundance were homogenously dispersed and non-significant between 0 – 30 and 30 – 53 m, coinciding with abundance peaks in those strata and its comparative rarity in deeper depths (Supplementary Materials, Table A).

Table 4. Average abundance (mean *MaxN*) and standard error (SE) of select roving predator species sampled on hard-bottom vs. unconsolidated substrate in the Hawaiian Archipelago. *Seriola sp*[†]: pooled totals of *Seriola dumerili*, *Seriola rivoliana*, and unidentified *Seriola sp*.

	Main Hawaiian Islands			Northwestern Hawaiian Islands	
Species	Depth Strata (m)	Hard-bottom	Unconsolidated sediment	Hard-bottom	Unconsolidated sediment
Aprion virescens	0-30	0.21±0.07	0.50±0.50	0.74±0.10	na
	30-53	0.57±0.21	0.40±0.40	1.21±0.16	0.33±0.33
	53-100	0.40±0.16	0.54±0.36	0.91±0.15	2.50±1.91
Caranx melampygus	0-30	0.79±0.19	-	0.67±0.14	na
	30-53	0.43±0.19	0.80±0.58	1.16±0.47	0.47±1.00
	53-100	-	-	-	-
Carangoides orthogrammus	0-30	0.08±0.06	-	0.11±0.08	na
	30-53	0.52±0.24	1.20±0.80	0.63±0.30	-
	53-100	0.28±0.24	0.57±.40	-	-
Caranx ignobilis	0-30	-	-	1.70±0.70	na
	30-53	0.13±0.07	-	1.20±0.60	-
	53-100	0.10±0.10	0.18±0.08	-	-
Seriola sp.†	0-30	0.05±0.05	-	0.11±0.08	na
	30-53	0.04±0.04	-	0.47±0.23	-
	53-100	0.40±0.22	0.18±0.15	2.39±1.28	2.50±2.11
Pseudocaranx cheilio	0-30	-	-	-	na
	30-53	-	-	0.16±0.04	-
	53-100	-	-	0.43±0.16	4.00±1.63
Carcharhinus plumbeus	0-30	-	-	-	na
	30-53	-	-	-	-
	53-100	0.10±0.10	0.43±0.17	0.22±0.09	0.33±0.21
Carcharhinus galapagensis	0-30	-	-	0.41±0.17	na
	30-53	-	-	1.26±0.48	-
	53-100	-	-	0.35±0.13	0.83±0.65
Triaenodon obesus	0-30	-	-	0.44±0.11	na
	30-53	-	-	0.68±0.23	-
	53-100	-	-	0.04±0.04	-

Roving Predator Length Estimates

Overall, *Aprion virescens* (519 ± 40 and 626 ± 13 mm) and *Caranx melampygus* (367 ± 19 and 507 ± 24, Table 5 and Figure 6) were significantly smaller (both species, $p = 0.0014$) in the MHI versus NWHI. While *Aprion virescens* recorded no depth-based differences ($p = 0.5412$) in either region, *Caranx melampygus* were an average 29% larger in MHI mesophotic versus

shallow depths (435 ± 23 versus 337 ± 23 mm, p = 0.0007). In addition, *Caranx ignobilis* were 26% smaller between the MHI (650 ± 36 mm) and NWHI (878 ± 30 mm, p < 0.01, Table 5 and Figure 6), primarily driven by larger individuals in the NWHI occupying mesophotic strata. Finally, *Carcharhinus galapagensis* were 45% larger in mesophotic (1361 ± 43; 934 ± 15 mm) versus shallow depths in the NWHI, contrasting with *Triaenodon obesus* which recorded no significant depth-based size differences (1189 ± 20; 1088 ± 55 mm, p > 0.05). Comparisons made with less than 10 measurements (*Aprion virescens*: MHI, 0 – 30 m and *Triaenodon obesus*: NWHI, 0 – 30 m) should be treated with caution.

Table 5. Mean average length (L_{mean}) and standard error (±) for five major roving predator species in Hawaii. Minimum (L_{min}) and maximum (L_{min}) lengths are noted for each species, within each depth strata (shallow, mesophotic) and region (MHI, NWHI).

