Faculty of Science and Engineering
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A Deeper Look at Hawaiian Coral Reef Fish Assemblages: A Comparison of Survey Approaches and Assessments of Shallow to Mesophotic Communities

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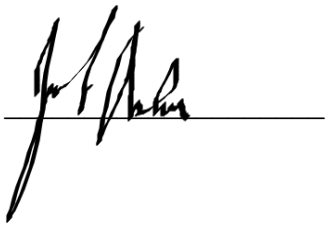
Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgement has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8th edition (2013). The proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number # AEC_2014_09.

Signature:  Date: 26 April 2017

Thesis abstract

Research, monitoring and management of Hawaiian coral reef fishes remains heavily reliant on data collected using underwater visual censuses by SCUBA divers. However, diver-based visual sampling is subject to limitations, including: 1.) Biases caused by different responses of fishes to divers at fished versus remote locations. For example increased wariness of target fishes at heavily fished locations could lead to substantial undercounts. Equally, the attraction of large bodied roving predatory species, such as sharks and jacks, to divers at remote locations has likely led to inflated predator biomass estimates; and 2.) Domains limited to 'shallow' depths that can be readily surveyed by divers on open-circuit SCUBA – i.e. ~30m or less. As many 'depth generalist' coral reef fish species are distributed across a broad range of depths, and in some cases more abundant in deeper 'mesophotic' waters > 30 m, underwater visual censuses do not assess large portions of coral reef fish populations, and potentially overlook important conservation or management information (e.g. mesophotic depths may act as refuges from fishing). Conversely, 'depth specialist' species may be constrained to shallow or deeper depth strata, affecting overall community structure and limiting refuge potential.

Baited Remote Underwater Stereo-Video systems (stereo-BRUVs, herein denoted as 'BRUVS') represent one widely-used, alternative approach to bridge these knowledge gaps. However, this method has not been adopted as a standard tool surveying and monitoring reef fish and large-bodied roving predators in the Hawaiian Archipelago. While BRUVS may be capable of generating valuable information in data-deficient areas, concerns over additional biases relating to use of baited video surveys (e.g. attraction of predators, herbivore avoidance) have yet to be addressed in Hawaii. There is a need to increase the use of remote survey methods for surveying and monitoring reef fish and large-bodied roving predators and to critically assess the strengths, advantages, weaknesses, limitations and biases of BRUVS in comparison with other underwater visual census approaches. The interpretation of data collected from different methods, which have disparate biases and depth limitations, may result in very dissimilar estimates of coral reef fish populations leading to conflicting management actions.

This thesis combines several novel methodological and ecosystem-based comparisons for the Hawaiian Archipelago. Chapter 2 compares and contrasts the functional group composition of coral reef fish communities and a subset of predatory target species over a range of soak time intervals (i.e. 0 – 20, 0 – 40, and 0 – 60 minute sampling intervals) for both BRUVS and its unbaited analogue (RUVS). I also investigate the time of first arrival ('TOFA') and the time to maximum abundance ('MaxN_T'). I conclude that while shorter RUVS or BRUVS soak times of 20 minutes are sufficient to capture overall assemblage group structure and to survey resident or "fast reacting" species, longer BRUVS soak times (i.e. 60 minutes) improve herbivore assessments, and are better at capturing predatory sessile macropiscivores (eels belonging to Muraenidae and Ophichthidae) and generalist macropiscivores (large-bodied, roving sharks, jacks, and snapper), particularly targeted jack species that are considered depleted around human population centers.

In Chapter 3, I use BRUVS to compare and contrast reef fish communities between shallow water and mesophotic depths in the Main Hawaiian Islands (MHI), with continued emphases on functional groups

and fishery-targeted species, and expanded to include Hawaiian endemics and linkages between assemblage counts and environmental features. A combination of multivariate PERMANOVA, pair-wise permutational ANOVA, and Canonical Analysis of Principal Components (CAP) analyses showed that while significant community shifts were detected when transitioning from shallow water to mesophotic depths, relative abundance and species richness were highest in $\leq$ 30 m habitats. Two functional groups (mobile invertivores, generalist macropiscivores) were notable exceptions, having higher abundance and richness values in mesophotic depths. Multivariate regression trees (MRT) and distance-based linear modeling (DistLM) indicated that depth, habitat complexity, unconsolidated sediment (sand), and macroalgae act as structural reef fish assemblage drivers, with indicator species assigned to specific environmental node breaks. There was also evidence of depth-based shifts in the composition and abundance of endemic species, and mesophotic refugia for target species belonging to several functional groups (using length-based kernel density estimates). Finally, I discovered a mesophotic ground fish interface in *Halimeda* beds that are utilized by juvenile *Pristipomoides filamentosis*.

Chapter 4 focuses exclusively on reef-associated generalist macropiscivores (roving predators) from shallow to mesophotic depths, and includes BRUVS assessments from both the (populated) MHI and the (unpopulated) NWHI. Through a combination of tests (Bootstrapping, PERMANOVA, Hierarchical Clustering, SIMPER, non-parametric quantile regression splines), I found clear shifts in roving predator community composition, and differences in relative abundance between regions and depth zones. For example, I observed that there was up to an order of magnitude more jacks and five times more sharks sampled in the NWHI compared to the MHI. In addition, differences in target species length-distributions between depth zones and regions were examined using non-parametric Kolmogorov-Smirnov tests, which provided evidence for;

1.) Depth-based predator refuges around populated areas in the MHI – e.g. that target fishes tended to be larger in deeper waters. This assertion was complemented by stark differences between shallow and mesophotic predator abundances in the MHI (e.g. *Caranx ignobilis* solely encountered in mesophotic zones); and

2.) The prevalence of smaller *Carcharhinus galapagensis* and *Caranx ignobilis* in $\leq$ 30 m depths in the NWHI suggests possible body size and depth segregation, or potential avoidance of intra- or inter-specific predation pressures in deeper waters.

In Chapter 5, I investigate the scope for diver-based underwater visual censuses to properly assess the abundance of large-bodied, roving predators across the Hawaiian Archipelago. Specifically, there are recurring, long-standing concerns that (i) divers are typically limited to only a narrow part of the depth range used by these species; and (ii) acquired behavioral differences of roving predatory species – such as avoidance of divers at fished locations – seriously and substantially bias estimates of relative abundance between populated and remote locations. Here, I compared roving predator abundance estimates gathered by shallow water point-count and towed-diver surveys in $\leq$ 30 m against data collected using RUVS and BRUVS across the Hawaiian Archipelago, including comparisons among

datasets collected in shallow depths exclusively, as well as with data from RUV-BRUV spanning 0 – 100 m. The 'boot' and 'boot.ci' functions were used from the boot package in R, Version 3.3.0, with 10,000 iterations to produce adjusted 95% confidence intervals (type = "bca") for each diver census and video assessment method used. Although RUVS and BRUVS data showed significantly higher roving predator densities in the remote NWHI, they also generated substantially lower NWHI:MHI ratios than were generated from diver data – i.e. significantly decreased scales of difference. Comparative example include (but are not limited to) the snapper *Aprion virescens* (SPC NWHI:MHI ratio was 62:1, towed-diver 24:1, RUVS 5:1, BRUVS 3:1), reef sharks (SPC 142:1, towed-diver 76:1, RUVS 20:1, BRUVS 11:1), and jacks (e.g. trevallies: SPC 5:1, towed-diver 17:1, RUVS 2:1, BRUVS 2:1). Clearly, these results corroborate concerns about the limitations of data that can be readily collected by divers for those groups of fishes, and emphasizes the need to further evaluate diver-based predator estimates in order to foster effective management policies for predatory species.

In conclusion, I demonstrate that BRUVS are an appropriate alternative and/or complement to diver-based visual censuses that provide a means to gain a more holistic representation of reef fish communities and higher-level predator groups. As a relatively new approach to US coral reef fish assessment strategies, the use of BRUVS could be further expanded to include comparatively understudied mesophotic coral reefs and other associated habitats in the Hawaiian Archipelago, along with other poorly studied deep-water regions in the US Pacific Territories (Pacific Remote Islands, American Samoa, Guam and the Commonwealth of the Northern Marianas). Lastly, the extension of BRUVS surveys to other areas hosting large, sustained roving predator populations would allow for a more nuanced assessment of the plausibility of 'inverted biomass pyramids' as part of future monitoring procedures and management approaches.

Statement of Contributors

Published Chapters

Chapter 3: Asher, J., Williams, I. & Harvey, E.S. (2017). Mesophotic Depth Gradients Impact Reef Fish Assemblage Composition and Functional Group Partitioning in the Main Hawaiian Islands. *Frontiers in Marine Science* **4**, doi:10.3389/fmars.2017.00098.

Author contributions: JA, IW, and EH designed the study. JA collected the data, conceived/executed the data analyses, and wrote/edited the manuscript. All co-authors reviewed and commented on the manuscript.

Chapter 4: Asher, J., Williams, I. D., & Harvey, E. S. (2017). An Assessment of Mobile Predator Populations along Shallow and Mesophotic Depth Gradients in the Hawaiian Archipelago. *Scientific Reports*, 7(1), 3905.

Author contributions: JA, IW, and EH designed the study. JA collected the data, conceived/executed the data analyses, and wrote/edited the manuscript. All co-authors reviewed and commented on the manuscript.

Chapters in Review

Chapter 2: Currently in review with *Methods in Ecology and Evolution*: Asher, J., Williams, I. D., & Harvey, E. S. To Bait, or Not to Bait. A Comparison of Underwater Video Survey Techniques over Increased Sampling Durations in the Hawaiian Archipelago

Author contributions: JA, IW, and EH designed the study. JA collected the data, conceived/executed the data analyses, and wrote/edited the manuscript. All co-authors reviewed and commented on the manuscript.

Chapters in Preparation

The following are currently in review with the NOAA Fisheries, Pacific Islands Fisheries Science Center Editorial Division in preparation for journal submission:

Chapter 5: Is seeing believing? Diver-based and videographic censuses reveal inconsistencies in roving predator estimates between regions

Author contributions: JA, IW, and EH designed the study. JA collected the data, conceived/executed the data analyses, and wrote/edited the manuscript. All co-authors reviewed and commented on the manuscript.

Abbreviations

ACL	Annual Catch Limit
AUV	Autonomous Underwater Vehicle
BotCam	Bottom Camera Bait Stations
BRUVS (Stereo-BRUVs)	Baited remote underwater stereo-video systems
CCR	Closed-circuit rebreather
CREP	Coral Reef Ecosystem Program
CPUE	Catch per unit effort
EBFM	Ecosystem-Based Fisheries Management
FBSAB	Fishery Biology Stock Assessment Branch
MCE	Mesophotic Coral Ecosystem
MHI	Main Hawaiian Islands
MOUSS	Modular Optical Underwater Survey Systems
MSA	Magnuson-Stevens Fishery Conservation and Management Act
NOAA	National Oceanic and Atmospheric Administration
NWHI	Northwestern Hawaiian Islands
PIFSC	Pacific Islands Fisheries Science Center
PMNM	Papahānaumokuākea Marine National Monument
RAMP	Reef Assessment and Monitoring Program
ROV	Remotely Operated Vehicle
RUVS (Stereo-RUVs)	(Unbaited) remote underwater stereo-video systems
SCUBA	Self-Contained Underwater Breathing Apparatus (open-circuit)
SPC	Stationary Point Count (underwater visual surveys)
TOAD	Towed Optical Assessment Device
UVC	Underwater Visual Census
WPRFMC SSC	Western Pacific Fishery Management Council, Scientific Statistical Committee

Acknowledgments

I didn't grow up particularly close to any body of water, outside of the slow meandering of the Potomac River inside of Washington, DC. Thankfully, my parents had the foresight to take weekend trips to nearby golf-course ponds to fish for blue gills when I was old enough to hold a rod and reel, followed by forays to the Chesapeake Bay and Assateague Island in Maryland and Virginia when I got older. Mucking about in tidal swamps, fossil hunting for shark teeth at Calvert Cliffs, surf casting in the winter, and hunting for crayfish during the summer remain entrenched as early memories. But it was catching sight of my first hammerhead shark cruising off a pier in North Carolina that I suspected I'd be making a life tied to these remembrances. So: to mom and dad, thanks for planting the original seeds. It changed my life for the better.

Steve Lindfield deserves a particular mention, as working with him during underwater video censuses around Guam and the Marianas in 2010 provided the initial spark for returning to graduate school. I was comfortably nested in a growing and productive career after seven years with NOAA; however, your work inspired me to take a leap of faith, returning to one of the core tenets of marine science research: to always be curious, and to never stop challenging yourself.

In terms of the work assigned to this PhD thesis, my sincerest of thanks go to my advisors. Euan Harvey and Ivor Williams, your guidance during the course of developing and producing the outputs of this research were invaluable. You were there during numerous professional and personal challenges in and outside of traditional work spaces, balancing reassurance and support with constructive criticism, and putting the stresses assigned to pursuing a mid-40's degree in appropriate perspectives and context. You forever have my gratitude.

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Finally, a bit of advice for those wanting to pursue a PhD. Doing this mid-life is a great deal harder than originally expected. For anyone reading this: if you have questions in need of answering through a dissertation or thesis? Start younger than I did!

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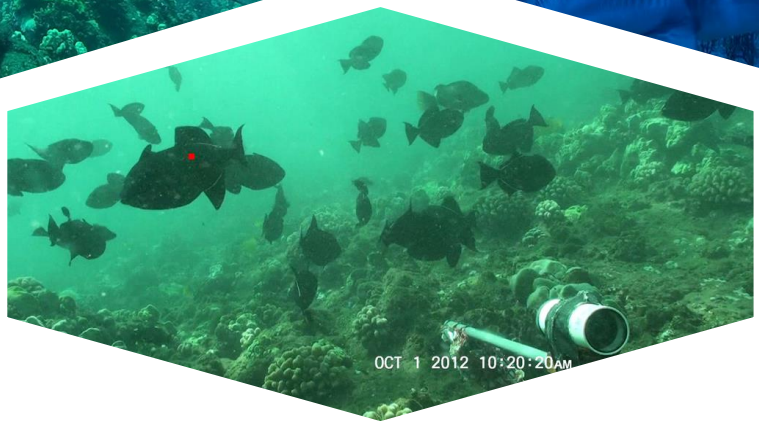
Chapter 1 – General Introduction



Background and rationale: incentives for thesis research

The basis for this work came as a result of several policy, methodological, and ecological drivers. In particular, US Fishery Management Councils were tasked to develop management plans, set catch limits, and develop stock recovery plans (where applicable) for local fisheries resources. In Hawaii, the management and implementation of catch limits for coral reef fishes was inhibited by two limitations. The first was the methodological constraints assigned to the types of information collected, with managers remaining dependent on diver-based and commercial catch data. The second was an absence of information beyond 30 m depths. Additional details are expanded upon in: "Policy drivers", "Underwater sampling practices in Hawaii", and "Knowledge gaps associated with mesophotic coral ecosystem reef fishes".

Policy drivers

Fishery stock assessments in the United States have historically relied on fishery-dependent and extractive data, i.e. commercial or recreational catch records. For the first time, the revised Magnuson-Stevens Fishery Conservation and Management Act (Congress 1996; Conservation 2007) required the Western Pacific Fishery Management Council (WPRFMC) to specify annual catch limits (ACLs[1]) for a much wider range of federally managed fisheries in Hawaii and US Pacific Territories than before. These included many inshore and coral reef associated species with typically poor or limited fishery dependent data, especially for waters deeper than 30 m, which represents the maximum feasible working depth for underwater visual surveys by divers on open-circuit SCUBA. As many coral reef fishes (including the numeric majority of some species) are found in deeper waters (Lindfield et al. 2014; Lindfield et al. 2016), there was a clear data gap that could not readily be filled by the existing survey programs (NOAA Coral Program 2014). In addition, while catch statistics were accessible in the Main Hawaiian Islands (MHI), fishery dependent data was not available for the large, remote portions of the Hawaiian Archipelago where fishing is prohibited (e.g. Northwestern Hawaiian Islands (NWHI)/Hawaii's Papahānaumokuākea Marine National Monument). Given the lack of information necessary to make management or regulatory decisions on coral reef fish stocks (Donovan et al. 2011) there was increased interest in developing supplementary fishery-independent approaches capable of sampling in waters deeper than are generally surveyed by divers on open-circuit SCUBA.

Underwater sampling practices in Hawaii

Diver-based censuses

In the absence of robust fishery dependent information (e.g. catch per unit effort [CPUE]), diver stationary point count (SPC) and towed-diver visual surveys (Bohnsack et al. 1986; Richards et al. 2011; Ayotte et al. 2015b) have been increasingly used for assessment of shallow-water reef fishes in the

[1] ACL is defined as defined by the MSA is "the level of annual catch of a stock or stock complex that serves as the basis for invoking accountability measures. Accountability measures (AMs) are defined as "management controls that prevent ACLs or sector-ACLs from being exceeded where possible and correct or mitigate overages if they occur."

Pacific. Since around 2011, coral reef scientists at the NOAA Fisheries, Pacific Islands Fisheries Science Center (PIFSC) Coral Reef Ecosystem Program (CREP) and Fisheries Biology and Stock Assessment Branch (FBSAB) incorporated diver-based, visual survey data, combined with commercial catch data (MHI only), to generate stock assessments for a number of coral reef fishes, tying together length-based stock indicators of mortality rates and modeling survival estimates (Ault et al. 2005; Gedamke and Hoenig 2006; Nadon et al. 2015; Nadon 2017).

Strengths of diver SPCs and towed-diver survey programs (NOAA Coral Program 2014) include consistent methodology and survey design, along with the use of frequently calibrated/trained and relatively fixed number of long-term personnel to reduce inter- and intra-observer related biases. In addition, stratified randomized sampling across $\leq$ 30m hard bottom means that data are credibly representative of a large portion of coral reef habitat. However, as with any survey methods, there are potential weaknesses. These include, but are not limited to:

1.) Possible behavioral differences of target fishes in the presence of divers (Chapman 1974; Chapman 1976; Chapman 1986; Kulbicki 1998; Cole et al. 2007; Watson and Harvey 2007; Dickens et al. 2011). These could range from generalized behavioral avoidance of divers where there is substantial fishing, to diver attraction in remote or well protected locations, particularly of large bodied roving predators such as sharks and jacks (Cole et al. 2007; Richards et al. 2011; Januchowski-Hartley et al. 2012; Lindfield et al. 2014; Gray et al. 2016);

2.) Safety considerations associated with SCUBA diving limit the feasibility of survey operations beyond ~30 m, whereas coral reef fish species can be highly abundant in deeper habitats down to 100 m or more (Fitzpatrick 2012; Fukunaga et al. 2016; Lindfield et al. 2016). As a consequence, there is uncertainty about the extent to which shallow water data are representative of species' status across their entire depth distributions; and

3.) In cases where diver information is insufficient and catch data is used, data only comes from exploited locations and depth ranges , and therefore may not properly represent the status of the wider population (Nadon et al. 2015; Nadon 2017).

Underwater video surveys

Since 2005, the NOAA PIFSC CREP and FBSAB have used fishery-independent, alternative methods to characterize bottom fishery resources between 75 – 250 m (Merritt 2005; Merritt et al. 2011). Bottom Camera Bait Stations (BotCam) and Modular Optical Underwater Survey Systems (MOUSS), autonomous underwater and remotely operated vehicles (AUVs and ROVs respectively), and towed-cameras, e.g. towed optical assessment devices (TOAD), showed promise as fishery-independent methods for sampling deep-water species and in some cases, coral reef fish assemblages beyond 30 m (Ellis and Demartini 1995; Singh et al. 2004; Rooney et al. 2010; Misa et al. 2013; Moore et al. 2013; Richards et al. 2016). However, these techniques were a.) Not optimized for coral reef fish sampling, being primarily engineered for deeper environments (i.e. BotCam, MOUSS) and/or for benthic assessments (AUV, ROV,

TOAD); and b.) Remain vulnerable to environmental hazards (e.g. shallow water, waves, and currents) in shallow depths ≤ 30 m, either by dragging or directly impacting cameras suspended over the bottom (MOUSS/BotCam), increased potential for instrument drift or signal loss (AUV), or amplified entanglement risks to tethered equipment (ROV, TOAD). Finally, large gear footprints, small equipment inventories, and high per-unit costs act as major impediments to use of these technologies at greater spatial scales.

Baited remote underwater stereo-video systems (Stereo-BRUVs, herein denoted as 'BRUVS') represents an alternative, fisheries-independent approach which was utilized in the majority of work presented in this thesis. They are functionally similar to existing BotCam and MOUSS technologies; however, BRUVS are smaller and easier to deploy, and can be used in both shallow and deep-water coral reef environments. BRUVS have been widely used to collect data on fish assemblages, providing a repeatable, low cost, and non-extractive method for assessing tropical and temperate fish communities across depth and habitat strata (Harvey et al. 2001a, 2001b, 2002a; Cappo et al. 2004; Watson et al. 2005). Finally, they have been used to provide information within an Ecosystem-Based Fishery Management (EBFM) framework in Western Australia, which governs fishery-related resources within the context of whole-ecosystem and bioregional boundary administration (Fletcher et al. 2011; Smale et al. 2011).

Important considerations for using BRUVS include unknown bait attraction effects, as plume areas are dependent on currents and wave action and are challenging to quantify. Other potential sources of variability include bathymetry/habitat, bait type, varying responses to bait between species, density of fish that can be observed within the visible sampling areas in front of cameras, and the potential for competitive exclusion of some species by others (Willis and Babcock 2000a; Bailey and Priede 2002; Stobart et al. 2007; Dorman et al. 2012; Ghazilou et al. 2016; Walsh et al. 2016).

Unbaited stereo-video systems (Stereo-RUVs, herein denoted as 'RUVS') are similar to BRUVS, BotCam and MOUSS, albeit RUVS collect video data without the presence of bait (Myers et al. 2016). This approach reduces concerns associated with baiting, i.e. attracting fishes outside of visible sampling areas or from adjacent habitats, resulting in biased estimates of abundance, biomass, and/or species richness (Bradley et al. 2016; Sheaves et al. 2016). Studies requiring relative density estimates (used in some stock assessments) may see RUVS as a preferred alternative, at least until accurate bait plume modeling becomes readily available (Priede and Merrett 1996; Watson et al. 2005). Finally, RUVS may be better suited for specialist research projects where baiting would confound results interpretation, e.g. monitoring predator encounters at aquaculture sites (Loiseau et al. 2016). Conversely, RUVS abundance estimates are typically subject to higher spatial and temporal variability than BRUV, as a byproduct of lower encounter rates and potentially greater impacts from small-medium scale differences in oceanography or habitat that are not dampened by the mitigating effects of bait attractants (Watson et al. 2005).

Results from baited and unbaited video station comparisons vary and are likely region-dependent (Langlois 2011); however, the use of BRUVS has generally been favored over RUVS. Contrary to some of

concerns highlighted above, there is evidence that BRUVS are capable of sampling as many or more herbivorous species and individuals in temperate and tropical habitats than RUVS, with apparent attraction of non-carnivorous species attributed to increased activity around video stations rather than to the bait itself (Watson et al. 2005; Cappo et al. 2006a; Harvey et al. 2007). Similarly, BRUVS may be better suited to detect spatial and temporal changes because of lower variances, whereas RUVS require more samples to produce data with comparable statistical power (Watson et al. 2005; Harvey et al. 2007).

Despite limitations associated with both RUV and BRUV, underwater video surveys were deemed to have potential for generating additional data necessary for fishery-independent assessments of Hawaiian coral reef fish stocks, providing information to inform the development of robust reef fish ACLs, and generating highly accurate size data that can be measured against diver-based data streams. In particular, underwater video surveys appear well-positioned to address questions regarding coral reef fish population dynamics in deeper, poorly-assessed mesophotic coral reef ecosystems.

Knowledge gaps associated with mesophotic coral reef ecosystem fishes

The majority of coral reef research to date has focused on ecosystems between 0 – 30 m (Friedlander and DeMartini 2002; Nadon et al. 2012; Heenan 2014; Jouffray et al. 2015; Williams et al. 2015). However, mesophotic coral ecosystems (MCEs), which are found in 30 – 150+ meter depths, contain much larger area of habitat than their shallower counterparts (Ginsburg 2007; Hinderstein et al. 2010; Kahng et al. 2010; Kahng et al. 2014; Pyle et al. 2016). While MCEs have garnered increased attention over the past decade, they remain comparatively understudied. In addition, benthic and geomorphological components – rather than fish assemblages - have been the principal areas for research (Bak et al. 2005; Kahng and Kelley 2007; Bare et al. 2010; Rooney et al. 2010). As such, most MCEs in the Pacific region remain relatively unexplored or infrequently sampled, with only a few studies dedicated to examining MCE fishes (Bridge et al. 2012; Kahng et al. 2014; Wagner et al. 2014; Pyle et al. 2016)

The Hawaiian Archipelago represents something of an exception in comparison with other parts of the Pacific, as there has been a combination of TOAD surveys, closed-circuit rebreather (CCR) and technical dive assessments, as well as submersible censuses focused on extensive MCE research between the MHI of Maui, Lanai, and Molokai (Maui-Nui). Noteworthy discoveries include evidence of depth zonation among Maui-Nui *scleractinian* corals between shallower (30 – 50 m) and deeper MCEs (50 – 80 m), paralleling patterns seen in mesophotic reefs in other parts of the world, albeit with considerable regional and geological variation (Rooney et al. 2010; Pinheiro et al. 2016; Englebert et al. 2017). Additional depth zone breaks have been described for communities of octocorals, sponges, brachyuran crabs, and algae, both in the MHI and elsewhere (Bridge et al. 2011; Bridge et al. 2012; Spalding 2012; Hurley et al. 2016)

However, patterns in mesophotic depth zonation with respect to reef fish communities, functional

group partitioning, and differences in food web structure are less clear in the MHI, and have not been extensively addressed in comparison with other locations (Bradley et al. 2015; Pyle et al. 2016). The majority of Hawaii MCE research to date has centered on exploration, surveys of specific taxa or target species, spatially focused investigations, e.g. mesophotic black coral (*Antipathes*) reef fish communities or artificial reefs, or linkages between mesophotic reef fish groupings and environmental drivers at localized, small scales (Grigg 1965; Brock and Chamberlain 1968; Moffitt et al. 1989; Grigg 2004; Boland and Parrish 2005; Kahng and Grigg 2005; Kane 2016). While there are a number of studies which highlight changes in reef fish assemblage structure, including functional group and endemic-level shifts, along shallow to mesophotic gradients in the NWHI, there has been little such research in the MHI (Kosaki 2011; Kane et al. 2014; Fukunaga et al. 2016; Kosaki et al. 2016).

Depth refuges

MCEs are physically and biologically linked to nearby shallower habitats, and may act as depth refuges for shallow water coral reef taxa (Riegl and Piller 2003; Hinderstein et al. 2010). Modeling of coral larvae movements indicates that some MCEs may be less prone to disturbance events, with vertical broadcasting and dispersal from MCE habitats being a source of larvae to shallow reefs following environmental or anthropogenic impacts, and thus providing protection from disturbances (Glynn 1996; Ginsburg 2007; Lesser et al. 2009; Bare et al. 2010; Bongaerts et al. 2010; Slattery et al. 2011; Holstein et al. 2015; Pyle et al. 2016). However, it is important to note that not all MCE communities are protected from environmental disruption, with sedimentation impacting reefs proximal to river outflow or dredge disposal sites, and some groups (e.g. foliose corals) being as vulnerable to typhoon damage in mesophotic depths as their shallower counterparts (White et al. 2013; Appeldoorn et al. 2016).

Similarly, coral reef *depth generalist* fishes, which are found in both shallow and mesopotic ecosystems, have been documented around Maui-Nu and from aquarium collectors, with some species (e.g. *Chromis verater*) exhibiting genetic homogeneity between shallow vs. mesophotic populations (Moffitt et al. 1989; Boland and Parrish 2005; Lumsden et al. 2007; Boland 2011; Tenggardjaja et al. 2014; Bridge et al. 2016; Pyle et al. 2016). Deeper coral reefs in the MHI may also harbor commercially or recreationally targeted generalists, including those that are threatened either locally or globally (Feitoza et al. 2005; Bejarano et al. 2014; Lindfield et al. 2014; Lindfield et al. 2016).

Conversely, MCEs are likely not capable of providing broad brush protection to all taxa, being limited to species with broad reseeding or vertical movement capabilities (Bongaerts et al. 2017). As such, both shallow and mesophotic reefs in the MHI also host *depth specialists*, those being fish species that are constrained to specific depth ranges, and hence may not be have scope for depth refuge effects (Kahng et al. 2014; Laverick et al. 2016). Lastly, in the case of coral reef fish stock assessments generated from diver censuses and commercial data as previously described, the full extent of species' ranges deeper than 30 m remains largely unidentified (Nadon et al. 2015; Nadon 2017).

The decline of large-bodied, coral reef roving predators

There is evidence that appropriate management can promote the recovery of overfished coastal shark species, given controlled monitoring of populations and enforcement of fishing guidelines (Peterson et al. 2017). However, there is a large body of research that highlights substantial and widespread declines of both pelagic and inshore shark species, with estimates of 90 – 97% historic reductions in the most heavily impacted areas, and overfishing (including bycatch) cited as the source of localized shark extinctions, even in remote areas once host to abundant populations (Sminkey and Musick 1995; McElroy et al. 2006; Myers et al. 2007; Luiz and Edwards 2011; McCauley et al. 2012; Dulvy et al. 2014; Francini 2014).

Populations of large-bodied sharks, jacks, and snapper in the MHI are similarly believed to be depleted in comparison with the NWHI, with supporting evidence primarily coming from diver-based underwater visual censuses on open-circuit SCUBA in $\leq$ 30 m (Friedlander and DeMartini 2002; Holzwarth et al. 2006; Nadon et al. 2012). As for other fish groups – in fact potentially more so, given their wide depth ranges – mesophotic coral ecosystems may act as depth-refuges and population reservoirs for roving large-bodied predators, with the capacity to provide additional foraging resources, i.e. prey-bases (Friedlander and Dalzell 2004; Papastamatiou et al. 2015; Lindfield et al. 2016). To date, while coral reef associated sharks (e.g. *Carcharhinus galapagensis, Triaenodon obesus, Galeocerdo cuvier*) and jacks (e.g. *Caranx ignobilis*, *Caranx melampygus*) are known to reside in mesophotic depths in Hawaii and elsewhere, their population distributions outside of shallow water depths remain largely unknown, representing a considerable informational gap (Wetherbee et al. 1996; Meyer et al. 2007a; Meyer et al. 2009a; Meyer et al. 2010b; Nakamura et al. 2011; Wagner et al. 2014; Papastamatiou et al. 2015).

Research questions

It is clear that the use of alternative approaches, outside of diver or catch-based surveys, are required to address knowledge gaps in Hawaii, particularly with respect to mesophotic reefs in the MHI and predator populations across the Hawaiian Archipelago in order to better serve management. As such, the overall scientific objective of this thesis was to improve our understanding of shallow to MCE reef fish assemblages for the purposes of enhancing stock assessments and ecosystem based management.

As a result, research in this thesis proceeded along two tracks: 1.) Methodological analysis comparing fishery-independent, video and diver-based survey methods; and 2.) ecosystem research, with a particular focus on how reef fish assemblages, functional groups, and target species are structured along gradients from shallow water (0 – 30 m) to mesophotic (30 – 100 m) habitats.

Specifically, I address the following core questions:

- How do Hawaiian coral reef fish assemblages in surveys vary between RUVS and BRUVS, and what are the effects of different soak time intervals?

- How are reef fish communities, including component functional groups, endemics, and fishery target species distributed along gradients from shallow to mesophotic depths in the MHI? What evidence is there of refuge effects? Aside from depth, what environmental drivers influencing assemblage structure among those habitats?
- How does roving predator abundance and community composition vary along depth gradients, and in particular how – if at all – does that differ between the inhabited islands (MHI) and the remote uninhabited islands (NWHI). Are regional differences evident in shallow water, similar for mesophotic assemblages, and are there refuge effects for these predatory species in mesophotic habitats in the MHI?
- How does changing the survey methodology, including the sampled depth range, affect estimates of relative abundance of roving predators between MHI and NWHI? Specifically, to what extent do results from video-based surveys across relatively wide depth ranges align with regional patterns documented in existing studies, that have so far been based on diver surveys in ≤ 30m (Friedlander and DeMartini 2002; Nadon et al. 2012; Williams et al. 2015)?

A simple thesis work flow is visualized in Figure 1.1.

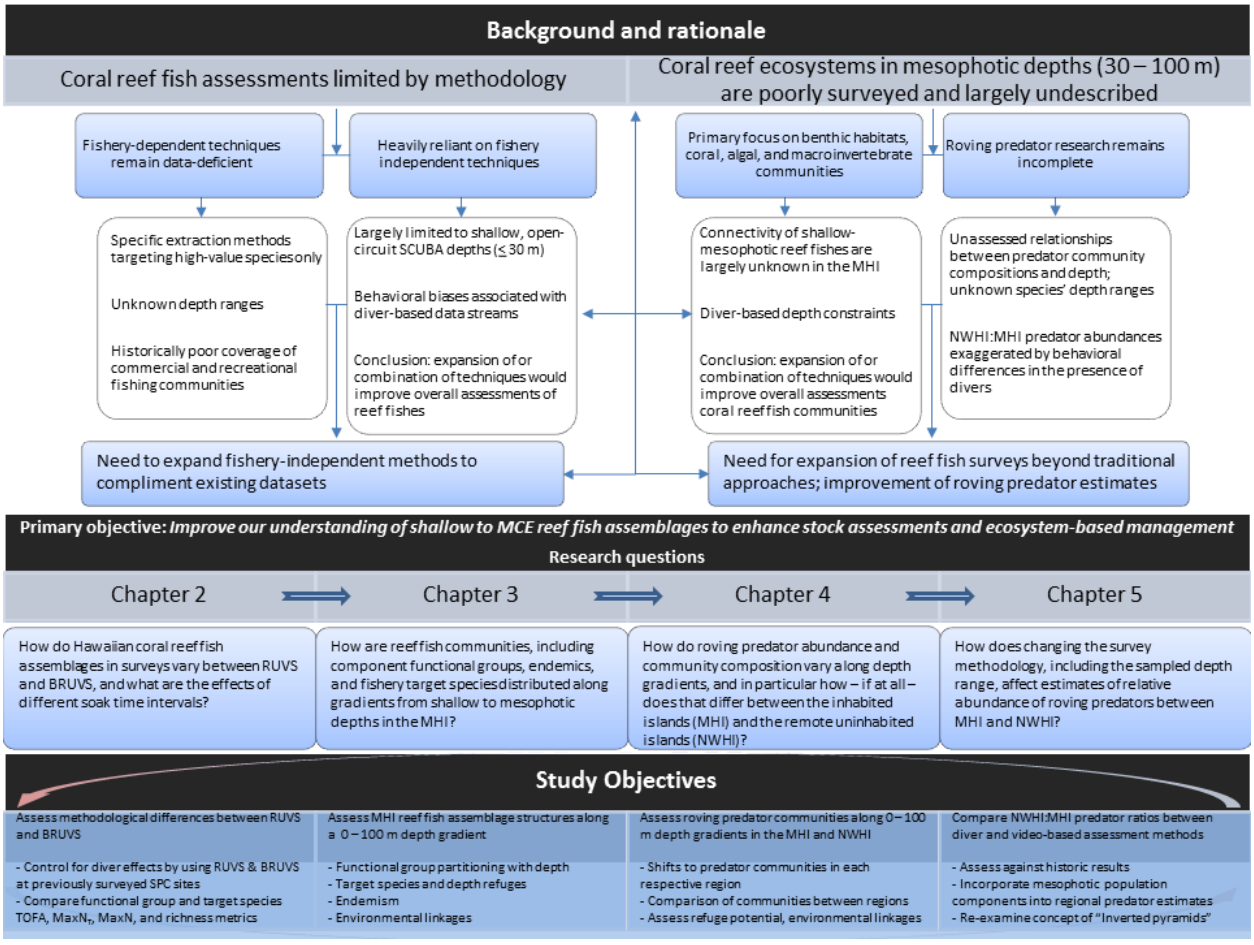


Figure 1.1. Flow diagram outlining thesis background, rationale and structure.

Study area

All research presented in the following chapters was conducted in the Hawaiian Archipelago. The Archipelago is geographically isolated, stretching a total distance of over 2,400 kilometers, and is by convention split into two separate sub-regions. The MHI consist of eight major, geologically young, high volcanic islands and with the exception of Kahoolawe, host relatively high human population densities, with over 70% of the state residing on Oahu and over 7 million visitors visiting the islands each year (Friedlander et al. 2008). In terms of direct economic importance, coral reefs around the MHI are estimated to provide upwards of $360 million annual revenue through fisheries and tourism activities, with an overall value estimated between $10 - 35 billion (Cesar and Van Beukering 2004; Friedlander et al. 2008; Brander 2013). However, MHI coral reefs, particularly those in shallow water, have been impacted by stressors including habitat destruction, nutrient runoff, overfishing, and invasive species introductions as a result of human influences (Grigg 1994, 2004; Friedlander et al. 2008; Stock et al. 2014; Yoshioka et al. 2016; Bierwagen et al. 2017).

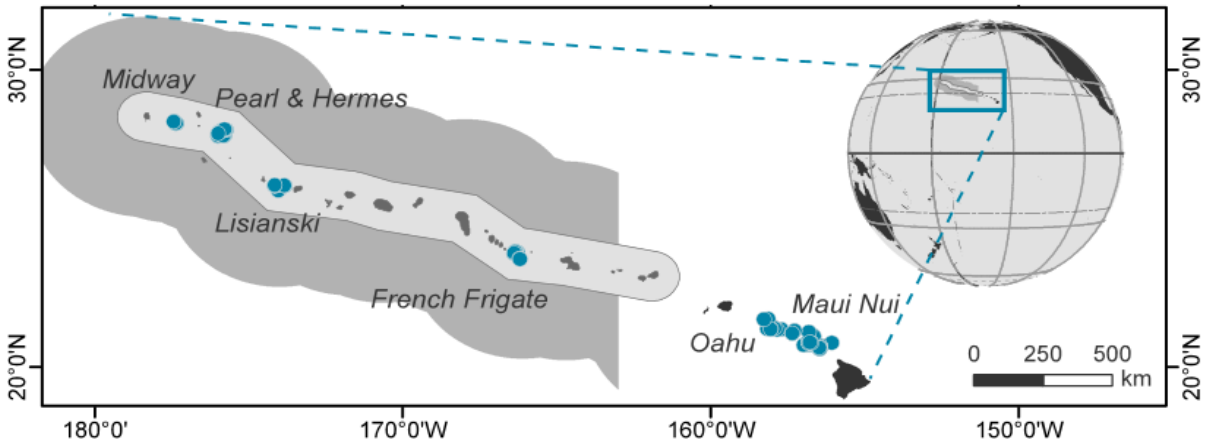


Figure 1.2. Map of the Hawaiian Archipelago, delineated by the populated Main Hawaiian Islands (MHI; lower right) and remote Northwestern Hawaiian Islands (NWHI; middle and upper left). The light-grey shading around the NWHI illustrates the protected area with the establishment of the Papahānaumokuākea Marine National Monument, while the dark-grey shading delineates the protection area expansion. Blue circles indicate RUVS and BRUVS deployment locations in the MHI (Oahu, Maui-Nui [Maui, Molokai, Lanai]), and the NWHI (French Frigate Shoals, Lisianski, Pearl and Hermes, Midway).

In contrast, the remote NWHI consist of a series of older, low-lying atolls, and smaller islands or islets that are difficult to access without long-range vessel capabilities. Historically, fishing activities within the NWHI were largely limited to bottom fish and lobster; however, the State of Hawaii established the NWHI Marine Refuge in 2005, effectively closing the majority of nearshore areas to fishing (except for Midway Atoll). The NWHI was further protected with the establishment of the Northwestern Hawaiian Islands Marine National Monument Presidential Proclamation 8031 in 2006 (Bush 2006), which was renamed as the Papahānaumokuākea Marine National Monument (PMNM) in 2007. The PMNM was expanded further in 2016, with access limited to scientific researchers and Native Hawaiian cultural practitioners. Finally, the NWHI is removed from most direct anthropogenic impacts present the MHI; however, there may still be impacts from point-source pollution from uncharacterized landfills, i.e. from decommissioned Navy installations and LORAN stations, and the effects of annual derelict fishing gear accumulations, albeit in highly localized areas (Friedlander et al. 2005; Dameron et al. 2007; Friedlander

et al. 2009).

Aims and thesis structure

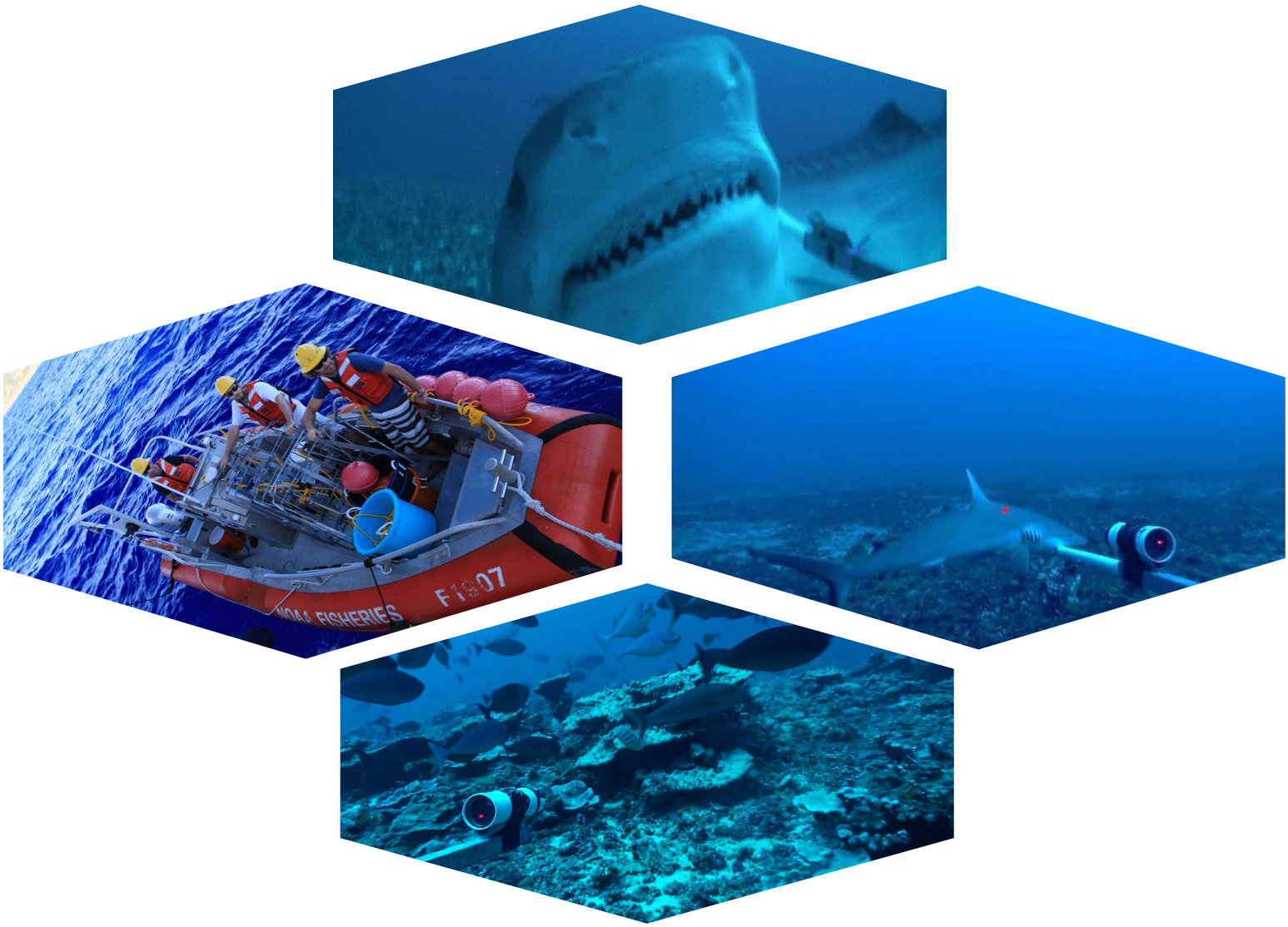
In order to address the uncertainties associated with underwater video sampling in the Hawaiian Archipelago, I focus on the utility and trade-offs between RUVS and BRUVS through a series of comparative assessments in Chapter 2, following a similar approach to that used by Misa et al. (2016), with the goal of identifying a preferred survey approach for subsequent ecology-focused chapters in this thesis. In addition to comparing baited and unbaited sampling, I examined optimum soak time duration over cumulative, 20-minute intervals (0-20, 0-40, 0-60 minutes). This approach was also used to determine if patterns reported by other RUVS versus BRUVS studies were emulated at the functional group level, and added an additional focus on several roving predator species of interest (sharks, jacks, and snapper). Prior to this thesis, no comparison studies between RUVS and BRUVS had been completed in Hawaii.

In Chapter 3, I explore coral reef fish assemblages across shallow and mesophotic coral reefs and associated benthic habitats, from 0 – 100 m in the MHI using BRUVS. Given the data-gaps in MHI reef fish populations in mesophotic depths, I pay particular attention to functional group partitioning across the shallow to mesophotic depth gradient described above, with an additional focus on several targeted species that are the focus of recent stock assessment publications. In Chapter 4, I focus wholly on large-bodied, roving predators, extending the shallow-mesophotic community work as described for the MHI in the previous chapter, and expanding that approach to include the NWHI. While several published works have previously compared shark, jack, and snapper populations between the MHI and NWHI, those have been primarily based on diver-based surveys in <30 m, and thus mesophotic predator assemblages had not previously been accounted for.

Lastly, my final research emphasis in Chapter 5 compares the outcomes of different survey and depth range approaches. Here, I expand upon the regional, roving predator comparisons in the MHI and NWHI, including visual abundance estimates obtained from unbaited and baited camera surveys, along with data collected from diver SPC and towed-diver surveys. Using a broad suite of methods to assess predator abundances between regions, I consider the ecological implications resulting from scales of differences obtained from each survey type, and tie-in the historic context of previous predator research outcomes.

Given thesis structure, there is some repetition between chapters. All chapters were generated with the intention of present or future publication, and with the assistance of co-authors. However, I performed all fieldwork, principal data analyses, and retain primary authorship for the writing presented in the body of this work. Chapter 6 is a discussion of thesis outcomes and future research direction. References for all chapters are cited at the end of the thesis.

Chapter 2 – To bait, or not to bait. A comparison of underwater video survey techniques over increased sampling durations in the Hawaiian Archipelago



Abstract

Baited remote underwater video sampling is widely used to provide conservative estimates of fish abundance, biomass, and richness across tropical, sub-tropical, and temperate ecosystems. While several studies have examined the effects of different soak times for baited sampling, we extend that work by using different soak time intervals for both unbaited and baited sampling surveys of coral reef fishes in the Hawaiian Archipelago. Specifically, we investigated the arrival times, species richness and relative abundance metrics, and the power to detect differences for reef fish assemblages, functional groups, and for a subset of targeted and/or vulnerable predatory species for a range of soak time durations at both unbaited and baited camera stations. Both methods sampled similar overall assemblages and major functional groups in as little as 20 minutes, but with arrival and maximum abundance rates (within one standard deviation) occurring within 40 and 45 minutes respectively. However, baited soak times of 60-minutes were considerably more powerful for sessile macropiscivores and generalist macropiscivores. We conclude that while the use of either 20-minute baited or unbaited sampling designs may be sufficient to gauge general reef fish assemblage structure and quantify resident locally abundant species, 60-minute baited surveys are better at capturing predatory species, particularly in high-fishing pressure locations where roving predators are likely to be depleted.