Species	MHI Shallow				MHI Mesophotic				MHI Total		NWHI Shallow				NWHI Mesophotic				NWHI Total	
	n	L_{mean}	L_{min}	L_{max}	*n*	L_{mean}	L_{min}	L_{max}	*n*	L_{mean}	*n*	L_{mean}	L_{min}	L_{max}	*n*	L_{mean}	L_{min}	L_{max}	*n*	L_{mean}
Snappers (*Lutjanidae*)																				
Aprion virescens	7	502±105	222	1072	18	526±40	222	817	25	519±40	21	638±30	289	830	47	621±13	471	817	68	626±13
Jacks (*Carangidae*)																				
Caranx melampygus	25	337±23	213	733	11	435±23	346	623	36	367±19	12	527±45	315	752	14	491±23	365	627	26	507±24
Caranx ignobilis	-	-	-	-	8	650±36	519	770	8	650±36	27	828±42	578	1348	14	974±18	857	1126	41	878±30
Sharks (*Carcharhinidae*)																				
Carcharhinus galapagensis	-	-	-	-	-	-	-	-	-	-	9	934±15	857	994	21	1361±43	1082	1810	30	1233±47
Triaenodon obesus	-	-	-	-	-	-	-	-	-	-	6	1088±55	946	1241	13	1189±20	1093	1330	19	1157±19

Table 6. Results of Kolmogorov-Smirnov (K-S) tests of differences between pairs of fish length density distributions sampled by region and depth strata. Bonferroni corrections were applied to for multiple depth comparisons (*Aprion virescens* and *Caranx melampygus*, □=0.0083; *Caranx ignobilis*, □= 0.017). Values in bold are significant at < 0.05.

Aprion virescens			*Caranx melampygus*		*Caranx ignobilis*		*Carcharhinus galapagensis*		*Triaenodon obesus*	
Region, Depth Strata	D Statistic	P	D Statistic	P	D Statistic	P	D Statistic	P	D Statistic	P
MHI, NWHI (Totals)	0.4465	**0.0014**	0.4915	**0.0014**	0.6341	**0.0092**	-	-	-	-
MHI 0-30m, MHI 30-100m	0.3571	0.5412	0.7200	**0.0007**	-	-	-	-	-	-
MHI 0-30m, NWHI 0-30m	0.7143	**0.0094**	0.6400	**0.0026**	-	-	-	-	-	-
MHI 0-30m, NWHI 30-100m	0.6717	**0.0082**	0.7200	**0.0002**	-	-	-	-	-	-
MHI 30-100m, NWHI 0-30m	0.4841	**0.0213**	0.4167	0.2719	0.4444	0.1745	-	-	-	-
MHI 30-100m, NWHI 30-100m	0.4019	**0.0299**	0.4610	0.1457	1.0000	**<.0001**	-	-	-	-
NWHI 0-30m, NWHI 30-100m	0.3202	0.1020	0.4167	0.2119	0.6296	**0.0013**	1.0000	**<.0001**	0.5000	0.2562