Introduction

Remote underwater video sampling has become commonly utilized in marine research, ranging from demersal coral reef fish assemblage and apex predator studies to pelagic and bottom fish assessments (Cappo et al. 2004; Merritt 2005; Merritt et al. 2011; Espinoza et al. 2014; Santana-Garcon et al. 2014; Richards et al. 2016). Baited remote underwater stereo-video (stereo-BRUVs; herein denoted as 'BRUVS') represents one non-destructive method used in a variety of benthic environments including refuges and marine protected areas (Cappo et al. 2003; Willis et al. 2003; Mclean et al. 2011; Goetze et al. 2015), with the ability to access depths that are beyond the feasible limits of underwater visual censuses (UVC) on open-circuit SCUBA (Merritt et al. 2011; Harvey et al. 2012b; Lindfield et al. 2014; Lindfield et al. 2016). Additional benefits of using BRUVS include the generation of permanent video archives and the capacity to derive reliable relative abundance, richness, and length-based frequency metrics for demersal reef fish assemblages and commercially valuable species, along with top-level carnivores and roving predators (Cappo et al. 2003; Watson et al. 2010; Lowry et al. 2011; Wraith et al. 2013; Rizzari et al. 2014; Bornt et al. 2015).

However, the use of bait as an attractant raises concerns over potential biases, which include the alteration of fish behaviors, inflation of density estimates due to fish being drawn from outside visible sampling areas, competitive exclusion, and/or preferential sampling of predator and scavenger populations with commensurate reductions in herbivorous, omnivorous, or other functional groups (Harvey et al. 2007; Colton and Swearer 2010). Several studies have compared BRUVS against other approaches, e.g. traps and trawling, diver-based UVC, and diver operated video in an attempt to quantify methodological biases associated with those different sampling methods (Willis et al. 2000b;

Watson et al. 2005; Harvey et al. 2012b; Rizzari et al. 2014; Goetze et al. 2015). However, only a few have directly explored the differences between unbaited and baited remote underwater stereo-video stations (stereo-RUVs; herein denoted as 'RUVS' and stereo-BRUVs; herein denoted as 'BRUVS'), and none to date have been comparative assessments of coral reef fishes in the Hawaiian Archipelago (Watson et al. 2005; Harvey et al. 2007; Bernard and Götz 2012; Ebner and Morgan 2013).

In the Hawaiian Archipelago, RUVS represent one possible alternative to BRUVS, removing uncertainties over baiting effects and associated behavioral influences, along with challenges posed by variable plume quantification and defining areas of attraction (Bailey and Priede 2002; Cappo et al. 2003; Cappo et al. 2004; Heagney et al. 2007; Stobart et al. 2007; Colton and Swearer 2010; Rizzari et al. 2014). However, the potential benefits from elimination of baiting effects may be undermined by reduced encounter rates in unbaited surveys (Watson et al. 2005; Bernard and Götz 2012). As a result, a greater number of RUVS samples are generally required to achieve comparable statistical power and sampling precision when compared with BRUVS (Cappo et al. 2003; Watson et al. 2005; Harvey et al. 2007; Bernard and Götz 2012).

Previous studies utilizing BRUVS have also varied in sampling duration (hereafter 'soak time'), largely as a byproduct of ecosystem and research focus (Gladstone et al. 2012). For example, BRUVs with $\leq$ 20 minute soak times have been recommended for temperate reef fish and tropical bottom fish, as a result of benefits associated with limiting bait plume dispersion distance, lowered costs associated from shorter video annotation times, and/or generated from species accumulation rates (Gledhill 2001; Watson et al. 2005; Stobart et al. 2007; Misa 2012; Campbell et al. 2015; Misa et al. 2016). However, other soak time recommendations range widely, from 25 – 36 minutes for the collection of carnivorous reef fish densities and biodiversity assessments of lagoonal areas or rocky reefs (Willis and Babcock 2000a; Cappo et al. 2004; Watson et al. 2007; Langlois et al. 2010; Bernard and Götz 2012; Birt 2012; Harasti et al. 2015), to upwards of 48 – 60 minutes for collecting data on other fish communities, target groups, or collective species of interest (Watson et al. 2005; Watson et al. 2007; Bernard and Götz 2012; Birt 2012).

To assess the effects of using bait and how sampling efficiency varied with soak time, we examined the ability of RUVS and BRUVS to discriminate Hawaiian coral reef fish species richness and functional-level relative abundances among sites in the Main Hawaiian Islands (MHI) following the approach used by Harvey et al. (2007) and Misa et al. (2016). In addition, we focused on the ability of RUVS and BRUVS to discriminate large-bodied roving predator populations (e.g. sharks, jacks) between areas of relative scarcity, i.e. the MHI, and those where they are abundant, i.e. Northwestern Hawaiian Islands (NWHI) (Friedlander and DeMartini 2002; Holzwarth et al. 2006; Nadon et al. 2012). We hypothesized that a) species richness and relative abundance estimates would be higher with BRUVS compared to RUVS; b) species richness and abundance of carnivorous fishes would be higher with BRUVS compared to RUVS; c) BRUVS would generate lower variances (and therefore higher power to detect assemblage, functional group, and species-specific differences in abundance), in comparison with RUVS; and d) soak times of 20 minutes would be able to effectively sample site-associated and more common species groups, albeit at lower sampling power. However, longer soak times would be required to document uncommon or

patchily-distributed species (e.g. sharks and jacks in the MHI).

Methods

Survey Areas

All BRUV and RUV surveys were conducted in the Hawaiian Archipelago (Figure 2.1). The populated MHI are composed of eight main islands covering nearly 550 km between Hawaii (Big Island; 19°43' N, 155°05'W) and Niihau (21°54'N 160°10'W). Sampling efforts occurred between September – October 2013 around the islands of Oahu, Maui, Molokai and Lanai, with additional Oahu sampling completed in November 2014.

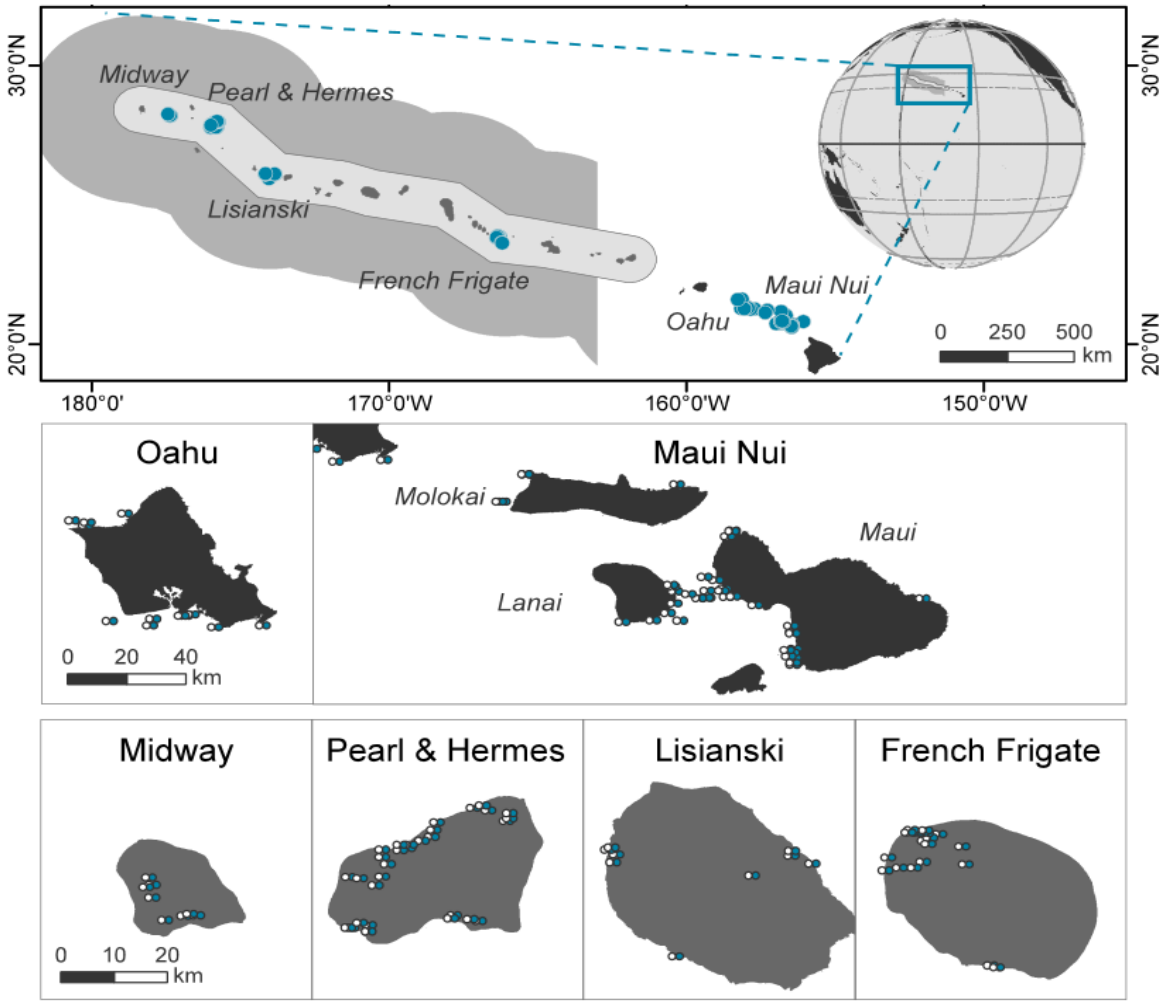


Figure 2.1. RUVS and BRUVS survey locations in the Hawaiian Archipelago. Top panel: MHI and NWHI, with the NWHI highlighted in grey shade. Middle panel: islands sampled in the MHI. Shaded black areas indicate island outlines. Lower panel: islands and atolls sampled in the NWHI. Shaded areas indicate 100 m depth contours. All deployments occurred in pairs at the same location, with light circles indicating RUVS (deployed and retrieved first), and dark circles indicating BRUVS.

The Northwestern Hawaiian Islands (NWHI) comprise a series of ten islands and atolls located to the northwest of the populated MHI, spanning nearly 2000 km between Nihoa (23°03'N and 161°55W) and

Kure Atoll (28°25'N and 178°20'W). Sampling efforts occurred between May – October2014 at French Frigate Shoals, Lisianski, Pearl and Hermes Atoll, and Midway Atoll.

Experimental Design

As reef fishes were the target community, sampling was restricted to hard-bottom habitats across two depth strata. In depths ≤ 30 m, RUVS and BRUVS deployments were randomly selected from locations previously surveyed by SCUBA divers conducting routine randomized monitoring operations for reef fishes (Ayotte et al. 2015b; Williams et al. 2015). In depths ≥ 30 m, deployment sites were randomly selected from a pool of 500 x 500 m grid cells generated from bathymetric and backscatter data products produced by the University of Hawaii, School of Earth and Ocean Sciences (SOEST), Hawaii Mapping Research Group (Main Hawaiian Islands Multibeam Bathymetry and Backscatter Synthesis, http://www.soest.hawaii.edu/HMRG/multibeam/). Grid cells were constrained within a 100 m contour line using data derivatives from SOEST HMRG 50 m bathymetry and topography grid cells, with at least 500 m between all sites in order to minimize potential confounding effects, e.g. overlapping BRUVS bait plumes or structural attraction of fish from one RUVS to another (Ruppert et al. 2013; De Vos et al. 2015). Grid cells containing > 35% unconsolidated sediment - based on backscatter values - were excluded.

Surveys incorporated a paired design, whereby RUVS and BRUVS deployments were conducted at each survey site. All surveys were completed between 8 AM – 3 PM, with at least 20 minutes allocated between the completion of RUVS sampling and the subsequent deployment of BRUVS. RUVS were always deployed first (RUVS, then BRUVS), because we assumed that bait would bias a subsequent RUV deployment (Harvey et al. 2007).

All survey sites and depth strata were binned at the regional level (MHI, NWHI). While RUV-BRUV pairs were deployed and retrieved at predetermined GPS coordinates and targeted depth strata, the drift of cameras on their way to the seafloor and the intrinsic patchiness of MHI benthic habitats in depths exceeding 30 m (Rooney et al. 2010) resulted in several benthic mismatches (e.g. one deployment landing on hard-bottom substrate, the other on unconsolidated sediment), or both deployments encountering 100% unconsolidated sediment. These pairs were excluded from the analysis. In the MHI, a total of 51 RUV-BRUV pairs (102 total deployments) were analyzed. In the NWHI, a total of 67 RUV-BRUV pairs were analyzed (134 total deployments), with generalist macropiscivores/roving predators as the primary survey focus (as part of Chapter 4, which focuses exclusively on predator populations across the Hawaiian Archipelago).

Video Collection, Processing, and Annotation

Paired RUV-BRUV samples were collected using pairs of high definition Sony CX7 or CX12 handycams, calibrated using the software package CAL™ prior to deployment (Harvey and Shortis 1995; Shortis and Harvey 1998; Seager 2008). Cameras were placed 0.7 m apart on a base bar mounted inside a galvanized steel roll-bar frame inwardly converged at 8°, covering approximately 51 m^2 when annotating reef fish

within ≤7 m sampling distance from the cameras (Harvey et al. 2007). BRUVS incorporated a 1.2 m PVC pipe-arm, which was locked into a 0.5 m metal mounting sleeve in front of the stereo-video cameras, with approximately 800 g of crushed Japanese sanma (*Cololabis saira*) in a mesh vinyl coated bait bag attached at the end. In contrast, RUVS only incorporated the metal mounting sleeve, and did not incorporate a pipe-arm or bait bag. Video was converted into .AVI format using Xilisoft™ following field collection efforts, and reef fish annotation completed using EventMeasure-Stereo™ (Seager 2008).

The *MaxN* metric was used as the principal relative abundance benchmark for inferring population structure for coral reef fish assemblages from underwater video sampling (Ellis and Demartini 1995; Priede and Merrett 1996; Willis and Babcock 2000a; Willis et al. 2000b; Cappo et al. 2004; Cappo et al. 2006a; Gledhill et al. 2006; Stoner et al. 2008; Langlois et al. 2010). MaxN is defined as: "the maximum number of fish in a single frame during a set viewing interval" (Ellis and Demartini 1995). It represents a conservative estimator of relative abundance, but ensures that individual fishes are not counted multiple times.

In this study, we define *soak time* as the amount of time between camera station bottom contact (Time on Seabed, TOS) and the conclusion of pre-defined sampling durations (Misa et al. 2016). The *time of first arrival* (TOFA) was defined as the time from TOS to the first species sighting, while the *time to MaxN* ($MaxN_T$) was the interval (minutes) between TOS and the recording of MaxN (Ellis and Demartini 1995). Each RUV and BRUV deployment was executed over 60 minutes, with TOFA and $MaxN_T$ reviewed over the full video duration. Soak time subsets of 20 (0 – 20), 40 (0 – 40), and 60 minutes were used for generating comparisons of species richness and MaxN between methods (see analysis section).

Reef Fish Assemblages and Target Species

In the MHI, reef fish TOFA and MaxN measurements were annotated from both RUV and BRUV samples down to the lowest possible taxonomic level (Randall 2007) for each soak time. All fishes were subsequently binned into nine groups based on similarity of functional traits and feeding regime, which were primarily derived from FishBase (v. 11/2014) and the NOAA PIFSC CREP reef fish database for the Hawaiian Archipelago (Tilman 2001; Harvey et al. 2007; Bernard and Götz 2012; Froese and Pauly 2014; Heenan 2014). These included herbivores, planktivores, corallivores, sessile invertivores, mobile invertivores, and omnivores. Carnivorous species were subdivided into three groups, driven primarily by diet, body-size, and feeding behavior. These encompassed small-bodied piscivores (e.g. trumpet fish, lizardfish, peacock grouper), sessile macropiscivores (eels belonging to Muraenidae and Ophichthidae), and generalist macropiscivores (large-bodied, non-planktivorous jacks, sharks, barracuda, and the snapper *Aprion virescens*), as specified in Friedlander and DeMartini (2002).

Identifications were made to genus or species level for common taxa, except for species that are difficult to discriminate below family level during video analysis (e.g. Gobiidae, Bothidae, or Kyphosidae). Unknown identifications were removed prior to conducting statistical analyses. As a consequence of its schooling behaviors, the carangid *Decapterus macarellus* was excluded from MHI abundance analyses as a result of consistent MaxN values > 100, which would skew assemblage and planktivorous variance

estimates. Similarly, a singular sighting of > 250 *Sphyraena helleri* was also excluded from generalist macropiscivore abundance analysis in the NWHI. Finally, the snapper *Pristipomoides filamentosus* is a bottom fish typically disconnected from shallower reef fish communities, and was also omitted from generalist macropiscivore comparisons (in both the MHI and NWHI).

Several generalist macropiscivores were selected for single-species regional analysis (MHI, NWHI) between RUV-BRUV pairs. These included the green jobfish (*Aprion virescens*) and bluefin trevally (*Caranx melampygus*), which were encountered in sufficient numbers in the MHI and NWHI to allow for regional comparisons between methods and soak times. While the giant trevally (*Caranx ignobilis*) was encountered in RUV-BRUV sampling across the Archipelago, analysis was limited to NWHI methods comparisons only as encounters in the MHI were rare and primarily limited to mesophotic depths. Finally, the Galapagos shark (*Carcharhinus galapagensis*) was frequently encountered and further assessed for NWHI deployments only, as none were encountered in the MHI.

Analysis

TOFA and MaxN$_T$

The primary motives for assessing TOFA and MaxN$_T$ were to evaluate the arrival and peak abundance times over 60-minute sampling periods for assemblage, functional group, and species-level categories. Although TOFA has been used as an analog for recording fish abundance, detailed metric analysis was not specifically intended for that purpose here, and requires sophisticated arrival-departure models to overcome uncertainty levels prior to generating predictive abundance estimates (Priede et al. 1994; Ellis and Demartini 1995; Priede and Merrett 1998; Farnsworth et al. 2007).

Mean TOFA and MaxN$_T$ values (±SD) were calculated for pooled assemblage, functional groups, and target species encountered over the course of full RUV-BRUV soak times (60-minutes), with proportional and cumulative proportional TOFA and MaxN$_T$ observations occurring within 5 minute intervals plotted across the entire 60 minute soak time. Generalist macropiscivore mean TOFA and MaxN$_T$ values were also compared between regional MHI and NWHI site pools, while target species were individually and independently assessed depending on regional presence.

Finally, differences in assemblage composition, species richness (N_{sp}) and number of individuals (MaxN$_i$) assessed by MHI RUVS and BRUVS were investigated over 20, 40 and 60 minute soak times. These durations broadly represent the three most common RUV and BRUV soak times used in previous reef fish studies. For each soak time, MaxN estimates were recorded for each species and subsequently pooled at assemblage and functional-group levels.

For the varying functional-groups and target species identified for univariate analysis between methods, RUVS and BRUVS sites were only included if at least one of the methods (RUV or BRUV) had recorded that functional group or target species within the overall 60-minute soak time (i.e. response groups must have been present at that site, according to at least one method). As a result, the number of TOFA

and $MaxN_T$ values (and consequently, the number of sites examined) varied per assessment level.

Richness and Relative Abundance

A two-way permutational multivariate analysis of variance (PERMANOVA; (Anderson 2001; Anderson 2008a) with 9999 permutations was used to assess differences in N_{sp} and MaxN using the factors *bait treatment* (fixed, 2 levels) and *soak time* (fixed, 3 levels: 0-20, 0-40, and 0-60 minutes), constructed using a Type III sums of squares in the PERMANOVA+ package in PRIMER 7 (Anderson 2008a; Clarke and Gorley 2015). PERMANOVA has the advantage over customary ANOVA and MANOVA tests in that no assumptions of normality are made, and it is robust to correlations with heterogeneous variances (Anderson and Walsh 2013).

RUV and BRUV data were tested for differences in fish abundances over different soak time intervals using a *modified Gower Log base 10* dissimilarity measure (Anderson et al. 2006). Modified Gower Log base 10 tests detect and interpret order of magnitude changes in abundance as shifts in assemblage composition, and are well-suited for addressing multivariate heterogeneity of variances (Anderson 2008a; Harvey et al. 2012b). Homogeneity of dispersions (PERMDISP; (Anderson 2006) were completed with 9999 permutations to further assess variation between RUV-BRUV samples. Finally, a plot of the constrained canonical analysis of principal coordinates (CAP) (Anderson and Robinson 2003; Anderson and Willis 2003) was generated to: a) visualize outputs generated by PERMANOVA; b) investigate minimum misclassification errors using leave-one-out allocation tests (Lachenbruch and Mickey 1968; Anderson and Willis 2003; Anderson 2008a); and c) identify which functional groups drove the differences between RUVS and BRUVS and soak times. Functional groupings with a Pearson's product momentum correlation > 0.4 were plotted, those being the groupings that contributed most to dissimilarities between methods and soak times (Anderson and Willis 2003).

An unpacked series of main and pair-wise comparisons were used to examine species richness and total number of individuals for 'all fishes' and for functional groups between bait treatment and soak time (Anderson and Millar 2004; Harvey et al. 2007). Richness and abundance data were square root and *log(x+1)* transformed respectively, prior to generating Euclidean measures (Sokal and Rohlf 1981). When the number of unique permutations was less than 100, a Monte Carlo P value was generated as the interpretative result (Anderson 2008a). Additional PERMDISP tests were utilized to test for equality of variances, akin to a Levene's test (Levene 1960).

In a non-parametric final test series, a third factor *region* (fixed, 2 levels: MHI, NWHI) was used to evaluate differences in generalist macropiscivore populations and RUV-BRUV soak time patterns, with individual, regional CAP outputs and species contributions values $\geq$ 0.4 used to visualize dissimilarities between factors using *log(x+1)* and a zero-adjusted Bray-Curtis dissimilarity measure. Subsequent univariate tests further evaluated NWHI functional group-level richness and abundance values using previously described approaches and compared with MHI results.

Power

Differences between RUV and BRUV reef fish assemblages, functional groups, and species level abundances ($MaxN_i$) over 20, 40, and 60 minute soak times was tested using the application G-Power™ (Faul et al. 2009) with the target of having an 80% chance of detecting a 100% change in relative abundance at an α of 0.05 (Westera et al. 2003; Watson et al. 2007; Watson et al. 2009). Power was calculated in 5 sample increments between a minimum of 5 and a maximum of 75 samples for overall assemblage, herbivore, and mobile invertivore abundance, and 10 sample increments – between 10 and 150 samples – for less abundant functional groups: planktivores, corallivores, omnivores, piscivores, sessile macropiscivores, generalist macropiscivores, and target species between the MHI and NWHI. Particular attention was paid to generalist macropiscivores and their component species between regions, as those are typically difficult to adequately sample around human population centers due to low abundance and relatively high variability (Langlois et al. 2010; Harvey et al. 2012b).

Results

Fish Assemblage Description

A total of 175 species belonging to 39 families were observed in the 51 paired RUV and BRUV surveys in the MHI. Between 123 - 146 total species (all deployments pooled) were recorded for RUVS (mean 10.2 ± 1.0 SE to 14.8 ± 1.2 per deployment), and 126 – 156 species (mean 12.5 ± SE to 18.7 ± 1.5) for BRUVS, with lower RUV-BRUV values logged during 20 minute soak times and higher values during 60 minute soak times. Of these, 14 species were recorded exclusively by RUVS, and 28 were recorded solely during BRUVS deployments (Supplementary Materials, Table S2.1). These species discrepancies were partially driven by uncommon, singular encounters (e.g. RUVS-only herbivores: *Chanos chanos*, *Cantherhines sandwichiensis*, *Lactoria diaphana*), or through perceived baiting influences (BRUVS-only: nearly all sessile macropiscivore species, i.e. eels). Similarly, relative abundances ranged from 1358 – 1905 individual fishes (mean 26.6 ± 3.8 SE to 37.4 ± 4.3) for RUVS, and 2041 – 3170 individual fishes (mean 40.0 ± 5.2 SE to 62.2 ± 7.3) for BRUVS.

Among all soak times, species richness and abundance for RUVS and BRUVS were dominated by herbivores (25 – 28% of species, 18 – 25% of total individuals), planktivores (10 – 11% of species, 27 – 40% of total individuals), and mobile invertivores (39 – 44% of species, 30 – 36% of total individuals; Supplementary Materials, Figure S2.1 A, B). The six remaining functional groups constituted a total of 17 – 24% of species, and 9 – 14% individuals.

Of the 67 NWHI sites, where only generalist macropiscivores were quantified, 14 species from 3 families were recorded by RUVS, and 15 species from 4 families by BRUVS (Supplementary Materials, Table S2.1). Comparatively, for RUVS surveys in the MHI, we recorded 12 generalist macropiscivore species from 4 families, and 16 species belonging to 5 families during BRUVS surveys. While most species were encountered in both regions, generalist macropiscivore compositions diverged between MHI and NWHI with some species solely - and infrequently - encountered in the MHI (*Scombroides lysan*, *Gnathanodon*

speciosus, *Scombridae* sp.) and others exclusively, and generally frequently, sighted in the NWHI (*Pseudocaranx cheilio*, *Carcharhinus galapagensis*, *Triaenodon obesus*, *Seriola lalandi*).

TOFA and MaxN$_T$

Mean TOFA and MaxN$_T$ values were broadly consistent between RUVS and BRUVS for the assessed MHI functional groups (Figure 2.2), with several notable patterns. First, total assemblage (all species pooled) and the more numerically dominant functional groups (herbivores, planktivores, mobile invertivores) were highly right-skewed towards early arrivals for both RUV and BRUV, with ≤ 20 mean TOFAs (Figure 2.2) and a general leveling of cumulative TOFAs around the 15 – 20 minute mark (Figure 2.3). A closer examination revealed 40 – 43% of species' TOFA occurred within the first five minutes and between 73 – 75% within the first 25 minutes of RUV and BRUV sampling, with herbivores, planktivores, and mobile invertivores acting as primary drivers (40 – 50% TOFA within five minutes, 71 – 80% within 25 minutes). Mean TOFA for the remaining functional groups occurred in < 26 minutes, but was more variable, with sessile invertivores (RUV) and MHI generalist macropiscivores (RUVS and BRUVS) taking between 40 – 45 minutes to achieve cumulative species arrival > 75%. In contrast, NWHI generalist macropiscivores and a subset of target species generally had much lower TOFA (Figure 2.2 and Supplementary Materials, Figures S2.3 – S2.5). Mean MaxN$_T$ values were ≤ 30 minutes for all functional groups (Figure 2.2), irrespective of method, being strongly related to TOFA patterns (Figure 2.2 and Supplementary Materials, Figures S2.2 – S2.5).

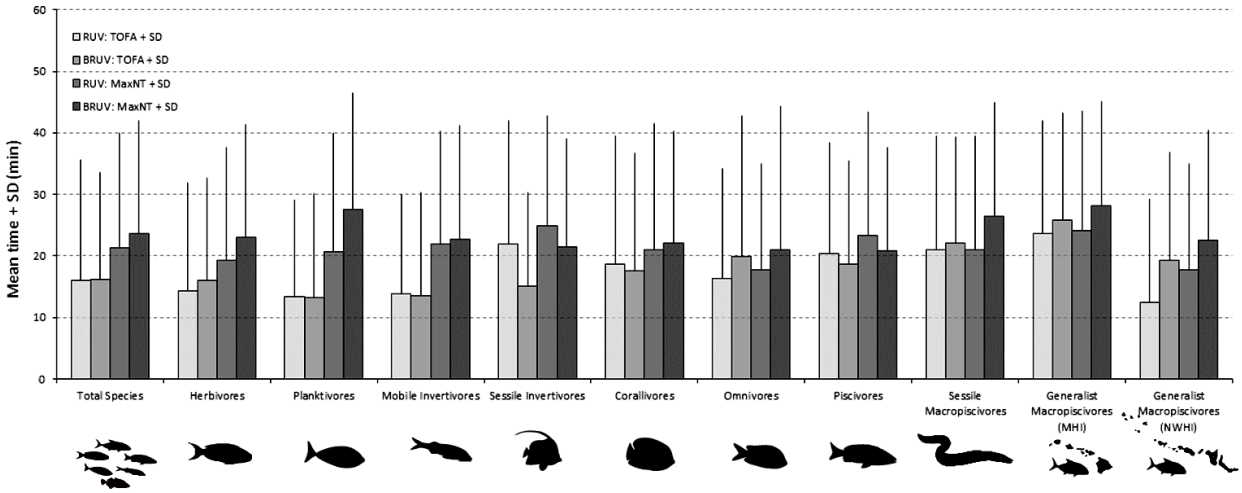


Figure 2.2. Mean time of first arrival (TOFA) and time to MaxN (MaxN$_T$) for MHI total species and each of nine functional groups recorded from 51 RUV-BRUV (paired) deployments. NWHI generalist macropiscivore values recorded from 67 RUV-BRUV (paired) deployments.

When incorporating one standard deviation into TOFA and MaxN$_T$ values, TOFA for 6 of 9 MHI functional groups and NWHI generalist macropiscivores were covered within 40 minutes, which was exceeded only by MHI sessile invertivores (RUVS), omnivores (BRUVS), and MHI generalist macropiscivores (RUVS and BRUVS). In comparison, soak times of 45 minutes were required to encompass the majority of mean MaxN$_T$ values within one standard deviation, which was only exceeded by planktivores (27.5 ± 19.0), sampled during BRUVS surveys.

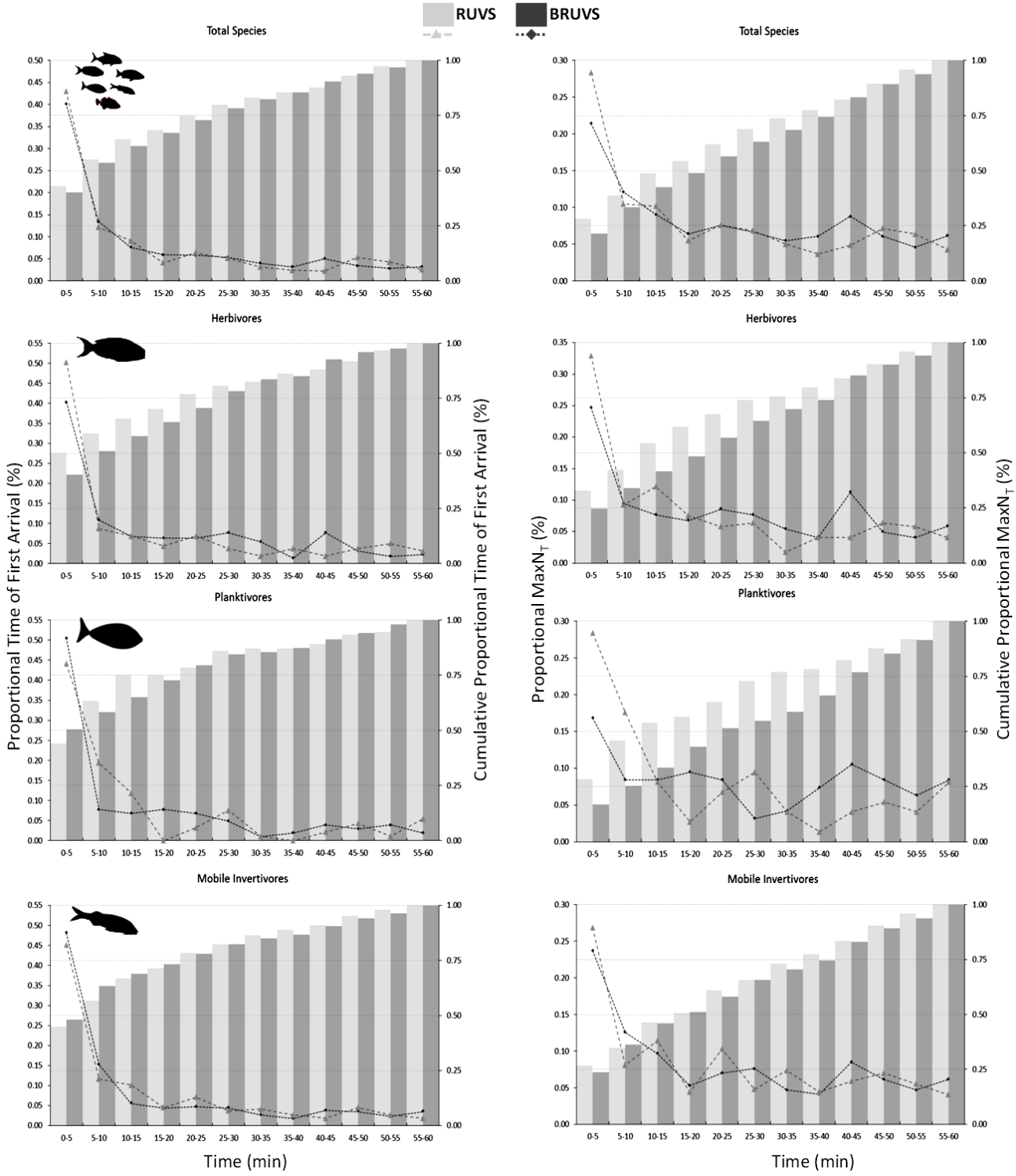


Figure 2.3. Proportional (lines) and cumulative proportional (bars) TOFA (left) and MaxN$_T$ (right) for Total Species, Herbivores, Planktivores, and Mobile Invertivores, binned into 5-minute intervals from Time on Seabed (minute 0) up to 60 minutes. Recorded from 51 RUV-BRUV sites surveyed from 2012 – 2013.

Species Abundance and Richness

Assemblage composition differed by method (PERMANOVA, $p < 0.0001$) and soak time ($P < 0.001$), with no interactive effects ($p > 0.05$) (Table 2.1). Those differences were primarily driven by mobile invertivores and the three carnivorous functional groups (piscivores, sessile and generalist macropiscivores, Pearson's r values ≥ 0.4, Supplementary Materials, Figure S2.6 and Table S2.4). However, overall leave-one-out allocation success (Anderson and Willis 2003) showed high statistical estimates of overall misclassification error (69%). Allocation success was highest between RUVS, 0-20 minutes (53%) and BRUV, 0-60 minutes (53%), which represents the farthest sampling distances between methods and soak times. Allocation success for remaining classifications ranged between 9-29%, and while the majority of these (except for RUV, 0-40 minutes) exceeded values attributed to chance alone, these are indicative of general assemblage similarities for the remaining functional groups between methods and timed sampling intervals. A subsequent distance-based test for homogeneity of multivariate dispersions (PERMDISP) revealed higher assemblage variability (heterogeneous test, $p > 0.05$) for some methods and soak times versus others, which was driven by the four functional group differences identified in the CAP and Pearson's R tests. When these groups were removed, dispersions between methods and soak times reverted to homogeneity ($p < 0.05$).

Among MHI sites, species richness and $MaxN_i$ predictably increased over cumulative RUV and BRUV 20-minute sampling intervals (Figure 2.4), irrespective of groupings (Table 2.2, Supplementary Materials, Tables S2.2 and S2.3). Subsequent assessments of total proportional functional richness (% N_{sp} contribution to overall richness by functional group) illustrated the continued prevalence of herbivore (25 -28%; soak time $p < 0.001$), planktivore (10 - 11%; NS for both factors) and mobile invertivore species (39 - 44%; method $p < 0.05$, soak time $p = 0.0001$), with no significance differences in richness detected in sessile invertivores, corallivores, and omnivores. Remaining carnivorous groups, which included piscivores (5 - 6%, soak time $p < 0.05$), sessile macropiscivores (0.6 - 5%, method $p = 0.0001$, soak time $p < 0.05$), and MHI generalist macropiscivores (3-6%, method $p < 0.05$ and soak time $p < 0.001$) were indicative of trends driving the differences recorded in previous CAP outputs that were heterogeneously dispersed ($p > 0.05$) and more variable between RUV-BRUV sampling of these groups over time.

Subsequent tests for mean number of individuals ($MaxN_i$) at assemblage and functional group levels recorded varying levels of significance between RUVS and BRUVS sampling intervals (Table 2.2), although patterns commonly seen with species richness were emulated with $MaxN_i$. For the MHI, the total number of individuals of all functional group levels pooled (assemblage level), herbivores, mobile and sessile invertivores, sessile macropiscivores (including interactive effects), and generalist macropiscivores were significant for both method and soak time. Planktivorous and piscivorous species recorded significant differences in one factor (method) or the other (soak time) respectively, while omnivores and corallivores recorded no changes irrespective of method and sampling time ($p > 0.05$). MaxN dispersion patterns were similar to those for assemblage and richness tests, with carnivorous functional groups being the primary outliers. Pairwise outputs from MHI mean N_{sp} and $MaxN_i$ functional groupings and NWHI generalist macropiscivores are presented in more detail in Figure 2.4 and Supplementary Materials, Tables S2.2 and S2.3.

Table 2.1. PERMANOVA of Modified Gower log base 10 assemblage composition, square root transformed total number of species, and *log(x+1)* transformed total number of individuals relative abundance data for MHI RUV-BRUV samples over increased 20-minute sampling intervals. Euclidean distance based measures were utilized for univariate data.

Source	*Assemblage Composition*				*Total Number of Species (N_{sp})*			*Total number of Individuals ($MaxN_i$)*		
	df	MS	F	P(perm)	MS	F	P(perm)	MS	F	P(perm)
Method (Unbaited, Baited)	1	3.94	8.95	**0.0001**	11.78	9.56	**0.0025**	9.74	14.32	**0.0004**
Soak Time (0-20, 0-40, 0-60)	2	1.67	3.80	**0.0005**	14.71	11.94	**0.0001**	5.70	8.38	**0.0006**
Method x Soak Time	2	0.18	0.40	0.9606	0.15	0.12	0.8854	0.03	0.05	0.9542
Res	300	0.44			1.23			0.68		

Significant P values (P < 0.05) indicated in bold.

Table 2.2. PERMANOVA of square root transformed number of species (Nsp) and *log(x+1)* transformed number of individuals (MaxNi) for MHI RUV-BRUV samples over increased 20-minute sampling intervals. Method and soak time are fixed factors. Individual functional groups based on univariate, Euclidean distance-based measures. Significant values (P < 0.05) are indicated in bold.

Source	*Total Number of Species (N_{sp})*				*Total number of Individuals ($MaxN_i$)*		
	df	MS	F	P(perm)	MS	F	P(perm)
Herbivores							
Method (Unbaited, Baited)	1	3.12	3.81	0.0516	4.16	3.99	**0.0471**
Soak Time (0-20, 0-40, 0-60)	2	5.61	6.85	**0.0007**	5.57	5.33	**0.0058**
Method x Soak Time	2	0.14	0.18	0.8359	0.32	0.31	0.7341
Res	300	0.82			1.04		
Planktivores							
Method (Unbaited, Baited)	1	0.94	1.49	0.2189	14.18	6.31	**0.0121**
Soak Time (0-20, 0-40, 0-60)	2	1.01	1.60	0.2038	2.36	1.05	0.3621
Method x Soak Time	2	0.01	0.01	0.9891	0.01	0.01	0.9942
Res	300	0.63			2.25		
Mobile Invertivores							
Method (Unbaited, Baited)	1	2.18	6.43	**0.0122**	4.31	12.21	**0.0006**
Soak Time (0-20, 0-40, 0-60)	2	4.17	12.29	**0.0001**	4.10	11.61	**0.0001**
Method x Soak Time	2	0.02	0.07	0.9398	0.03	0.09	0.9150
Res	300	0.34			0.35		
Sessile Invertivores							
Method (Unbaited, Baited)	1	0.94	3.05	0.0852	1.39	4.39	**0.0381**
Soak Time (0-20, 0-40, 0-60)	2	0.72	2.34	0.0945	0.90	2.85	0.0612
Method x Soak Time	2	0.03	0.10	0.9137	0.10	0.30	0.7475
Res	300	0.31			0.32		
Corallivores							
Method (Unbaited, Baited)	1	0.18	0.47	0.4944	0.45	1.01	0.3068
Soak Time (0-20, 0-40, 0-60)	2	0.29	0.79	0.4567	0.29	0.65	0.5213
Method x Soak Time	2	0.01	0.03	0.9749	0.01	0.03	0.9748
Res	300	0.37			0.44		
Omnivores							
Method (Unbaited, Baited)	1	0.04	0.22	0.6352	0.67	2.32	0.1272
Soak Time (0-20, 0-40, 0-60)	2	0.16	0.81	0.4461	0.07	0.23	0.8080
Method x Soak Time	2	0.05	0.27	0.7655	0.03	0.09	0.9163
Res	300	0.20			0.29		
Piscivores							
Method (Unbaited, Baited)	1	0.01	0.03	0.8646	0.25	0.65	0.4048
Soak Time (0-20, 0-40, 0-60)	2	1.92	4.43	**0.0116**	1.86	4.86	**0.0082**
Method x Soak Time	2	0.17	0.40	0.6686	0.05	0.12	0.8875
Res	300	0.43			0.38		
Sessile Macropiscivores							
Method (Unbaited, Baited)	1	18.00	87.89	**0.0001**	11.39	85.75	**0.0001**
Soak Time (0-20, 0-40, 0-60)	2	0.80	3.92	**0.0231**	0.62	4.69	**0.0097**
Method x Soak Time	2	0.48	2.34	0.0926	0.43	3.22	**0.0418**
Res	300	0.20			0.13		
Generalist Macropiscivores							
Method (Unbaited, Baited)	1	3.60	9.39	**0.0020**	4.58	9.08	**0.0025**
Soak Time (0-20, 0-40, 0-60)	2	3.46	9.04	**0.0005**	4.85	9.62	**0.0002**
Method x Soak Time	2	0.42	1.10	0.3396	0.42	0.83	0.4429
Res	300	0.38			0.50		
Generalist Macropiscivores (NWHI)							
Method (Unbaited, Baited)	1	24.17	62.65	**0.0001**	26.15	45.04	**0.0001**
Soak Time (0-20, 0-40, 0-60)	2	5.387	13.97	**0.0001**	5.492	9.46	**0.0002**
Method x Soak Time	2	0.236	0.61	0.5386	0.2	0.34	0.7130
Res	396	0.386			0.581		

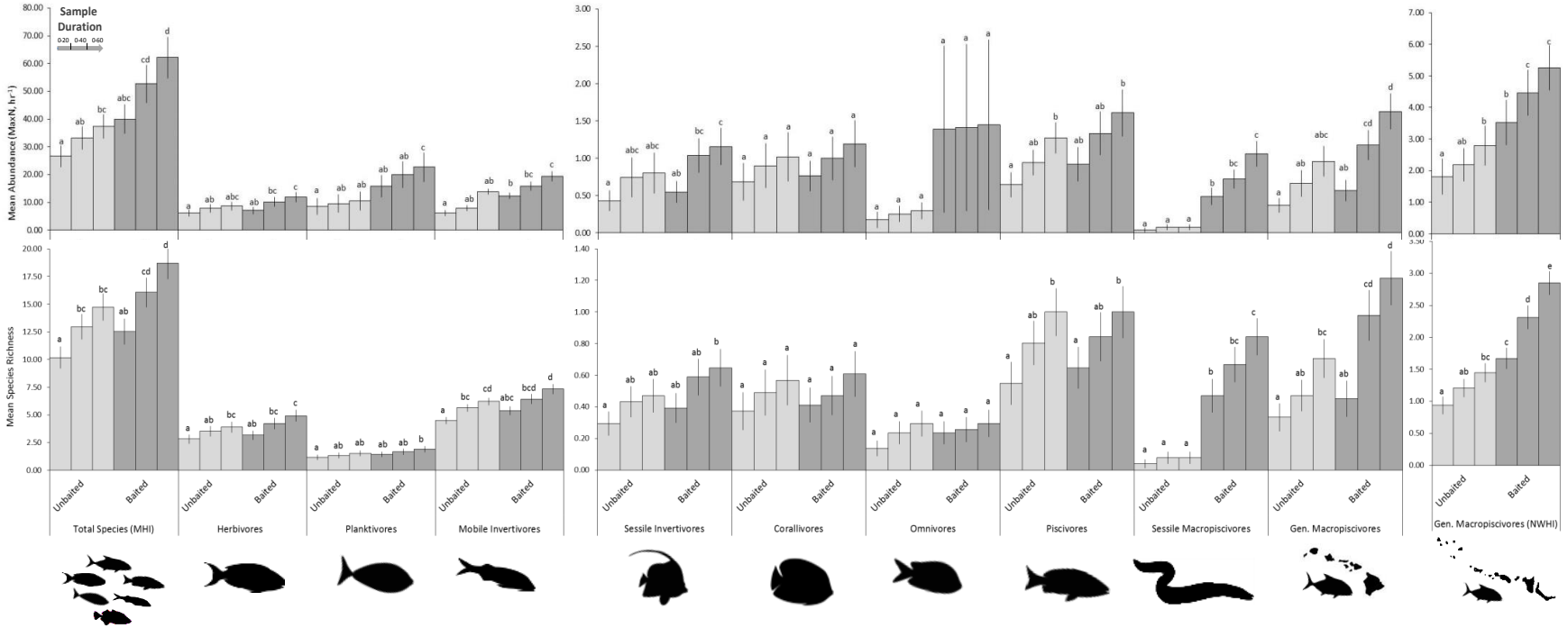


Figure 2.4. Species richness (number of species, Nsp, bottom panel) and mean abundance (MaxNi, top panel) and sand for 0-20, 0-40, and 0-60 minute camera soak times by method, for overall MHI reef assemblage (total species), MHI functional groups, and NWHI generalist macropiscivores. Note mean richness and abundance scales vary by functional group and region (generalist macropiscivores only). Results of PERMANOVA pair-wise tests depicted as letters, columns with the same letter are not significantly different ($P > 0.05$). See Tables S.2 and S.3 for numeric outputs of pair-wise tests.

For the comparison between MHI and NWHI generalist macropiscivore populations, there were significant regional, methodological, and soak time differences (all $p < 0.001$), and no significant interactions between factors (Tables 2.2 and 2.3, Supplementary Materials, Tables S2.2 and S2.3). Outputs from the canonical analysis of principal components identified *Aprion virescens* and *Caranx melampygus* with Pearson's R values ≥ 0.4 for the MHI and NWHI, along with *Caranx ignobilis*, *Carcharhinus galapagensis*, and *Triaenodon obesus* in the NWHI, as primary drivers of difference (Supplementary Materials, Figure S2.7, A-C and Figure S2.8, A-E). Unsurprisingly, overall leave-one-out misclassification errors between regional RUV and BRUV soak time comparisons were high (MHI: 76.0%, NWHI: 72.9%), likely as a result of mostly low abundance estimates (i.e. singular sightings or zero counts, especially for shorter sampling intervals). As similarly expected, correct classifications were highest along opposite ends of the methodological spectrum in each region (MHI RUVS 0-20: 73.5%, NWHI RUVS 0-20: 59.7%; MHI BRUVS 0-60: 55.9%, NWHI BRUVS 0-60: 59.7%, Table S2.4). Finally, when assessed as N_{sp} and $MaxN_i$ univariate measures, NWHI generalist macropiscivores revealed similar significant differences in methodologies and soak times (Table 2.3, Supplementary Materials, Tables S2.2 and S2.3, Figure 2.4) but divergent dispersion patterns, whereby N_{sp} and $MaxN_i$ was heterogeneous ($P < 0.05$) in the MHI and homogenous ($p > 0.05$) in the NWHI.

Table 2.3. PERMANOVA of square root transformed number of species (Nsp) and *log(x+1)* transformed number of individuals (MaxNi) for MHI and NWHI RUV-BRUV samples over increased 20-minute sampling intervals. Region, method and soak time are fixed factors. Individual functional groups based on univariate, Euclidean distance-based measures. Significant values ($P < 0.05$) are indicated in bold.

Source	*Total Number of Species (Nsp)*				*Total number of Individuals ($MaxN_i$)*		
	df	MS	F	P(perm)	MS	F	P(perm)
Generalist Macropiscivores							
Region (MHI, NWHI)	1	12880	45.01	**0.0001**	12061	41.14	**0.0001**
Method (Unbaited, Baited)	1	13519	47.25	**0.0001**	13001	44.34	**0.0001**
Soak Time (0-20, 0-40, 0-60)	2	6800	23.76	**0.0001**	6522	22.24	**0.0001**
Region x Method	1	412	1.44	0.2262	615	2.10	0.1317
Region x Soak Time	2	349.6	1.22	0.2889	241.7	0.82	0.4490
Method x Soak Time	2	455	1.59	0.2100	440.3	1.50	0.2162
Region x Method x Soak Time	2	208.6	0.73	0.4892	161	0.55	0.6045
Res	594	286.2			293.2		

Power

The power to detect a 100% effect size varied by assessment level (assemblage, functional groupings, and target species between regions), methods used, and soak time (Figures 2.5 – 2.6). For example, the number of samples required to have power ≥ 0.8 to detect a doubling of MaxN were generally similar for all species combined (between 20 – 30 video samples) and for mobile invertivores (10 – 15 samples), irrespective of method and soak time. In stark contrast, while mean richness and abundance was greater for omnivores sampled by BRUVS at all sampling intervals, RUVS had greater power, although neither method achieved our benchmark sampling power at the range of samples sizes used (e.g. with a maximum of 150 samples).