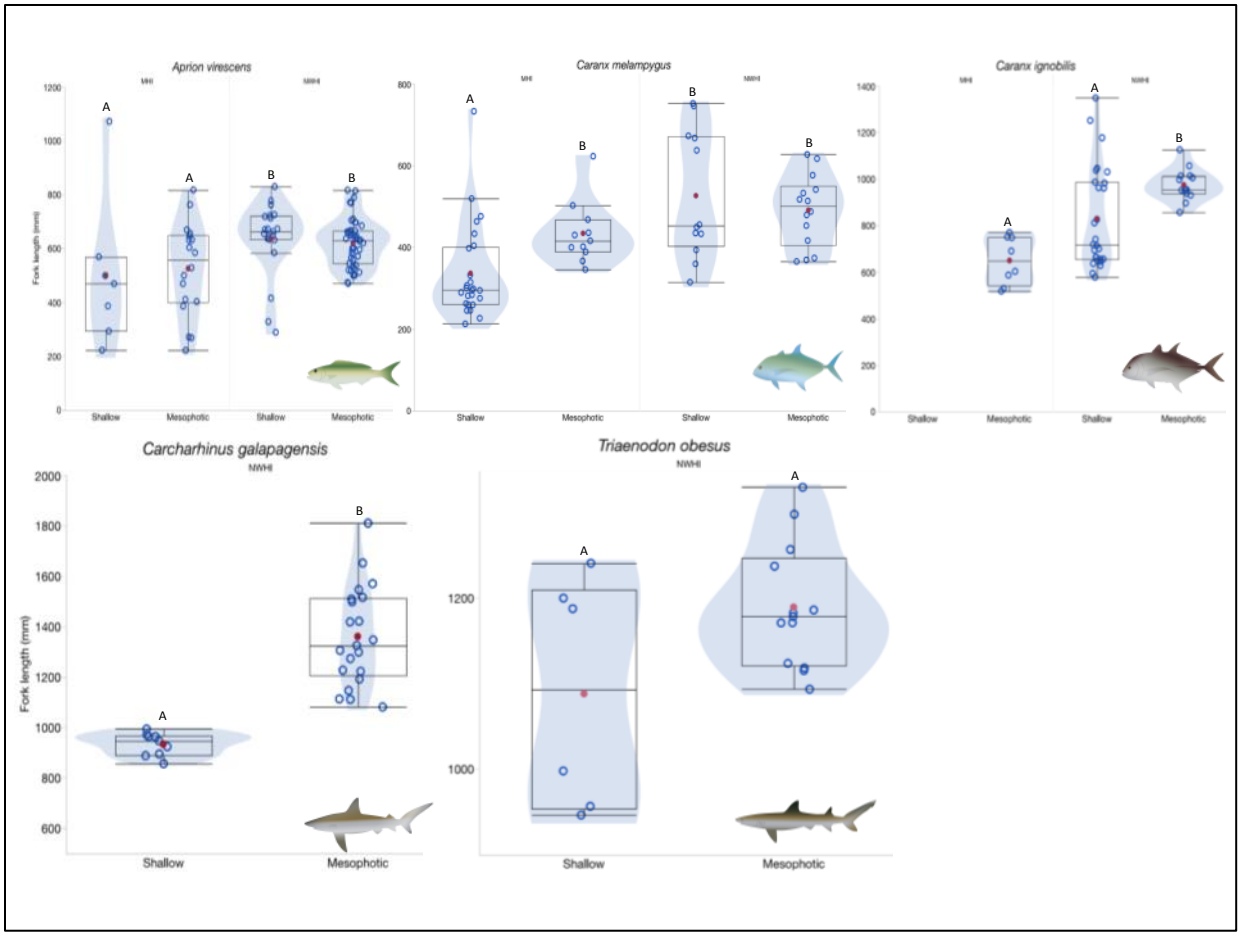

Figure 6. Box and whisker plots indicating fork-length size distributions for Aprion virescens, Caranx melampygus, Caranx ignobilis, Carcharhins galapagensis, and Triaenodon obesus. Whiskers indicate minimum and maximum values, the box specifies the lower interquartile range, and the solid black line indicates the median. Columns with the same letter are not significantly different (P > 0.05). Empty blue circles = individual fork-lengths, solid red circles = mean, shaded contour = density of measurements by length.

Habitat Description and Predator Linkages

Environmental variables were similar between shallow and upper mesophotic zones in the MHI and NWHI; However, linkages between roving predators (Pearson's r > 0.2, *Triaenodon obesus*, *Caranx melampygus*, *Carcharhinus plumbeus*, *Seriola sp*[†]) and environmental variables were weakly correlated, with 10.3% of the total variation accounted by depth, % hard coral, and % unconsolidated sediment cover. A summary of findings can be found in Supplementary Material, Figures A – C.