For the remaining functional groups, sampling power was mostly higher with BRUVS, and typically did not vary much between 0-40 and 0-60 minute soak times. The few instances that didn't fit that pattern were recorded with herbivores (maximum power for RUVS 0-60) and piscivores (maximum power for RUVS 0-40 and 0-60), and corallivores (maximum power for BRUVS 0-20 and 0-40).

For generalist macropiscivores and select target species, BRUVS required fewer samples and retained greater overall power to detect changes in relative abundance irrespective of region, with close parity between 0-40 and 0-60 minute soak time durations; however, finer-scale differences remained dependent on the species assessed. For example, the number of *Aprion virescens* samples required to achieve $\geq$ 0.8 power followed similar sampling trajectories for RUVS and BRUVS sampling times in the MHI and NWHI; however, the numbers of NWHI samples between 0-40 and 0-60 minute durations were much more closely aligned as a result of decreased sampling variability over longer soak time intervals. Interestingly, *Caranx melampygus* showed a similar pattern, albeit reversed between regions. Finally, remaining NWHI species (*Caranx ignobilis*, *Carcharhinus galapagensis*) higher power was achieved from longer BRUVS sampling durations, although *Caranx ignobilis* obtained much greater power from 60-minute soak time durations. As such, sampling *Caranx ignobilis* in the NWHI would require 56% more 40-minute replicates in order to achieve the same statistical power – in that case ~0.80 power to detect 100% effect size – as 60 minute replicates (90 x 40-minute versus 50 x 60-minute BRUVS; Figure 2.6).

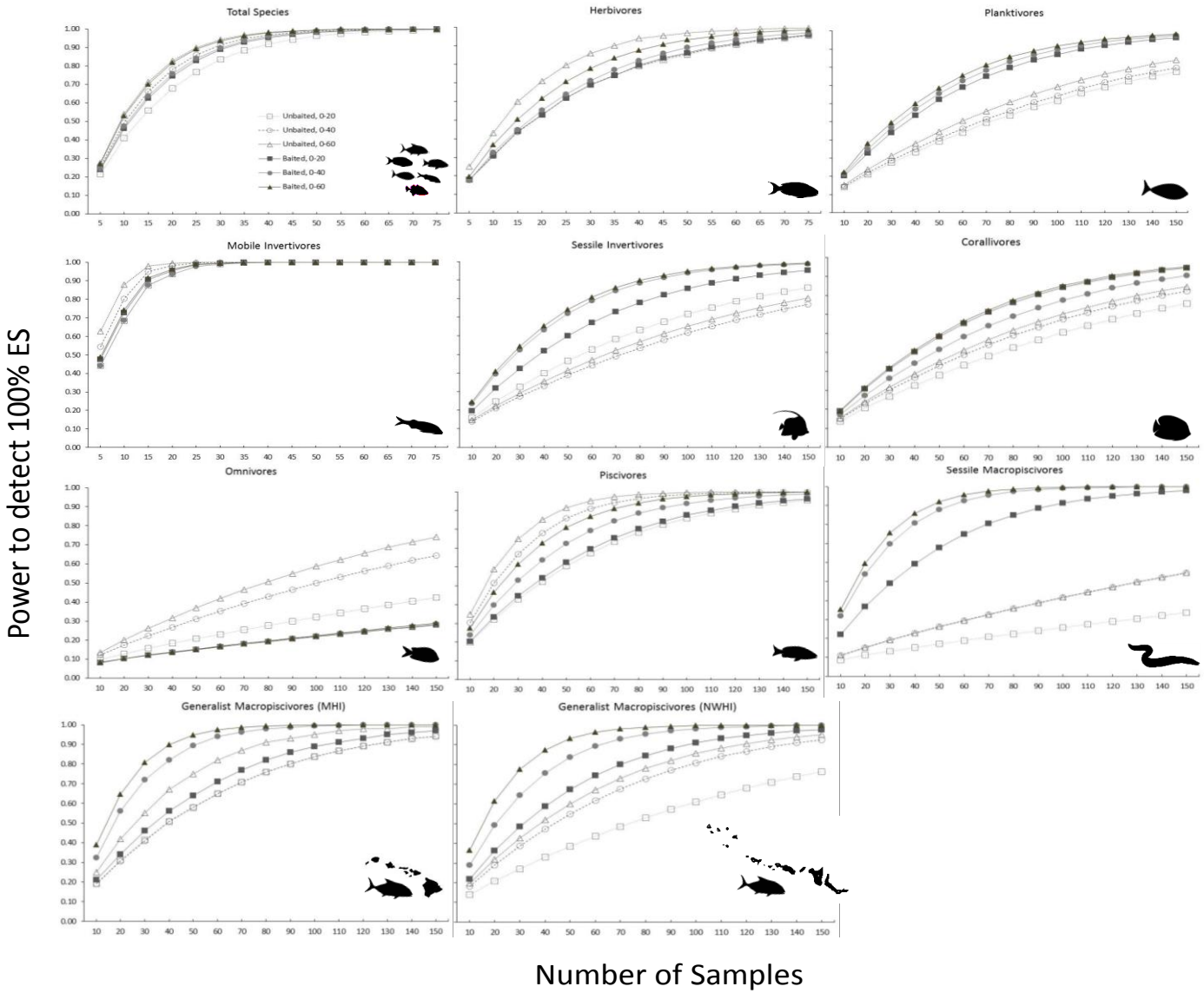


Figure 2.5. Statistical power for detecting a theoretical doubling (100% effect size [ES]) in relative abundance of total species and individual functional groups. Overlaps are a result of equal mean and SD values between soak times.

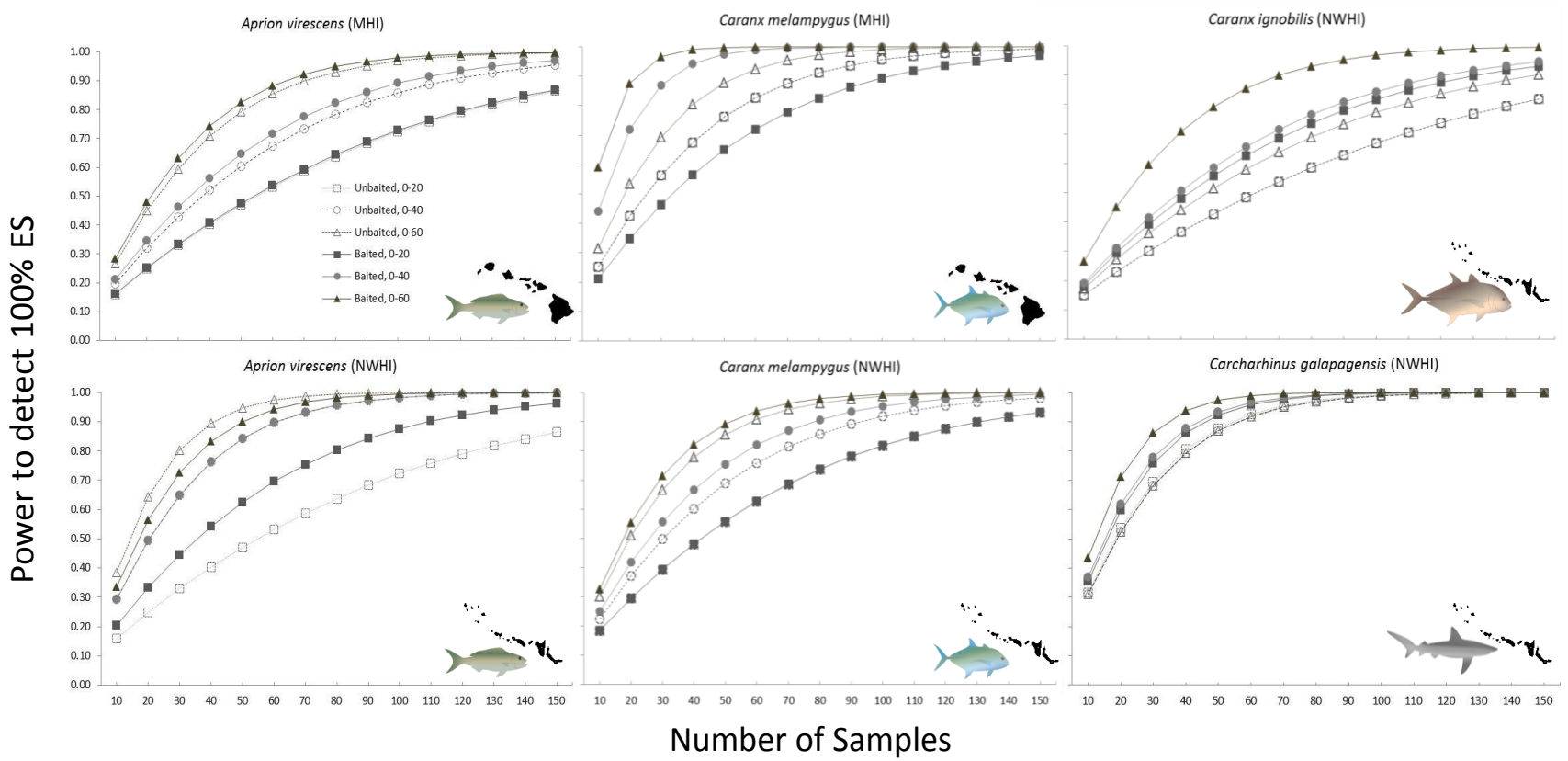


Figure 2.6. Statistical power for detecting a theoretical doubling (100% effect size [ES]) in relative abundance of total species and individual functional groups. Overlaps are a result of equal mean and SD values between soak times.

Discussion

This research augments other comparative methods studies, which contrast BRUVS with underwater visual census, trap, trawl, extractive fishing, diver-operated video, and other underwater assessment approaches (Cappo et al. 2004; Langlois et al. 2010; Watson et al. 2010; Goetze et al. 2015; Andradi-Brown et al. 2016b). However, comparisons between baited and unbaited methods remain vital in order to further understand the effects of baiting on reef fish assemblage structure and abundance-related effects. As such, this study represents one of only a small number of contrasting assessments between RUVS and BRUVS with respect to coral reef fishes and roving predator populations and, to our knowledge, remains the only underwater video comparison for coral reef fishes in the Hawaiian Archipelago.

TOFA and MaxN$_T$

For pooled MHI reef fish species, mean TOFA (RUV 16.0 ± 19.6, BRUV 16.2 ± 17.4) and MaxN$_T$ (RUV 21.4 ± 18.7, BRUV 23.4 ± 18.4) values were primarily driven by more numerically abundant functional groups (species of herbivores, planktivores, and mobile invertivores), and are similar to those recorded by Cappo et al. in 2004 (TOFA 16.0 ± 14.0, MaxN$_T$ 23.0 ± 16.0) during BRUVS surveys along the Great Barrier Reef. However, longer sampling durations, up to 45 minutes, were required for less-abundant groups to achieve cumulative, proportional TOFA and MaxN$_T$ values in excess of 70 – 75%. Proportional and cumulative proportional TOFA and MaxN$_T$ exhibited similar RUV and BRUV patterns, although arrival and abundance peaks occurred earlier with RUVS for most functional groups. This was a consequence of more species and individuals encountered by BRUVS, at assemblage and functional group levels, through the entire 60-minute survey durations, coupled with relative abundance metrics being proportionately higher for RUVS during the first 15 minutes of sampling.

Relative abundance metrics are known to be influenced by fish behaviors around camera stations (Cappo et al. 2003; Harvey et al. 2007; Misa et al. 2016). Here, functional group and species-level patterns followed one of three principal variants over time:

1.) Sharp peaks in TOFA and MaxN$_T$ within the first five minutes of sampling, likely due to species in closest proximity to the landing position of the RUVS or BRUVS. These were followed by abrupt TOFA and MaxN$_T$ declines at 5-10 minutes, and sustained 0-10% arrival and peak abundance accumulation rates for the remaining 5-minute sampling periods.

2.) Peaks in 0-5 minute TOFA and MaxN$_T$ values, followed by variable rates for the remaining periods. This was commonly observed for functional groups with generally few species and low abundance (e.g. omnivores).

3.) High variability through time (e.g. MHI sessile and generalist macropiscivores), which was associated with high mobility, inherent scarcity, patchy distribution, and/or time to bait plume olfactory detection in the case of BRUVS.

Of particular interest were the clear regional discrepancies in generalist macropiscivore mean, proportional, and cumulative proportional time of first arrival and time to MaxN values (sooner for NWHI RUV-BRUV, later for MHI). These results are broadly similar to patterns recorded by underwater visual censuses, in that videos with longer-duration were needed to detect uncommon, patchily distributed predators in the populated MHI, compared to the NWHI where predators are considerably more abundant and more frequently encountered (Friedlander and DeMartini 2002; Holzwarth et al. 2006). For example, *Aprion virescens* exhibited consistent earlier arrivals and maximum numbers (variant 1 above) in the NWHI, and much greater variability in arrival and maximum abundance values after the first five minutes of sampling (variant 2) in the MHI, as a result of large differences in abundance between regions. In contrast, *Caranx melampygus* mostly had highly variable arrival and MaxN rates (variant 3) in both regions, although MHI RUVS appeared more similar to variant 1.

Assemblage Composition, Richness, and Abundance

Results from RUVS and BRUVS were similar to a large degree, both in terms of richness and MaxN for most functional groups and in terms of contributions to coral reef fish assemblages across all soak time intervals (albeit with higher variability and thus lower power for 20-minute soak times). An advantage of RUVS was the ability to document fish behaviors unaltered by the potential biases associated with variable bait plumes. However, RUVS are reliant on the chance passage of more mobile and/or uncommon species (such as generalist macropiscivores), and therefore require greater number of samples to achieve the same statistical power as BRUVS. In addition, RUVS are not entirely free of survey biases. Fishes may be attracted by the physical structure provided by RUVS in low benthic complexity environments, e.g. prey fish species seeking shelter, or roving predatory species attracted to novel and somewhat conspicuous objects in otherwise featureless habitat (e.g. reef rubble flats, pavement, or areas of unconsolidated sediment).

Overall, BRUVS retained a number of distinct advantages over their unbaited counterparts in this study, including a greater number of species and individuals sampled in total assemblages and across the majority of assessed functional groups. Those results are consistent with other research on effects of baiting in video sampling (Willis and Babcock 2000a; Watson et al. 2005; Harvey et al. 2007; Watson et al. 2010; Bernard and Götz 2012). BRUVS also had increased power to detect changes in the total number of individuals for the general assemblage, the majority of functional groups, and specific target species. Lastly, BRUVS exhibited a consistent reduction in the coefficient of variation with longer soak time durations leading to increased similarities between sites (Harvey et al. 2007). Whether longer soak times dampen inter-site variability due to fishes coming from outside immediate BRUV sampling areas (~51 m^2) remains a topic for future investigation, as modeling of *in situ* environmental and oceanographic variables (shifting current speeds/direction, temperature, benthic topography), and their influence on bait plume sizes/dispersion rates (and subsequent impacts to reef fish abundance and richness estimates) remains particularly challenging without the inclusion of numerous assumptions (Heagney et al. 2007; Westerberg and Westerberg 2011; Dorman et al. 2012).

Despite concerns that herbivores (e.g. surgeonfish, parrotfish) would have lower abundance values in

BRUV surveys due to increased presence of predators or aggressive opportunistic omnivores, herbivore richness and relative abundance were not reduced by the use of bait in our study. In fact, BRUVS recorded higher herbivorous species richness and MaxN. Similarly, other studies have found few negative impacts of baiting on non-piscivorous groups in both temperate and tropical habitats (Harvey et al. 2007; Bernard and Götz 2012). Potential reasons for increased richness and abundance of non-piscivorous groups include "sheep effects", whereby species not directly attracted to the bait plume were nonetheless drawn to the feeding activities of others around BRUVS, or intra (conspecific) social attraction behavior (Watson et al. 2005; Harvey et al. 2007; Watson et al. 2010; Dorman et al. 2012). It was also notable that some members of nominally non-carnivorous groups appeared to feed or attempt to feed when presented with alternative food sources. For example, *Kyphosidae* are generally classified as herbivores (as in this study); however, we observed them feeding on BRUVS bait bags, as has been reported for members of this family in the Atlantic (Silvano and Güth 2006). Clearly, classifying all species into distinct functional group is somewhat simplistic, and further work on typical and potential diet is warranted.

It was somewhat surprising that there was no apparent baiting effect for the small number of lower-level piscivorous species observed. For that group there were only minor richness and abundance differences relating to soak times – in spite of that fact that feeding behaviors were observed for several such species around BRUVS (e.g. *Oxycheilinus unifasciatus*, *Lutjanus kasmira*, *Lutjanus fulvus*). Others exhibited non-feeding behaviors. These included appearing to be more interested in the cameras themselves (e.g. frequent close-in approaches by *Fistularia commersonii* irrespective of bait presence or absence), attraction to fish aggregation activities around RUVS and BRUVS (e.g. *Cephalopholis argus*), and transitory behaviors (e.g. *Aphareus furca*) or general lack of interest (e.g. *Paracirrhites forsteri*).

Differences in RUVS and BRUVS assemblage compositions, species richness, and relative abundance estimates were primarily driven by mobile invertivore and macropiscivore groups, which dovetails with previously published research that notes increased numbers of individuals and species of predatory and scavenging groups when bait is present (Harvey et al. 2007). Sessile macropiscivores (eels primarily belonging to Muraenidae), which are largely undetected during standard underwater visual censuses, were also rarely observed during RUVS surveys in our study. However, sessile macropiscivores were frequently observed by BRUVS, a result that matches the findings of research programs utilizing modified underwater censuses (Gilbert et al. 2005). Given how often eels were recorded during BRUV surveys, it seems likely that this ecologically important reef predator group remains greatly underrepresented in most unbaited surveys (i.e. standard diver censuses and RUVS) (Parrish et al. 1986).

Given their susceptibility to fishing pressures and intrinsic patchy distributions, highly mobile large-bodied roving predators can be inherently difficult to survey. They are also ecological important, and it remains imperative to adopt methods capable of sampling them efficiently. In this study, BRUVS observed more diverse and abundant assemblages of generalist macropiscivores in comparison to RUVS, and had greater power to detect changes. Optimal sampling for this group and for the particular target species assessed, were achieved with soak times of 40 minutes or more in both the populated MHI and remote NWHI.

As noted above, BRUVS are prone to inherent biases that are likely not to affect RUVS. While some BRUVS studies have quantified the dispersion of bait plumes, most programs assume equal sampling areas between stations - ignoring any potential differences in plume dispersion - or utilize mean or maximum current speeds to estimates ranges of diffusion, masking potentially widely dissimilar dispersion distances between deployments, which may vary by several orders of magnitude (Heagney et al. 2007; Taylor et al. 2013; Espinoza et al. 2014; Rizzari et al. 2014). Future research in the Hawaiian Archipelago would benefit from *in situ* benthic current measurements occurring simultaneously with BRUV sampling, in order to better understand bait plume dispersion patterns along a variety of benthic substrates, and their effects on the reef fish assemblages sampled.

In response to financial or logistics constraints and the time required to process large video datasets to the assemblage level, or because of a narrow focus on specific groups, some research programs opt to only assess commercially-harvested or preferentially target species with relatively early arrival and MaxN times – and by limiting the analysis in that way, increases the scope for a greater number of samples (Clarke and Warwick 1998; Langlois et al. 2010). One example is the NOAA PIFSC FRMD's reduction of MOUSS sampling periods from 40 minutes to 15 minutes (resulting in ~50% reduction in annotation time), for surveys targeting the seven commercially important bottom fish species in MHI. Another example is the use of 20 minute baited sampling for site-attached or resident reef species in the Atlantic (Bacheler and Shertzer 2015; Misa et al. 2016; Richards et al. 2016). However, some caution about reducing soak time is warranted, as higher sampling precision may be better achieved through longer soak times and therefore reduced among-sampled variability, rather than through increasing the number of replicates (Gladstone et al. 2012). As an example of the tradeoffs involved, a BRUVS survey program targeting *Caranx ignobilis* in the NWHI would require 56% more 40 minute replicates than 60 minute replicates to achieve the same statistical power (in this case, ~0.80 power to detect 100% effect size at 90 x 40-minute versus 50 x 60 minute BRUVS; Chapter 2, Figure 2.7).

Finally, it is worth noting that time-lags between video annotation and analysis can be pronounced, particularly when characterizing entire reef assemblages (i.e. identification and collection of MaxN for all species). The time required to analyze images (and the consequent delay before results are known) varies widely depending on the research focus, area or habitat being examined, experience of the video annotator, and the duration of the video samples. For example, an average of 5 hours is needed to process 40-minute bottom fish videos in the Hawaiian Archipelago, 3 – 5 hours per 50-minute sample to classify Caribbean reef fishes, and 2.5 hours of annotation time per 60-minute sample to categorize tropical continental shelf demersal fishes in Western Australia (Harvey et al. 2012b; Andradi-Brown et al. 2016a; Misa et al. 2016). In contrast, RUVS and BRUVS processing in the MHI ranged between 1.0 and 6.5 hours per 60-minute video, depending on habitat (rugose or simple), depth (higher processing time for lower ambient light environments) and the abundance and richness of encountered assemblages. RUVS and BRUVS annotation times were reduced to an average of 1.0 – 2.5 hours per 60-minute video when only sharks, jacks, and snapper were annotated from the NWHI surveys (Asher, unpublished data).

Conclusions

There are obvious benefits to reduced soak times, in terms of increased scope for replication (can redeploy equipment more times during a sampling period) as well as shorter associated image-analysis time and thus reduced "per-unit" costs (Misa et al. 2016). However, the choice of field sampling approach should remain dependent on the questions being asked. For example, RUVS and BRUVS sampling durations of 20 minutes may be sufficient for studies focused on the general structure of major functional groups, or for resident or "fast reacting" species (Stobart et al. 2007). RUVS may also be a preferred approach for assessing common and conspicuous taxa (Francour et al. 1999; Bernard and Götz 2012) while avoiding the biases associated with addition of bait. However, when assessing piscivorous species or the complete fish assemblage as a whole, we concluded that BRUVS surveys with at least 40-minute sampling periods outperformed RUV deployments of equal duration, and documented the majority ($\geq$70 - 75%) of species arrivals and MaxN estimates irrespective of assemblage, functional group, or target species designation. In addition, 40-minute BRUV surveys preserved the greatest similarity to other RUV and BRUV soak time sampling intervals observed in pair-wise testing, and dependably retained enough power to detect large-scale changes in population abundance given sufficient sample size collection. However, while 40-minute BRUVS might be optimal for future research on Hawaiian coral reef fishes, utilization of 60-minute surveys would maximize compatibility with other coral reef video research around the Pacific, facilitating multiregional comparisons.

Supplementary Materials

Table S.2.1. Functional group, family, genus and species of fish recorded during RUV-BRUV surveys over increased sampling intervals (0-20, 0-40, 0-60 minutes) in the MHI. X indicates species presence. Note: Generalist macropiscivores sightings are split to include roving predator data from the NWHI.

			Species Presence (X)					
Trophic Group	Family	Species	Unbaited, 0-20	Unbaited, 0-40	Unbaited, 0-60	Baited, 0-20	Baited, 0-40	Baited, 0-60
Herbivores	*Acanthuridae*	*Acanthuras blochii/xanthopterus*	X	X	X	X	X	X
		Acanthuridae sp	X	X	X	X	X	X
		Acanthurus blochii	X	X	X	X	X	X
		Acanthurus dussumieri	X	X	X	X	X	X
		Acanthurus leucopareius	X	X	X	X	X	X
		Acanthurus nigrofuscus	X	X	X	X	X	X
		Acanthurus nigroris	X	X	X	X	X	X
		Acanthurus nigroris/nigrofuscus	X	X	X	X	X	X
		Acanthurus olivaceus	X	X	X	X	X	X
		Acanthurus sp	X	X	X		X	X
		Acanthurus triostegus	X	X	X	X	X	X
		Acanthurus xanthopterus	X	X	X		X	X
		Ctenochaetus sp						X
		Ctenochaetus strigosus	X	X	X	X	X	X
		Naso lituratus	X	X	X	X	X	X
		Naso unicornis	X	X	X	X	X	X
		Zebrasoma flavescens	X	X	X	X	X	X
		Zebrasoma veliferum				X	X	X
	Balistidae	*Melichthys vidua*	X	X	X	X	X	X
	Chanidae	*Chanos Chanos*		X	X			
	Kyphosidae	*Kyphosidae sp*						X
	Monacanthidae	*Cantherhines sandwichiensis*			X			
		Cantherhines verecundus	X	X	X	X	X	X
		Centropyge fisheri	X	X	X	X	X	X
		Centropyge potteri	X	X	X	X	X	X
	Scarinae	*Calotomus carolinus*			X	X	X	X
		Chlorurus perspicillatus	X	X	X	X	X	X
		Chlorurus sordidus	X	X	X	X	X	X
		Scaridae sp	X	X	X	X	X	X
		Scarus sp	X	X	X	X	X	X
		Scarus dubius	X	X	X	X	X	X
		Scarus psittacus	X	X	X	X	X	X
		Scarus rubroviolaceus	X	X	X	X	X	X
	Tetraodontidae	*Canthigaster coronata*	X	X	X	X	X	X
		Canthigaster epilampra	X	X	X	X	X	X
		Canthigaster jactator	X	X	X	X	X	X
Planktivores	*Acanthuridae*	*Acanthurus thompsoni*	X	X	X			X
		Naso brevirostris	X	X	X	X	X	X
		Naso hexacanthus	X	X	X	X	X	X
	Balistidae	*Melichthys niger*	X	X	X	X	X	X
		Xanthichthys auromarginatus	X	X	X	X	X	X
		Xanthichthys caeruleolineatus	X	X	X			
	Carangidae	*Decapterus macarellus*	X	X	X	X	X	X
	Chaetodontidae	*Chaetodon kleinii*	X	X	X	X	X	X
		Chaetodon miliaris	X	X	X	X	X	X
		Heniochus diphreutes	X	X	X	X	X	X
	Diodontidae	*Chilomycterus reticulatus*		X	X			X
	Holocentridae	*Myripristis kuntee*				X	X	X
	Labridae	*Cirrhilabrus jordani*	X	X	X	X	X	X
	Lutjanidae	*Melichthys niger*				X	X	X
	Microdesmidae	*Gunnellichthys curiosus*	X	X	X	X	X	X
	Pomacanthidae	*Abudefduf abdominalis*	X	X	X		X	X
	Pomacentridae	*Abudefduf vaigiensis*		X	X	X	X	X
		Chomis leucura				X	X	X
		Chromis agilis	X	X	X	X	X	X
		Chromis hanui	X	X	X	X	X	X
		Chromis leucura	X	X	X	X	X	X
		Chromis ovalis	X	X	X	X	X	X
		Chromis vanderbilti	X	X	X	X	X	X
		Chromis verater	X	X	X			
		Dascyllus albisella	X	X	X	X	X	X
	Ptereleotridae	*Ptereleotris heteroptera*	X	X	X			
Mobile Invertivores	*Balistidae*	*Balistes polylepis*	X	X	X	X	X	X
		Balistidae sp	X	X	X		X	X
		Rhinecanthus aculeatus	X	X	X	X	X	X
		Rhinecanthus rectangulus	X	X	X	X	X	X
		Sufflamen bursa	X	X	X	X	X	X
		Sufflamen fraenatum	X	X	X	X	X	X
	Blenniidae	*Plagiotremus ewaensis*	X	X	X	X	X	X
		Plagiotremus goslinei			X	X	X	X
	Bothidae	*Bothidae sp*		X	X		X	X
	Chaetodontidae	*Chaetodon ephippium*					X	X
		Forcipiger flavissimus	X	X	X	X	X	X
		Forcipiger longirostris	X	X	X		X	X
	Cirrhitidae	*Cirrhitidae sp*				X	X	X
		Cirrhitops fasciatus						X
		Cirrhitus pinnulatus				X	X	X
		Paracirrhites arcatus	X	X	X	X	X	X
	Dasyatidae	*Dasyatis lata*					X	X
	Diodontidae	*Diodon hystrix*	X	X	X		X	X
	Gobiidae	*Gobiidae sp*			X			
	Labridae	*Anampses chrysocephalus*	X	X	X			
		Anampses cuvier	X	X	X			
		Bodianus bilunulatus	X	X	X	X	X	X
		Coris aygula				X	X	X
		Coris ballieui	X	X	X	X	X	X
		Coris flavovittata	X	X	X	X	X	X

Table S.2.1 Continued

			Species Presence (X)					
Trophic Group	Family	Species	Unbaited, 0-20	Unbaited, 0-40	Unbaited, 0-60	Baited, 0-20	Baited, 0-40	Baited, 0-60
Mobile Invertivores	*Labridae*	*Coris gaimard*	X	X	X	X	X	X
		Coris venusta	X	X	X	X	X	X
		Cymolutes lecluse		X	X	X	X	X
		Gomphosus varius	X	X	X	X	X	X
		Halichoeres ornatissimus			X	X	X	X
		Iniistius aneitensis					X	X
		Iniistius baldwini				X	X	X
		Iniistius pavo				X	X	X
		Iniistius umbrilatus		X	X	X	X	X
		Labridae sp	X	X	X	X	X	X
		Labroides phthirophagus			X	X	X	X
		Novaculichthys taeniourus			X		X	X
		Oxycheilinus bimaculatus	X	X	X	X	X	X
		Pseudocheilinus evanidus	X	X	X	X	X	X
		Pseudocheilinus octotaenia		X	X	X	X	X
		Pseudojuloides cerasinus	X	X	X	X	X	X
		Stethojulis balteata	X	X	X	X	X	X
		Thalassoma ballieui	X	X	X	X	X	X
		Thalassoma duperrey	X	X	X	X	X	X
		Thalassoma trilobatum		X	X			
	Lethrinidae	*Monotaxis grandoculis*	X	X	X	X	X	X
	Malacanthidae	*Malacanthus brevirostris*	X	X	X	X	X	X
	Mullidae	*Mullidae sp*	X	X	X	X	X	X
		Mulloidichthys flavolineatus	X	X	X	X	X	X
		Mulloidichthys pfluegeri	X	X	X	X	X	X
		Mulloidichthys vanicolensis	X	X	X	X	X	X
		Parupeneus chrysonemus	X	X	X			X
		Parupeneus insularis	X	X	X		X	X
		Parupeneus multifasciatus	X	X	X	X	X	X
		Parupeneus pleurostigma	X	X	X	X	X	X
	Myliobatidae	*Aetobatus narinari*			X	X	X	X
	Ostraciidae	*Lactoria diaphana*			X			
	Pinguipedidae	*Parapercis schauinslandii*	X	X	X	X	X	X
	Pomacentridae	*Plectroglyphidodon imparipennis*	X	X	X	X	X	X
		Stegastes fasciolatus	X	X	X	X	X	X
	Tetraodontidae	*Arothron hispidus*	X	X	X		X	X
		Torquigener randalli					X	X
Sessile Invertivores	*Chaetodontidae*	*Chaetodon auriga*		X	X	X	X	X
		Chaetodon fremblii	X	X	X	X	X	X
		Chaetodon lunula	X	X	X	X	X	X
	Ostraciidae	*Ostraciidae sp*	X	X	X			
		Ostracion meleagris	X	X	X			
	Pomacanthidae	*Apolemichthys arcuatus*	X	X	X	X	X	X
	Zanclidae	*Zanclus cornutus*	X	X	X	X	X	X
Corallivores	*Chaetodontidae*	*Chaetodon multicinctus*	X	X	X	X	X	X
		Chaetodon ornatissimus	X	X	X	X	X	X
		Chaetodon quadrimaculatus	X	X	X	X	X	X
		Chaetodon unimaculatus	X	X	X	X	X	X
	Pomacentridae	*Plectroglyphidodon johnstonianus*	X	X	X	X	X	X
Omnivores	*Monacanthidae*	*Aluterus scriptus*	X	X	X			X
		Cantherhines dumerilii	X	X	X	X	X	X
		Pervagor aspricaudus				X	X	X
	Pomacentridae	*Pomacentridae sp*	X	X	X	X	X	X
Piscivores	*Aulostomidae*	*Aulostomus chinensis*	X	X	X	X	X	X
	Cirrhitidae	*Paracirrhites forsteri*	X	X	X		X	X
	Fistulariidae	*Fistularia commersonii*	X	X	X	X	X	X
	Labridae	*Oxycheilinus unifasciatus*	X	X	X	X	X	X
	Lutjanidae	*Aphareus furca*	X	X	X	X	X	X
		Lutjanus fulvus	X	X	X	X	X	X
		Lutjanus kasmira	X	X	X	X	X	X
	Mullidae	*Parupeneus cyclostomus*	X	X	X		X	X
	Serranidae	*Cephalopholis argus*	X	X	X	X	X	X
Sessile Macripiscivores	*Muraenidae*	*Echidna nebulosa*					X	X
		Gymnothorax sp		X	X	X	X	X
		Gymnothorax flavimarginatus				X	X	X
		Gymnothorax meleagris		X	X	X	X	X
		Gymnothorax undulatus				X	X	X
		Muraenidae sp	X	X	X	X	X	X
		Scuticaria okinawae					X	X
		Scuticaria tigrina				X	X	X
	Ophichthidae	*Myrichthys magnificus*					X	X
		Ophichthus fowleri	X	X	X			
Generalist Macropiscivores	*Carangidae*	*Alectis ciliaris*				X	X	X
(Main Hawaiian Islands)		*Carangidae sp*	X	X	X		X	X
		Carangoides ferdau	X	X	X	X	X	X
		Carangoides orthogrammus	X	X	X	X	X	X
		Caranx ignobilis					X	X
		Caranx melampygus	X	X	X	X	X	X
		Gnathanodon speciosus			X		X	X
		Scomberoides lysan		X	X	X	X	X
		Seriola dumerili	X	X	X		X	X
		Seriola rivioiana				X	X	X
	Carcharhinidae	*Carcharhinidae sp*					X	X
		Carcharhinus amblyrhynchos		X	X		X	X
		Carcharhinus plumbeus	X	X	X		X	X
		Galeocerdo cuvier					X	X
	Lutjanidae	*Aprion virescens*	X	X	X	X	X	X
	Scombridae	*Scombridae sp*		X	X			
Generalist Macropiscivores	*Carangidae*	*Carangidae sp*	X	X	X		X	X
(Northwestern Hawaiian		*Carangoides ferdau*	X	X	X		X	X
Islands)		*Carangoides orthogrammus*	X	X	X	X	X	X
		Caranx ignobilis	X	X	X	X	X	X
		Caranx lugubris	X	X	X			
		Caranx melampygus	X	X	X	X	X	X
		Pseudocaranx cheilio	X	X	X	X	X	X
		Seriola dumerili	X	X	X	X	X	X
		Seriola lalandi	X	X	X	X	X	X
		Seriola rivioiana	X	X	X	X	X	X
		Seriola sp.			X	X	X	X
	Carcharhinidae	*Carcharhinidae sp*	X	X	X	X	X	X
		Carcharhinus amblyrhynchos				X	X	X
		Carcharhinus galapagensis	X	X	X	X	X	X
		Carcharhinus plumbeus	X	X	X	X	X	X
		Galeocerdo cuvier						X
		Triaenodon obesus	X	X	X	X	X	X
	Lutjanidae	*Aprion virescens*	X	X	X	X	X	X

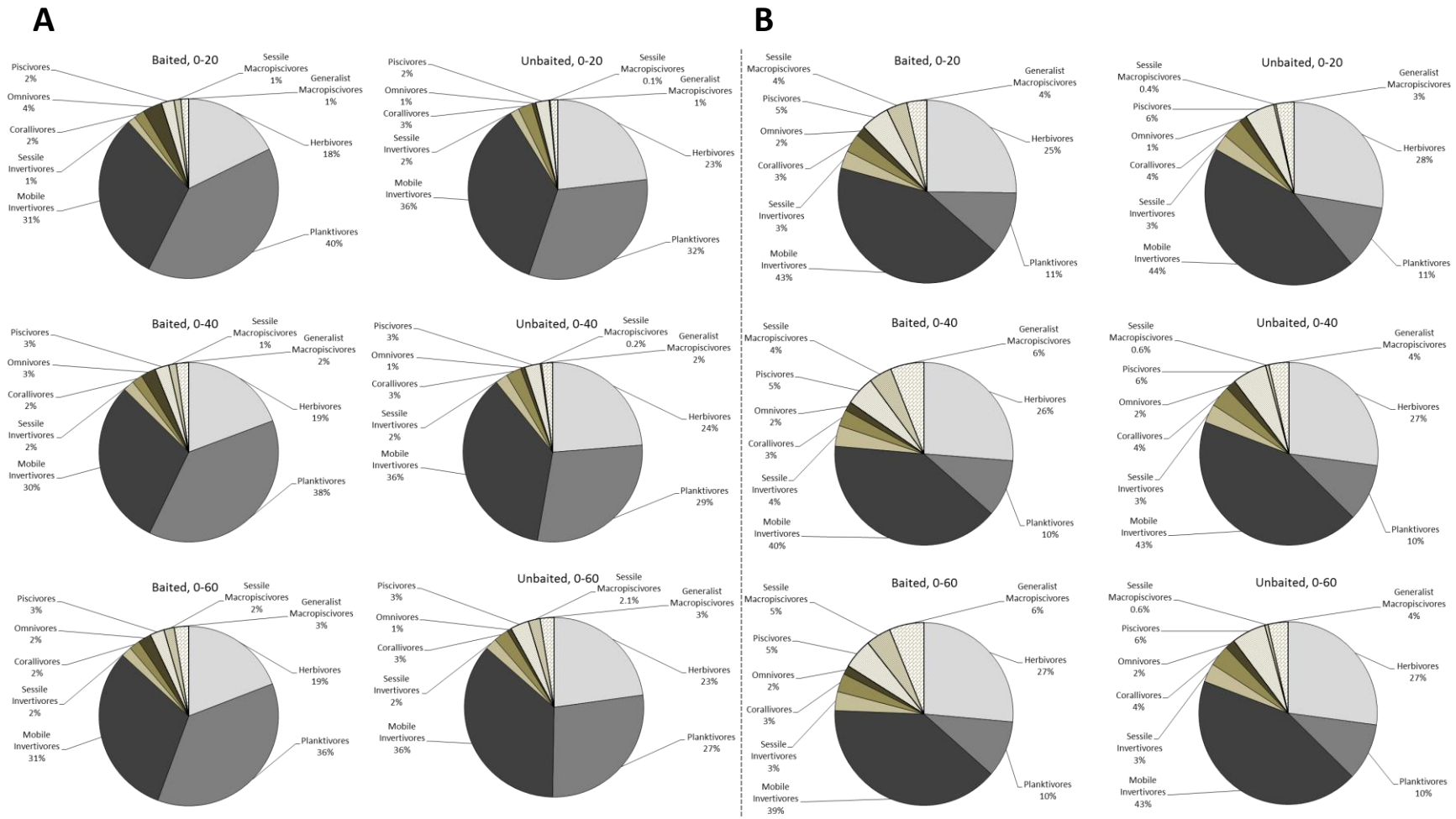


Figure S.2.1. A.) Proportional number of species contributing to total assemblage richness (% of total species, binned into functional groups) by method and soak time. B.) Proportion of fish abundance that contribute to total fish assemblage (% number of individuals, binned into functional groups) by method and soak time.

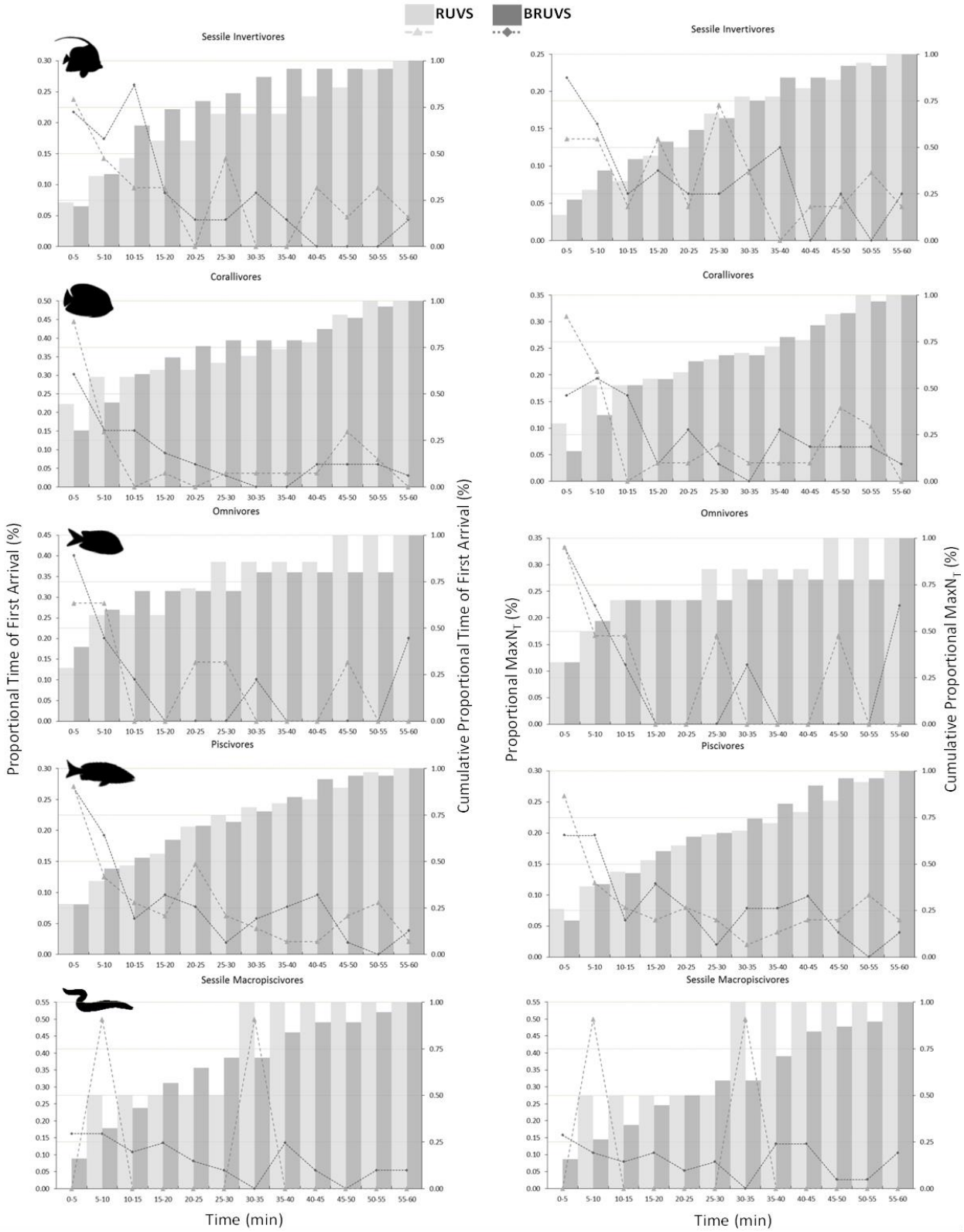


Figure S.2.2. Proportional (lines) and cumulative proportional (bars) TOFA and MaxN$_T$ (Sessile Invertivores, Corallivores, Omnivores, Piscivores, and Sessile Macripiscivores) binned into 5-minute intervals from Time on Seabed (minute 0) up to 60 minutes. Recorded from 51 RUV-BRUV sites surveyed from 2012 – 2013.

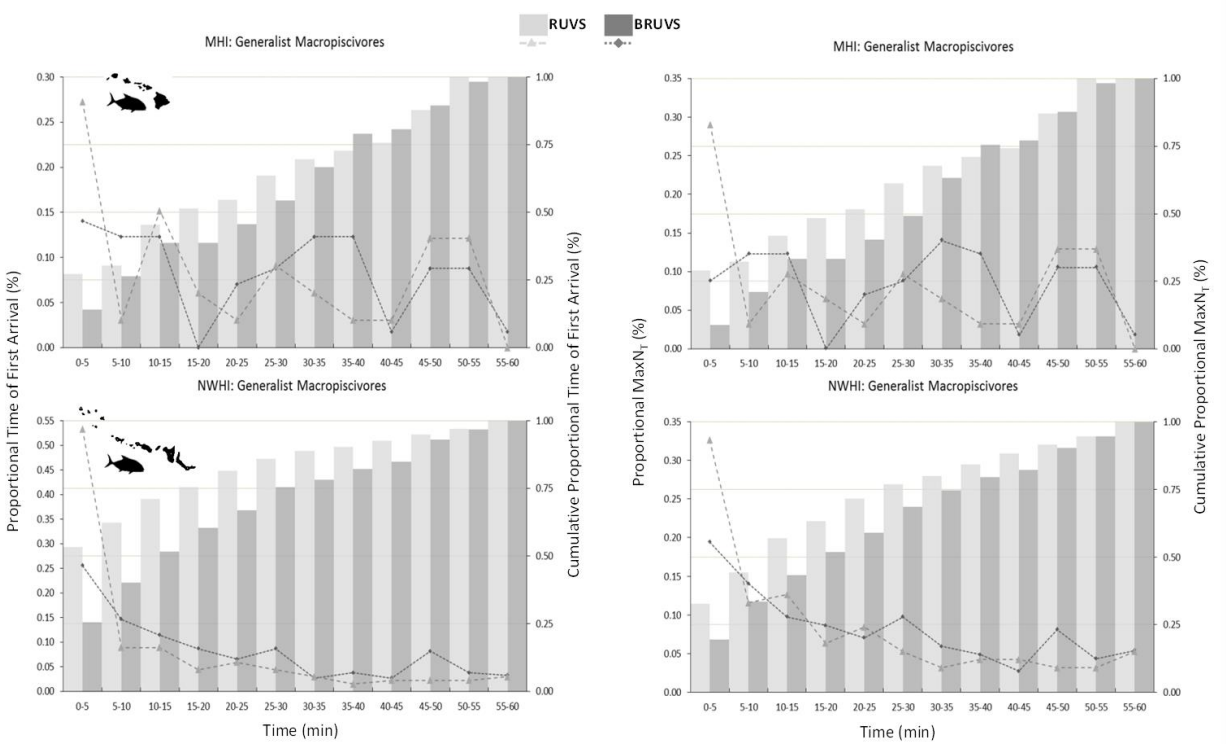


Figure S.2.3. Proportional and cumulative proportional TOFA and MaxN$_T$ (MHI and NWHI generalist macropiscivores) binned into 5-minute intervals from Time on Seabed (minute 0) up to 60 minutes. Recorded from 51 MHI and 67 NWHI RUV-BRUV sites surveyed from 2012 – 2014.