Discussion

When assessing predator populations, BRUVS retain several potential benefits over shallow water diver surveys. Aside from removing depth constraints attributed to open-circuit scuba

and diametric diver effects, i.e. predator avoidance in populated areas and attraction in remote areas which may act to bias relative abundance estimates in the Hawaiian Archipelago [66-68], and reducing concerns associated with diver instantaneous versus non-instantaneous predator counts [6], archived video can be used to extract data on other species or to verify the authenticity of predator identifications and length measurements [69]. Like all field survey methods, BRUVS host limitations including deployment challenges in vertical habitats, variable bait plume areas measured on holistic scales [42,70], and the potential for competitive exclusion of some species by others [44,70,71]. However, when considering the documentation of reef predators considered rare or absent during underwater visual censuses, BRUVS may provide a more community-wide representation of roving predator assemblage composition [29,42,44].

Survey results were consistent with predator abundance patterns documented in underwater visual censuses in the MHI and NWHI, albeit over a wider depth range (0 – 100 m). While pooled abundance values (all species) were three times higher in the NWHI (Table 2), differences were more pronounced for gregarious species. Specifically, *Caranx ignobilis* and pooled *Seriola sp*† were over an order of magnitude more abundant in the NWHI (all depths and habitats combined), which aligns with historic predator densities recorded by belt transect in $\leq$ 30 m [1], although reported belt-derived ratios for *Caranx ignoblis* alone were considerably higher than 10:1. The 5-fold difference in pooled shark abundances between MHI and NWHI (Table 2), and the pronounced absence of *Carcharhinus galapagensis*, *Triaenodon obesus* in the MHI, irrespective of depths or surveyed habitats, serves as additional anecdotal evidence towards reduced historic reef-shark baselines around populated areas [7].

Shallow water and upper mesophotic zone community overlaps, coupled with lower mesophotic zone separation, were largely similar between regions albeit with divergent species and depth distributions driving interzone connectivity. In the NWHI, *Aprion virescens* remained cosmopolitan between depth strata; However, shallow water-upper mesophotic zone overlaps for three jacks (*Caranx melampygus*, *Caranx ignobilis*, and *Carangoides orthogrammus*) and the numeric majority of two sharks (*Triaenodon obesus* and *Carcharhinus galapagensis*) between 0 – 53 m hint at several possible, interactive drivers, including prey-partitioning mechanisms [72], competition with more numerically prevalent species in the lower mesophotic zone (e.g. *Seriola sp*†, *Carcharhinus plumbeus*), and/or the reduced density or absence of preferred prey in deeper depths. While studies conclude that *Carcharhinus galapagensis* primarily forage in shallow water (Papastamatiou, Meyer et al. 2015), movements may be underestimated (Meyer, Papastamatiou et al. 2010) and runs contrary to longline studies which captured the majority of *Carcharhinus galapagensis* between 40 – 45m [73]. The prevalence of smaller *Carcharhinus galapagensis* and *Caranx ignobilis* in < 30 m depths suggests potential body size and depth

segregation, possibly avoiding intra- or inter-specific predation pressures [74] in deeper waters despite documentation of juvenile Galapagos sharks in mesophotic strata [75] and no evidence of nursery areas [73]. Predator alignments with thermocline position [22,76], and increases in mesophotic fish densities (i.e. prey availability) between 50 – 60 m [23,77] coincide with higher upper mesophotic abundances documented for the principal species encountered during NWHI BRUVS surveys. Finally, Hawaiian monk seal (*Neomonachus schauinslandi*) Crittercam™ surveys noted peak escort and foraging interactions for *Aprion virescens*, sharks, and jacks between 60 – 80 m, suggesting resultant predator depth adjustments were coupled to seal foraging as an exploitable resource [24,78]. The general absence of predator movements > 100 m depths or interisland transits [15,24,79,80] remain indicative of predatory spatial fidelity, and that BRUVS appear to capture overall depth-range demographics for these aforementioned species in the NWHI. This appears to be confirmed with historic bait station and submersible surveys in bottom fish depths (286 – 657 m), where shark sightings were rare and *Aprion virescens, Caranx ignobilis*, *Caranx melampygus*, and *Carangoides orthogrammus* were absent in contrast with common sightings of *Pseudocaranx cheilio* and *Seriola sp*[†] [81]. Whether size-differences or depth distributions directly relate to prey-partitioning, proportionately available habitats and host prey resources, competition with other species in deeper depths, or other causal source remains an important area for future research, along with continued investigations into diel and seasonal migrations and nutrient transport potential between depth zones [15].