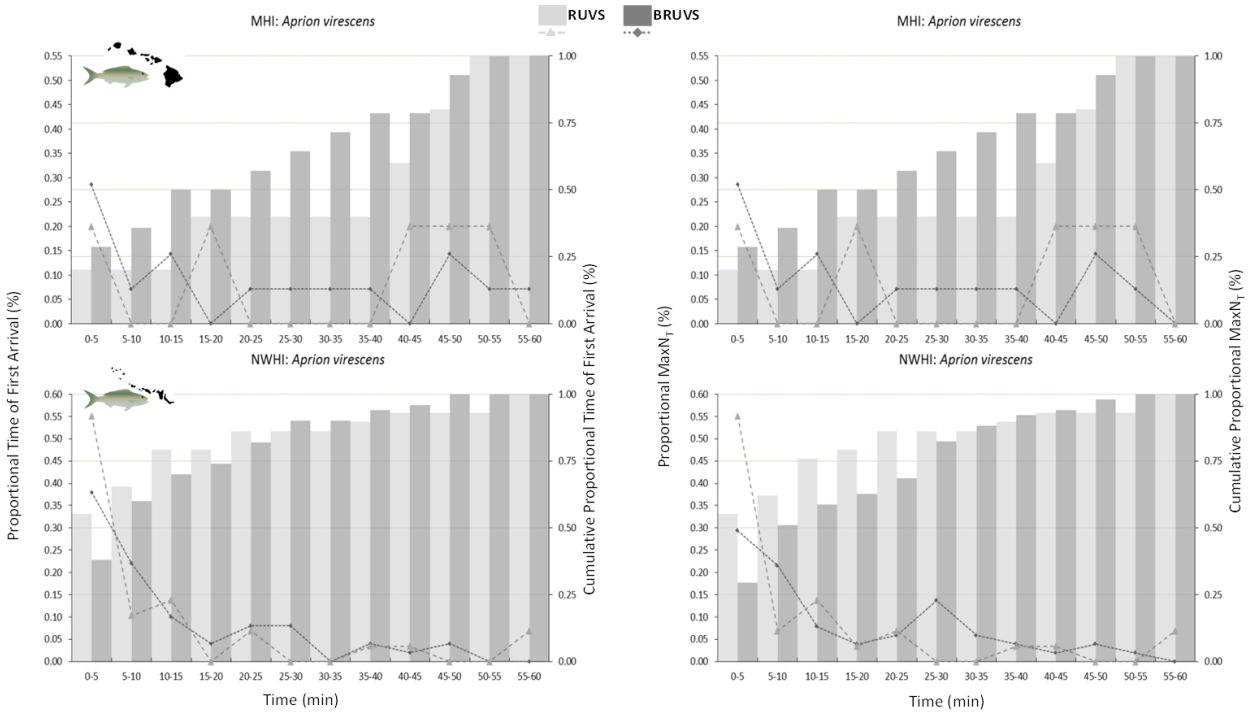


Figure S.2.4. Proportional (lines) and cumulative proportional (bars) TOFA and MaxN$_T$ of *Aprion virescens*, binned into 5-minute intervals from Time on Seabed (minute 0) up to 60 minutes. Recorded from 51 MHI and 67 NWHI RUV-BRUV sites conducted surveyed from 2012 – 2014.

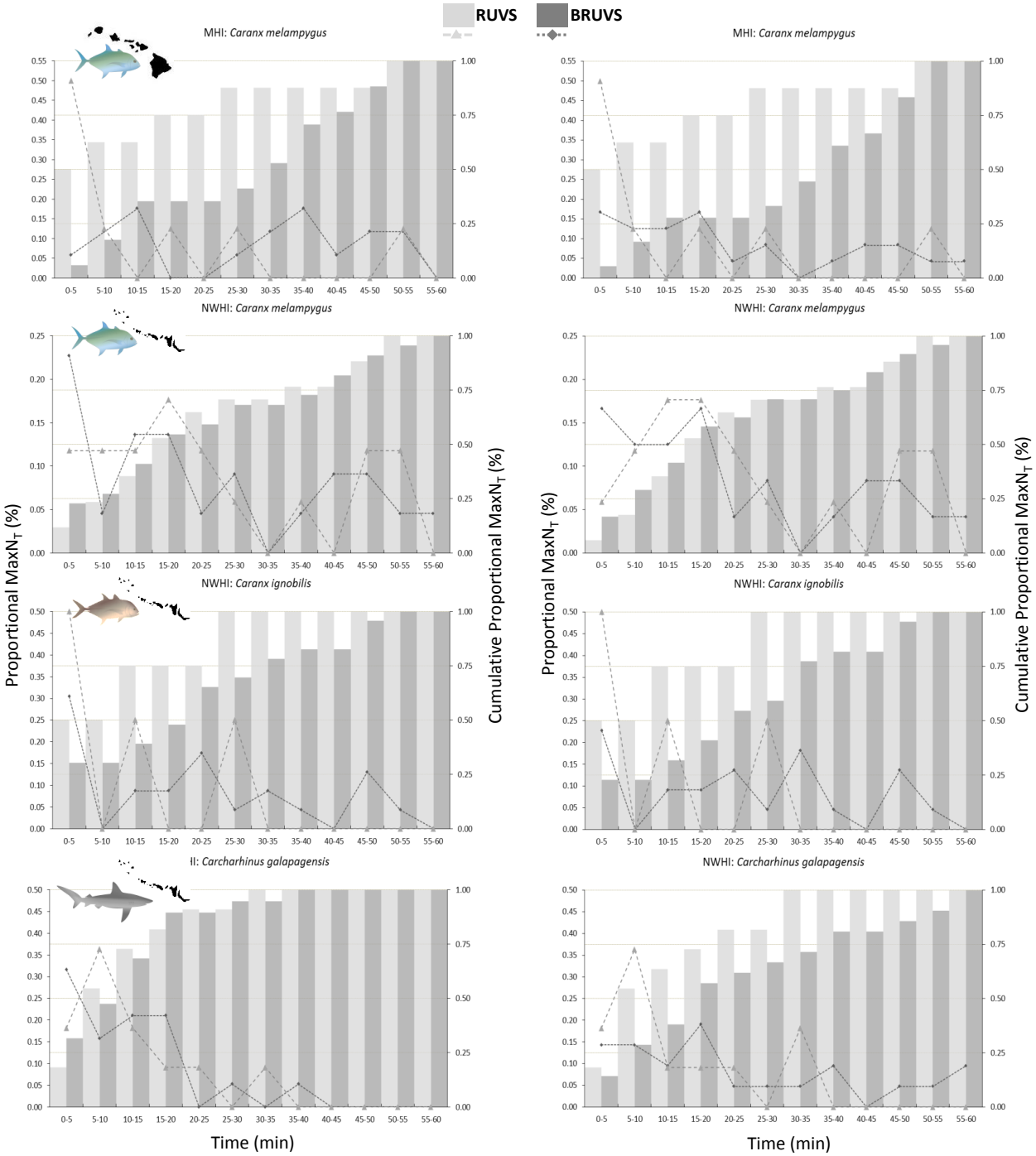


Figure S.2.5. Proportional (lines) and cumulative proportional (bars) TOFA and MaxN$_T$ of *Caranx melampygus*, *Caranx ignobilis*, and *Carcharhinus galapagensis* binned into 5-minute intervals from Time on Seabed (minute 0) up to 60 minutes. Recorded from 51 MHI and 67 NWHI RUV-BRUV sites surveyed from 2012 – 2014.

Table S.2.2. Pair-wise PERMANOVA tests of square root transformed number of species (Nsp) for RUV-BRUV MHI samples over increased 20-minute sampling intervals. Method and soak time are fixed factors. Individual functional groups based on univariate, Euclidean distance-based measures. Significant values (P < 0.05) are indicated in bold. Spaces indicate negative t-test (no P-value generated).

Pair-Wise Tests (MHI, N_{sp})	All Species (Pooled)	Herbivores	Planktivores	Mobile Invertivores	Sessile Invertivores	Corallivores	Omnivores	Piscivores	Sessile Macropiscivores	Generalist Macropiscivores	Generalist Macropiscivores (NWHI)
	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)
Baited, 0-20 vs. Baited, 0-40	**0.0331**	0.0515	0.5862	0.0788	0.2018	0.7945	0.9305*	0.4594	0.1411	**0.0071**	**0.0116**
Baited, 0-20 vs. Baited, 0-60	**0.0008**	**0.0051**	0.1829	**0.0013**	0.0910	0.3358	0.6981*	0.1503	**0.0092**	**0.0005**	**0.0001**
Baited, 0-20 vs. Unbaited, 0-20	0.1529	0.5255	0.5395	0.1295	0.4976	0.7006	0.3460*	0.5374	**0.0005**	0.5284	**0.0011**
Baited, 0-20 vs. Unbaited, 0-40	0.6023	0.4678	0.9029	0.4367	0.8198	1.0000	1.0000*	0.2647	**0.0009**	0.7021	**0.0436**
Baited, 0-20 vs. Unbaited, 0-60	0.1096	0.1316	0.5752	0.0618	0.6464	0.6931	0.6087*	**0.0337**	**0.0008**	0.1262	0.4754
Baited, 0-40 vs. Baited, 0-60	0.1553	0.2956	0.4505	0.1509	0.7072	0.4992	0.7627*	0.5158	0.2443	0.3794	**0.0442**
Baited, 0-40 vs. Unbaited, 0-20	**0.0003**	**0.0103**	0.2535	**0.0013**	**0.0477**	0.5151	0.3000*	0.1725	**0.0001**	**0.0004**	**0.0001**
Baited, 0-40 vs. Unbaited, 0-40	0.0744	0.2158	0.5095	0.2455	0.3024	0.8200	0.9244*	0.7528	**0.0001**	**0.0194**	**0.0001**
Baited, 0-40 vs. Unbaited, 0-60	0.5076	0.6256	0.9848	0.9286	0.4336	0.9057	0.6705*	0.1919	**0.0001**	0.2421	**0.0012**
Baited, 0-60 vs. Unbaited, 0-20	**0.0001**	**0.0004**	**0.0491**	**0.0001**	**0.0176**	0.1871	0.1918*	**0.0381**	**0.0001**	**0.0001**	**0.0001**
Baited, 0-60 vs. Unbaited, 0-40	**0.0016**	**0.0243**	0.1405	**0.0067**	0.1485	0.3610	0.7047*	0.6774	**0.0001**	**0.0017**	**0.0001**
Baited, 0-60 vs. Unbaited, 0-60	0.0357	0.1274	0.4238	0.0873	0.2384	0.6119	0.9066*	0.5630	**0.0001**	**0.0396**	**0.0001**
Unbaited, 0-20 vs. Unbaited, 0-40	0.0377	0.1753	0.6103	**0.0123**	0.3421	0.6986	0.3355*	0.0858	0.4002*	0.2930	0.1605
Unbaited, 0-20 vs. Unbaited, 0-60	**0.0015**	**0.0286**	0.2295	**0.0003**	0.2343	0.4456	0.1434*	**0.0060**	0.3995*	**0.0252**	**0.0028**
Unbaited, 0-40 vs. Unbaited, 0-60	0.2376	0.4394	0.5012	0.2077	0.8471	0.7106	0.6099*	0.2991	1.0000*	0.2336	0.1542

* Monte Carlo values presented where pair-wise permutations are ≤ 50

Table S.2.3. Pair-wise PERMANOVA tests of *log(x+1)* transformed number of individuals (MaxNi) for RUV-BRUV MHI samples over increased 20-minute sampling intervals. Method and soak time are fixed factors. Individual functional groups based on univariate, Euclidean distance-based measures. Significant values (P < 0.05) are indicated in bold. Spaces indicate negative t-test (no P-value generated).

Pair-Wise Tests (MHI, $MaxN_i$)	All Species (Pooled)	Herbivores	Planktivores	Mobile Invertivores	Sessile Invertivores	Corallivores	Omnivores	Piscivores	Sessile Macropiscivores	Generalist Macropiscivores	Generalist Macropiscivores (NWHI)
	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)	P(perm)
Baited, 0-20 vs. Baited, 0-40	0.1242	0.0803	0.6079	0.0954	0.0969	0.7112	0.9965	0.3268	0.1416	**0.0097**	**0.0489**
Baited, 0-20 vs. Baited, 0-60	**0.0059**	**0.0062**	0.3208	**0.0014**	**0.0383**	0.3467	0.8991	0.0951	**0.0059**	**0.0002**	**0.001**
Baited, 0-20 vs. Unbaited, 0-20	0.0556	0.5996	0.1650	**0.0344**	0.4897	0.5951	0.2465	0.3887	**0.0001***	0.3601	**0.0017**
Baited, 0-20 vs. Unbaited, 0-40	0.7503	0.5887	0.3590	0.9145	0.7767	0.9110	0.5143	0.5341	**0.0011***	0.7048	0.0653
Baited, 0-20 vs. Unbaited, 0-60	0.5177	0.2365	0.6712	0.2125	0.6163	0.8660	0.6824	0.0767	**0.0008***	0.1227	0.5056
Baited, 0-40 vs. Baited, 0-60	0.2239	0.2980	0.6331	0.1317	0.7089	0.5880	0.9301	0.4962	0.1547	0.2256	0.1376
Baited, 0-40 vs. Unbaited, 0-20	**0.0010**	**0.0219**	0.0551	**0.0007**	**0.0218**	0.3765	0.2373	0.0669	**0.0001**	**0.0008**	**0.0001**
Baited, 0-40 vs. Unbaited, 0-40	**0.0436**	0.2010	0.1544	0.0895	0.1899	0.6396	0.5043	0.6571	**0.0001**	**0.0297**	**0.0001**
Baited, 0-40 vs. Unbaited, 0-60	0.2453	0.5166	0.3322	0.5678	0.2634	0.8468	0.6611	0.5183	**0.0001**	0.3348	**0.0051**
Baited, 0-60 vs. Unbaited, 0-20	**0.0001**	**0.0017**	**0.0182**	**0.0001**	**0.0075**	0.1533	0.1842	**0.0097**	**0.0001**	**0.0001**	**0.0001**
Baited, 0-60 vs. Unbaited, 0-40	**0.0011**	**0.0228**	0.0531	**0.0007**	0.0913	0.3227	0.4314	0.2247	**0.0001**	**0.001**	**0.0001**
Baited, 0-60 vs. Unbaited, 0-60	**0.0113**	0.0876	0.1276	**0.0252**	0.1399	0.4653	0.5804	0.9053	**0.0001**	**0.0333**	**0.0001**
Unbaited, 0-20 vs. Unbaited, 0-40	0.0690	0.2944	0.6070	**0.0209**	0.3619	0.6967	0.4086*	0.1052	0.4119*	**0.2026**	0.1898
Unbaited, 0-20 vs. Unbaited, 0-60	**0.0038**	0.0836	0.2783	**0.0010**	0.2509	0.4949	0.2195*	**0.0044**	0.4068*	**0.013**	**0.0079**
Unbaited, 0-40 vs. Unbaited, 0-60	0.2722	0.5093	0.5867	0.2127	0.8431	0.7943	0.7054*	0.2132	1.0000*	0.2444	0.1991

* Monte Carlo values presented where pair-wise permutations are ≤ 50

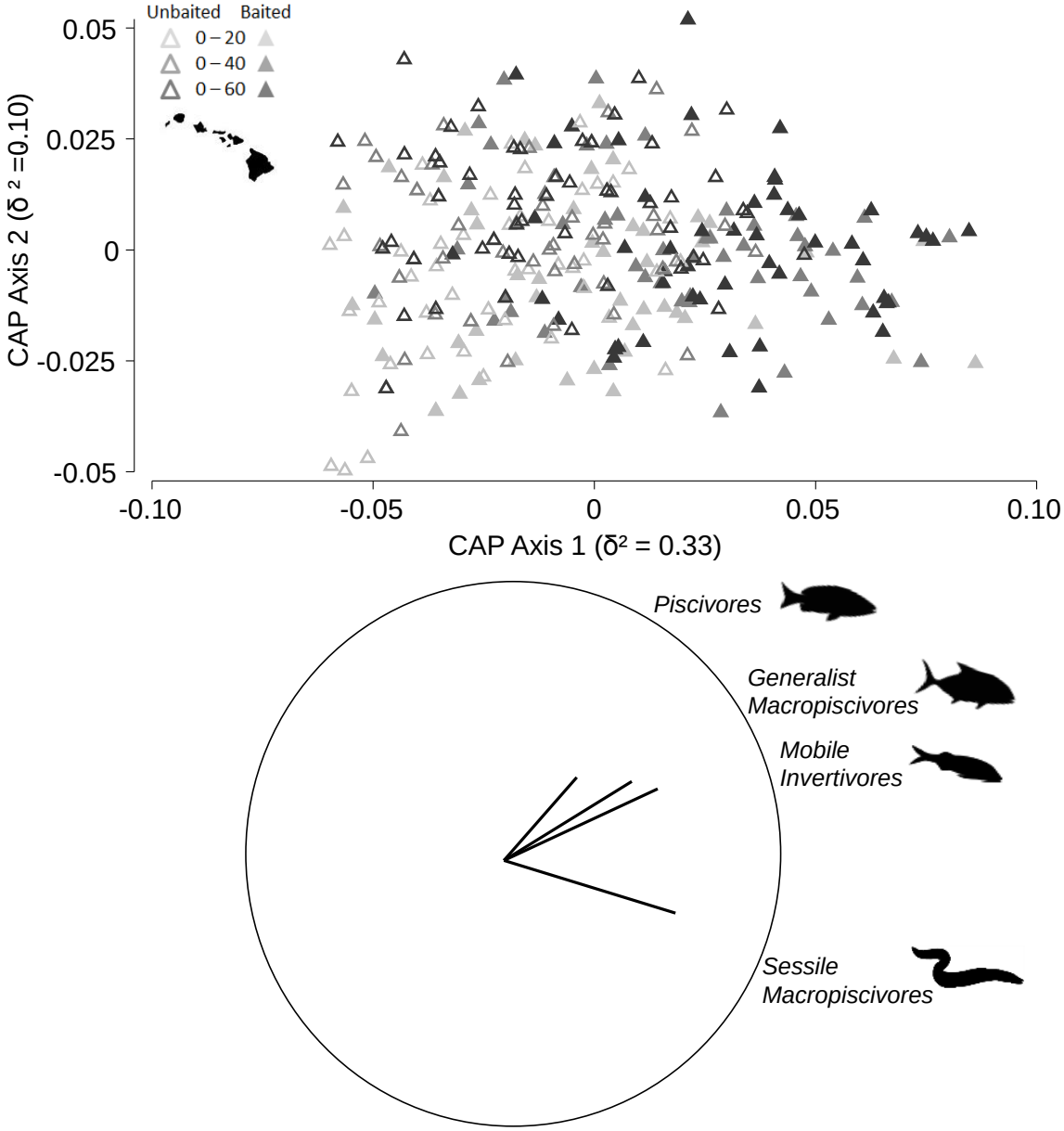


Figure S.2.6. Canonical analysis of principal components (CAP) generated from Modified Gower Log base 10 dissimilarity measures of functional groups across MHI RUV-BRUV soak times. Choice of m = 7. Functional groups with Pearson R values $\geq$ 0.4 are shown.

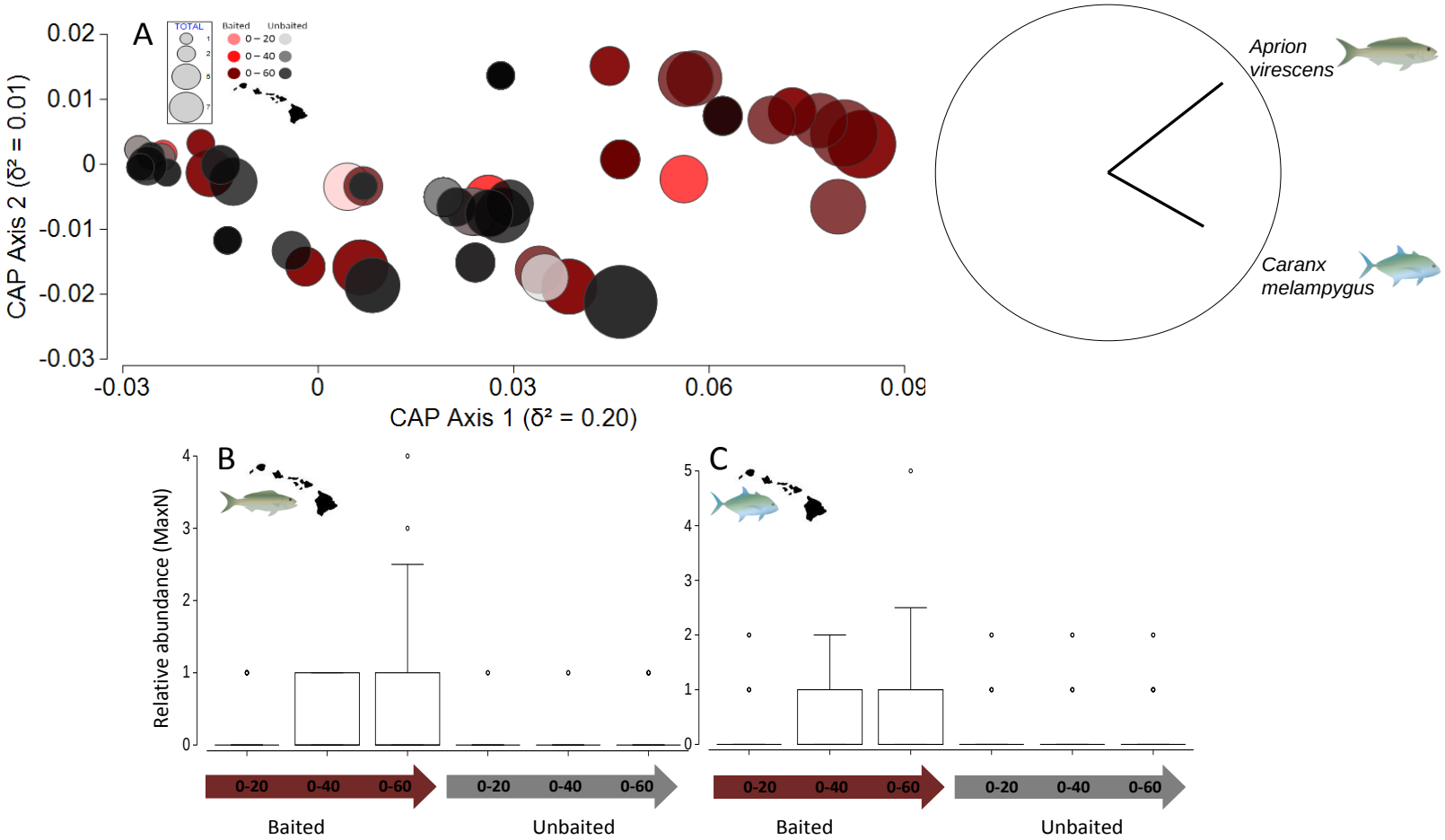


Figure S.2.7. A.) Canonical analysis of principal coordinates (CAP) ordination, testing for differences in generalist macropiscivore predator abundances between methods and soak times in the MHI. Species with Pearson R values > 0.4 are shown. Correlations with the canonical axis indicated by vector length and direction. *Boxplots* of relative abundance (MaxN) of contributory species, B.) *Aprion virescens* C.) *Caranx melampygus*.