Large-bodied snappers, jacks and sharks remain susceptible to fishing activities in the MHI, and changes in abundance and/or biomass can be viewed as an indicator of extraction pressures [12,23,82,83]. Mesophotic habitats may act as depth-refuges for species vulnerable to fishing pressures [23,25,84], and evidence remains suggestive of potential depth protection for several predators in the MHI mirroring patterns seen elsewhere [76,85-87]. In particular, *Caranx melampygus* represented one of the primary species responsible for shallow-upper mesophotic zone overlaps in the MHI in relatively equal numbers; however, overall mean fork-lengths were smaller in < 30 m than all other depth and regional strata tested in this study. *Carangoides orthogrammus* were 6 – 15 times more abundant in the upper mesophotic zone versus those recorded in diver depths, and *Caranx ignobilis* were singularly constrained to MHI mesophotic zones. In contrast, inferences on MHI shark population parameters remain limited due to low number of encounters recorded during this study. Sightings of *Carcharhinus plumbeus* aligns with previous research, which labeled sandbar sharks as the most common shark species in the MHI, primarily captured in 60 – 90 m depths, and rare when contrasted with other shark species in the NWHI [75]. However, mean abundance (0.12 ± 0.05 vs. 0.09 ± 0.03) and the percentage of sites present (8.4% vs. 9%) was similar between regions (Table 2) during this study, and when coupled with comparable longline catch-rates at French Frigate Shoals [26], suggests that sandbar sharks may not be as uncommon in the NWHI as previously suspected.

Of the remaining shark species in the MHI, only three singleton species were sampled in shallow water (*Carcharhinus melanopterus, Galeocerdo cuvier,* and *Carcharhinus amblyrhynchos*), dovetailing with drastically reduced baseline estimates [7], with the remainder encountered beyond 30 m. These consisted primarily of mature or small-bodied ($\leq$ 2m) female *Galeocerdo cuvier*, which may be indicative of migratory patterns documented from the NWHI to the MHI [88] or possible evidence of sex segregation [89]. While potential mesophotic effects may also be present, interpretations based on small sample sizes should be treated with caution.

Pooled environmental covariates delineated largely along *a priori* designated survey depth strata, with overlaps between regions, i.e. environmental variables generally appear similar between the MHI vs. NWHI (Supplementary Materials, Figures A-B). However, environmental linkages with roving predators were tenuous at best, and may be indicative of a.) the highly mobile nature of the roving predators and the utilization of multiple habitats; or b.) limited or asymmetric sampling frequencies between depths and habitats.

Finally, most open-circuit dive surveys focus exclusively on hard-bottom substrates, which may miss a proportion of the predator population occupying large areas of unconsolidated sediment in the Hawaiian Archipelago (especially the MHI). While roving predators may retain inherent preferences towards hard-bottom substrates [74], the assessed species presented here (except for whitetip reef sharks) retain a documented presence on shallower sandy habitats [13,79,80,90-92] and were encountered in mesophotic sand flats during the course of this study. *Caranx melampygus*, *Caranx ignobilis*, *Aprion virescens*, and *Seriola sp*[†] were all observed feeding in areas of 100% unconsolidated sediment (J. Asher, pers. obs.); however, the frequency of sand flat usage as foraging grounds, refugia, or as transitional habitats remains largely unaccounted for. Future BRUVS surveys would benefit from the inclusion of these areas in subsequent designs, as roving predators normally associated with reef and hard-bottom systems retained a considerable presence in unconsolidated sediment that cover underexplored and marginally assessed areas in deeper waters of the MHI.

In conclusion, roving predator research remain heavily reliant on underwater visual censuses, along with a smaller number of fishery independent remote underwater video surveys, and limited fishery-dependent or extractive surveys [26]. The use of BRUVS and the expansion of surveys into mesophotic depths augment our understanding of roving predator distributions across the Hawaiian Archipelago, and illustrate the need to expand long-term predator research and monitoring outside of traditional open-circuit SCUBA depths.

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