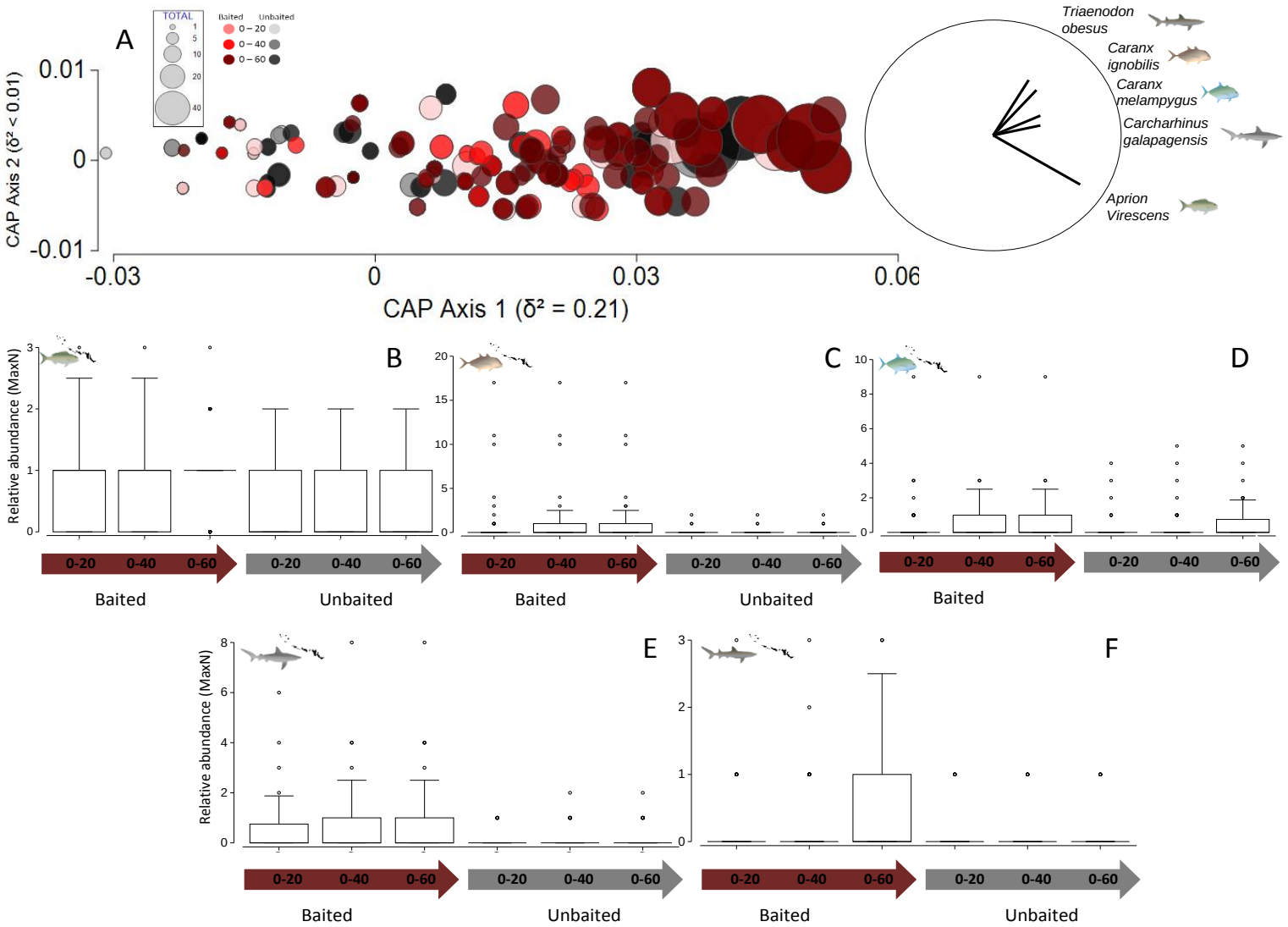


Figure S.2.8. A.) Canonical analysis of principal coordinates (CAP) ordination, testing for differences in generalist macropiscivore predator abundances between methods and soak times in the NWHI. Generalist macropiscivore species with Pearson R values > 0.4 are shown. Correlations with the canonical axis indicated by vector length and direction. *Boxplots* of relative abundance (MaxN) of contributory species, B.) *Aprion virescens* C.) *Caranx ignobilis* D.) *Caranx melampygus* E.) *Carcharhinus galapagensis* F.) *Triaenodon obesus*.

Table S.2.4. Canonical analysis of principal coordinates (CAP), leave-one-out allocation to groups. Tested at the functional group (MHI only) and generalist macropiscivore species-levels (MHI, NWHI).

Functional Groups (MHI)								
Original Group	Baited, 0-20	Baited, 0-40	Baited, 0-60	Unbaited, 0-20	Unbaited, 0-40	Unbaited, 0-60	Total	%correct
Baited, 0-20	10	7	9	14	4	7	51	19.608
Baited, 0-40	5	9	20	6	1	10	51	17.647
Baited, 0-60	6	10	27	2	1	5	51	52.941
Unbaited, 0-20	6	5	0	27	5	8	51	52.941
Unbaited, 0-40	8	5	3	19	5	11	51	9.804
Unbaited, 0-60	2	7	6	13	8	15	51	29.412
Generalist macropiscivores								
Original Group (MHI)	Baited, 0-20	Baited, 0-40	Baited, 0-60	Unbaited, 0-20	Unbaited, 0-40	Unbaited, 0-60	Total	%correct
Baited, 0-20	0	2	11	19	1	1	34	0.000
Baited, 0-40	0	2	17	13	0	2	34	5.882
Baited, 0-60	0	6	19	7	0	2	34	55.882
Unbaited, 0-20	0	2	6	25	1	0	34	73.529
Unbaited, 0-40	0	2	7	23	2	0	34	5.882
Unbaited, 0-60	0	2	11	17	3	1	34	2.941
Original Group (NWHI)	Baited, 0-20	Baited, 0-40	Baited, 0-60	Unbaited, 0-20	Unbaited, 0-40	Unbaited, 0-60	Total	%correct
Baited, 0-20	22	0	15	3	9	18	67	4.478
Baited, 0-40	9	2	14	1	9	32	67	13.433
Baited, 0-60	5	1	11	3	7	40	67	59.701
Unbaited, 0-20	40	2	11	0	8	6	67	59.701
Unbaited, 0-40	32	3	10	5	7	10	67	4.478
Unbaited, 0-60	26	2	14	4	8	13	67	20.896

Chapter 3 – Mesophotic depth gradients impact reef fish assemblage composition and functional group partitioning in the Main Hawaiian Islands

Abstract

Mesophotic coral ecosystem (MCE) research has increased considerably in recent years, as MCEs may provide partial insulation from the effects of climate change, localized anthropogenic stressors, and may dampen fishing pressures for target species depleted in shallower waters. However, few studies have examined coral reef fish assemblages and functional groups across shallow water to mesophotic depth gradients. In the Main Hawaiian Islands, we investigated coral reef fish communities between 0 and 100 m using baited remote underwater stereo-video. While significant community shifts were detected when transitioning from shallow water to mesophotic depths, relative abundance and species richness remained highest between 0 – 30 m. Mobile invertivores and generalist macropiscivores were exceptions, recording higher abundance and richness values in deeper waters. Depth, habitat complexity, and percent cover of unconsolidated sediment and macroalgae were the main reef fish community drivers in multivariate regression and distance-based linear models. Finally, several target species were more abundant and/or larger in deeper waters, suggesting stock assessment and resource management strategies are incomplete without the incorporation of mesophotic portions of stocks.

Introduction

Until recently, research, monitoring, and management of coral reef fishes primarily relied on data collected using underwater visual censuses on open-circuit scuba between 0 – 30 m (herein denoted as 'shallow water' in the context of this study). However, many fishes present in shallow water habitats are depth-generalists, able to reside in 'mesophotic' depths of 30 – 150 m or more (Thresher and Colin 1986; Ginsburg 2007; Brokovich et al. 2008; Kahng et al. 2010; Slattery et al. 2011; Bridge et al. 2013; Bejarano et al. 2014). In addition, while not fully protected from environmental or biological disturbance events, mesophotic coral ecosystems ('MCEs') may be partially shielded from some of the influences impacting shallow water coral reefs, and serve as population reservoirs for depth-generalists targeted by fishers in 0 – 30 m depths (Glynn 1996; Riegl and Piller 2003; Bak et al. 2005; Lesser et al. 2009; Bongaerts et al. 2010; Slattery et al. 2011; Kane et al. 2014; Lindfield et al. 2014; Tenggardjaja et al. 2014; Baker et al. 2016; Lindfield et al. 2016). Conversely, while shallow water coral reefs and associated habitats (e.g. pavement or rubble flats) may shelter depth-restricted specialist fishes incapable of inhabiting deeper depths, MCEs and other deep-water mesophotic benthic habitats ("MBHs") can likewise host distinct communities and species of reef fishes not found in 0 – 30 m depths, with depth, habitat type, structural complexity, and biotic cover acting in concert with geographic extent and oceanographic drivers to structure assemblages and functional-level groupings (Thresher and Colin 1986; Beukers and Jones 1998; Brokovich et al. 2008; MacNeil et al. 2009; Harvey et al. 2013b; Komyakova et al. 2013; Jankowski et al. 2015; Andradi-Brown et al. 2016a; Heyns-Veale et al. 2016; Rosa et al. 2016). As a result, limitations of many marine science research programs include missing portions of reef fish populations that are utilizing deeper habitats, or omitting species of potential conservation or management importance that are restricted to mesophotic depths. However, despite increased mesophotic research over the past two decades and the potential importance of these systems, Pacific MCEs remain understudied and relatively unassessed in comparison with their shallower counterparts (Bridge et al. 2013; Kahng et al. 2014).

Historic mesophotic research in the Main Hawaiian Islands ('MHI') has primarily focused on exploration

(Brock and Chamberlain 1968; Strasburg et al. 1968), surveys of specific taxa or target species (Grigg 2004; Kahng and Grigg 2005; Tenggardjaja et al. 2014), habitat and zone characterization (Locker et al. 2010; Rooney et al. 2010; Blyth-Skyrme et al. 2013; Costa et al. 2015; Veazey et al. 2016), spatially focused investigations, e.g. host reef fish assemblages inhabiting mesophotic black coral (*Antipathes*) patches and deep artificial reefs (Grigg 1965; Moffitt et al. 1989; Boland and Parrish 2005), or characterized localized reef fish assemblages, functional groups, and the effects of environmental variables limited to small areas (Kane 2016). While Fukunaga et al. (2016) characterized reef fish assemblage, functional group, and endemism patterns holistically across shallow water to mesophotic gradients in the Northwestern Hawaiian Islands (NWHI), similar investigations in the MHI remains comparatively sparse.

To a large degree, the lack of MCE research and monitoring, in comparison with shallow water coral reef ecosystems, has been due to logistical, technical, and financial constraints associated with the use of technical mixed-gas or closed circuit rebreather (CCR) diving and the use advanced remote sampling technologies, e.g. submersibles (Pyle 1996; Pyle 2000; Kahng et al. 2010). The advent of baited remote underwater stereo-video (stereo-BRUVs, herein denoted as 'BRUVS' as in Chapter 2) represents an alternative, cost-effective approach that has been increasingly used to assess MCE reef fish populations (Pearson and Stevens 2015; Lindfield et al. 2016). Here, we analyzed BRUVS data collected from 107 sites around the MHI, with the objective of characterizing changes in reef fish community structure from shallow water to mesophotic depths. We focus on changes to overall reef fish assemblages and functional-level partitions along depth gradients and their relationships to a range of habitat variables (Boland 2011; Kane 2016). We also explore the potential for mesophotic depth-refugia of reef fish 'target' species (those subjected to commercial or recreational fishing extraction) and whether relative abundance of endemic species or the proportion of the fish community they make up changes with depth (Kane et al. 2014; Fukunaga et al. 2016; Kosaki et al. 2016).

Methods

Survey Area

The MHI consist of eight volcanic islands with a resident human population of over 1.4 million people (census.hawaii.gov), stretched across a 650 km SE-NW gradient between 19°N, 155°W to 22°'N, 160°10'W.

Sites located around Oahu, Maui, Molokai, Lanai were surveyed during two NOAA research expeditions in September and October 2012, and by shore-based small boat sampling efforts around Oahu in November 2013 (Figure 3.1).

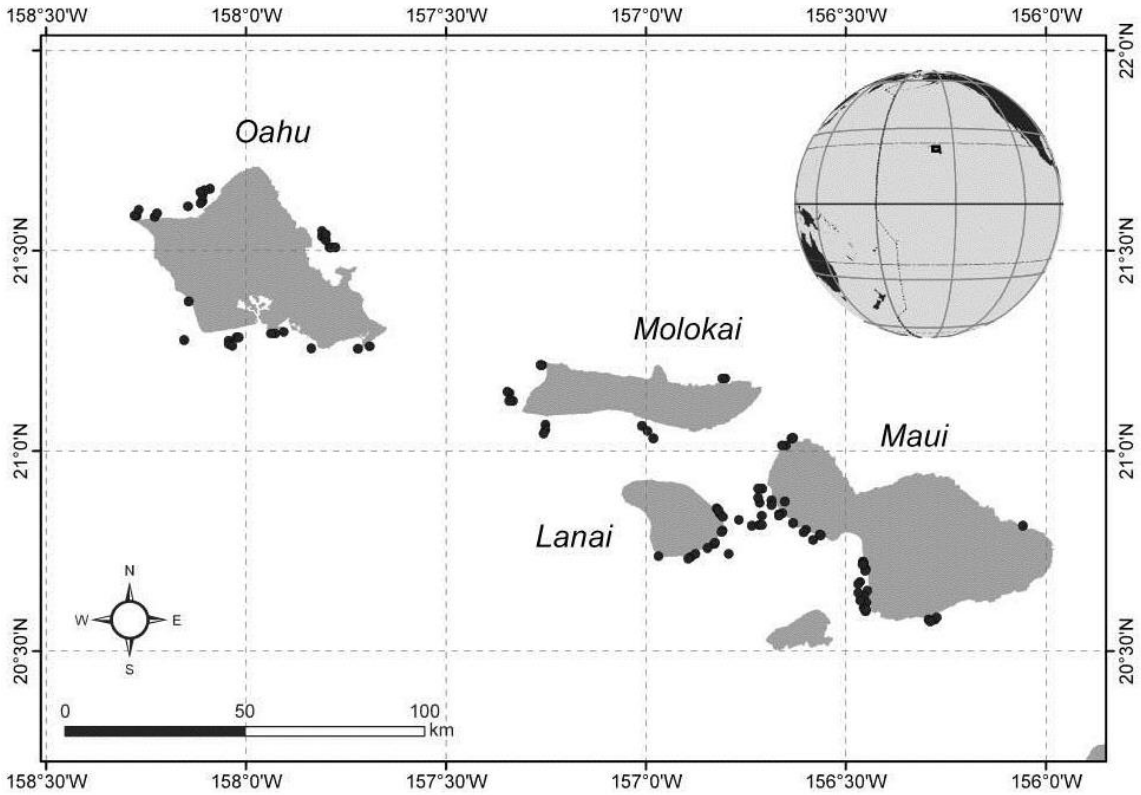


Figure 3.1. Stereo-BRUVs survey locations in the Main Hawaiian Islands. Dark circles indicate individual BRUVS deployment sites.

Sampling design

BRUVS are a widely-used fishery-independent technology, able to generate information on relative abundance and length-distributions of demersal fishes (Harvey and Shortis 1995; Harvey and Shortis 1998) . For this study, shallow water BRUVS sites between 0 – 30 m were a randomly selected subset of locations that had previously been surveyed by divers on SCUBA as part of routine monitoring surveys conducted by NOAA Coral Reef Ecosystem Program (CREP, Heenan et. al, 2014). Sites between 30 – 100 m were randomly selected from a pool of 500 x 500 m grid cell center points constrained within 100 m contour lines of each island. These sites were at least 500 m apart to reduce the likelihood of bait plume overlaps and stratified into three depth bins (30 – 53, 53 – 76, 76 – 100 m); however, the two deeper bins were combined *post hoc* (53 – 100 m, 'lower mesophotic') due to low hard-bottom sampling frequencies at those depths ('depth', fixed: 3 levels, *shallow water*, *upper mesophotic*, *lower mesophotic*).

Because the goal was to compare hard-bottom habitats, grid cells containing > 35% unconsolidated sediment derived from multibeam backscatter data (Pacific Islands Benthic Habitat Mapping Center 2006, 2007, 2009) were excluded from the survey domain. However, at many of the deeper deployment sites, bottom type information was not available or was inaccurate and thus many of those deployments were on what appeared to be 100% unconsolidated sediment (i.e. sand flats). While not targeted in this study, these sites were included in analyses with the addition of a two-level fixed factor ('habitat': *hard-bottom* versus *unconsolidated sediment*).

Each BRUVS was deployed for a 60 minute sampling period (Watson et al. 2005; Bernard and Götz 2012), using approximately 800 g of Japanese sanma (*Cololabis saira*) pulped into a wire mesh basket 1.2 meters in

front of the stereo-cameras. We selected *Cololabis saira* because it is locally available and functionally similar to the more commonly used pilchard (*Sardinops sagax*), as both are oily soft-fleshed fishes widely used by fishers as attractants. Pilchards have been shown to be an appropriate bait for studies using BRUVS (Cappo et al. 2007; Harvey et al. 2012b; Harvey et al. 2013b; Walsh et al. 2016), and although we recognize that the type of bait used will have some impact on survey outcomes, evidence suggests BRUVS surveys remain relatively robust to the bait used (Dorman et al. 2012; Ghazilou et al. 2016). While more work in this area would be desirable, overall we believe that *Cololabis saira* is likely to be a suitable general attractant, and one that provides scope for highly meaningful comparison with the majority of other BRUVS studies to date.

Stereo-cameras were placed on a base bar mounted 0.7 m apart inside a galvanized steel roll-bar frame, inwardly converged at 8° and covering ~51 m^2 when identifying reef fishes within $\leq$ 7 m distance from BRUVS (Harvey et al. 2007). Any individual fishes observed > 7 m from BRUVS were omitted from annotation and analysis. Lastly, two shallow water (0 – 30 m) sites were discarded, as nutrient outflows and runoff reduced in-water visibility to less than 7 m.

Data processing

Each BRUVS consisted of a paired Sony handycams that were calibrated using CAL™ software (www.seagis.com.au; Seager 2008) according to standard protocols before and after each data collection effort (Harvey and Shortis 1998; Shortis and Harvey 1998). Following completion of field sampling, stereo-video files were reviewed with species annotated to the lowest possible taxonomic level using the program EventMeasure-Stereo™ (Seager 2008).

The *MaxN* metric was used as the basis for abundance estimation (Ellis and Demartini 1995; Willis and Babcock 2000a; Willis et al. 2000b), and fork-length measurements were taken for a subset of target species at the time of MaxN. All species annotations were reviewed prior to data analysis, with quality control completed by one analyst to retain consistency (Wilson et al. 2007).

Group classification

Fish species sampled by BRUVS in the MHI were assigned to functional group categories, as described in Harvey et al. (2007) and Barnard et al. (2012), based on dietary, behavioral, and morphological traits. The NOAA PIFSC CREP MHI reef fish database (Heenan et al., 2014), and FishBase, ver. 11/2014 (Froese and Pauly 2014) served as primary classification sources, with a subset of species assignments cross-checked against functional classifications generated from isotopic analyses (Bradley et al. 2015). The nine functional groupings were: herbivores, planktivores, mobile invertivores, sessile invertivores, corallivores, omnivores, and lower-level piscivores. Sessile macropiscivores were additionally defined as a functional group encompassing large-bodied eel species belonging to Muraenidae and Ophichthidae, while generalist macropiscivores incorporated all large-bodied, roving predators following guidelines as specified in Friedlander and DeMartini (2002). These included the snapper *Aprion virescens*, non-planktivorous jacks, barracuda, and sharks (i.e. apex predators). Fishes that could only be identified to family or genus level were binned into groupings based on the NOAA PIFSC CREP classification system (Heenan 2014).

Species encountered during this study were further categorized as a) target species – being those with > 450

kg yr $^{-1}$ of landings between 2000 – 2010, based on information obtained from local commercial (CML) and recreational (Marine Recreational Information Program, MRIP) catch reports analyses in the MHI (Stamoulis 2016). Targets species identified as being below a sustainability threshold, i.e. potentially overfished with spawning potential ratio (SPR) < 30%, (Nadon et al. 2015) were additionally flagged within each respective functional group; and b) Hawaiian endemics, i.e. species found solely in the Hawaiian Archipelago and Johnston Atoll (DeMartini and Friedlander 2004; Randall 2007; Wagner et al. 2014). Additional details describing group assignments are given in Supplementary Materials, Table S3.1.

A total of 75 fish could not be identified even to family level, and were excluded from analysis. However, they only constituted between 0.5 (0 – 30 m hard-bottom) and 4% (30 – 53 m, unconsolidated sediment) of total abundance.

Habitat and Environmental Drivers

A number of habitat and environmental variables were gathered for each deployment: depth (obtained from attached depth-gauges; habitat complexity was rated on a five-point scale, with 1 = no vertical relief to 5 = high vertical relief (Wilson et al. 2007; Ayotte et al. 2015b); and percent cover of coral, macroalgae, turf, crustose coralline, and sand were visually estimated from BRUVS imagery. The metrics "distance from shore" and "distance from nearest boat ramp" were also derived for each site using ArcGIS, version 10.3 (http://www.esri.com/software/arcgis).

Statistical Analyses

All statistical analyses described below were conducted using PRIMER version 7.0.11 with the PERMANOVA+ add-on (Clarke and Warwick 2001; Anderson 2008a; Clarke and Gorley 2015), unless otherwise specified.

Both univariate and multivariate tests, and subsequent community and functional group inferences between depth and habitat strata, should be treated with caution as a result of asymmetric hard-bottom versus unconsolidated sediment sampling. In particular, while the small number of unconsolidated sediment surveys between 0 – 30 m (2) and 30 – 53 m (5) were included in statistical testing and graphics displays, they could only be peripherally interpreted. Similarly, while the primary focus remains centered around hard-bottom reef fish communities, conclusions derived from sites between 53 – 100 m (10), in comparison to shallow water (40) and upper mesophotic (24) hard-bottom strata, were limited.

Univariate Tests

All univariate statistical tests used pair-wise permutational analysis of variance (permutational ANOVA, Anderson 2008) based on Euclidean distance-based matrices with Type III sums of squares. Total abundance (summed MaxN) and species richness (summed total species, S) were calculated at community, functional, and endemic group levels across depth and habitat strata using untransformed, univariate datasets. Monte Carlo P-values were utilized for small sample sizes, i.e. where there were fewer than 100 permutations (Anderson 2008a).

Community assemblage and functional group structure

A canonical analysis of principal components (CAP) (Anderson and Willis 2003) was used as a global test to assess structural differences in overall fish assemblages and the precision of factored depth and habitat categories. A "leave-one-out" allocation and cross-validation test (Lachenbruch and Mickey 1968; Anderson 2008a) was generated to identify misclassification errors and measure the accuracy of depth and habitat assignments, with the number of axes (m) chosen by plotting the residual sum of squares. Pearson rank correlation values $\geq$ 0.4 were used to visualize associations between individual species and canonical axes.

A permutational multivariate analysis of variance (PERMANOVA) was further used to assess multivariate differences in the overall reef fish community (Anderson and Walsh 2013), with pair-wise tests completed *post hoc* to assess significance levels between the six potential depth-habitat combinations, with p-values obtained using permutation tests (9999 permutations) for each individual term in the model and Monte Carlo P-values employed if tests had fewer than 100 permutations (Anderson 2008a). Community abundance data was *log(x+1)* transformed to down-weight more abundant species prior to generating a Bray-Curtis dissimilarity matrix, which is appropriate for statistical tests utilizing abundance information (Faith et al. 1987). Metric multidimensional scaling ordinations (mMDS) of total reef fish assemblages, major functional group communities, and endemic group centroids were generated in order to further visualize relationships between communities and increasing depths and varying habitat strata. These were standardized and transformed via Index of Association (Whittaker 1960) and clustered along the y-axis using a Type III SIMPROF analysis with a complementary cophenetic correlation coefficient to assess clustering accuracy between pair-wise distances (Sokal and Rohlf 1962) and ordered along the x-axis according to depth and habitat categories. Unlike the more commonly used nonmetric multidimensional scaling (nMDS), which are 2-D ordinations generated from (dis)similarities on a monotonic scale of distances (Clarke and Warwick 2001), mMDS retains linear inter-point distances versus ranks of distances and may be more reliable when the number of group centroids is low. Finally, shade plots (heat maps) of the four most numerically abundant functional groups were plotted, with species summed, standardized, and transformed using protocol as described for mMDS plots (see above) and ordered along the x-axis according to depth and habitat categories. For mobile invertivores, only those species contributing to $\geq$ 20% abundance were depicted in graphic visualizations (i.e. excluding species which, for every site, account for < 20% of its total abundance) due to the disproportionately high number of species encountered in this functional group.

Length-based estimates

Fork-lengths of all generalist macropiscivores and stock-assessment targets were collected at the time of MaxN. Non-parametric kernel density estimates (KDEs) were used to approximate length frequency distributions between shallow water and pooled mesophotic zones following the approach used by Langlois et al. (2012), with a minimum requirement of 10 individuals measured per strata. KDE bandwidths were selected using Sheather-Jones assignment protocol (Sheather and Jones 1991) via the function *dpik* in the package *KernSmooth* in the R statistical program version 3.3.0 (Wand and Jones 1995; Wand 2011).

Habitat and Environmental Linkages

A principal components analysis (PCA) was used to evaluate and distinguish differences between normalized habitat variables along depth and habitat categories. Variation was depicted along the first two principal axes, with environmental vectors indicating strength and direction.

Two complementary models assessed the influence of environmental drivers, distance to boat ramp, and distance from shore on reef fish assemblage structures. A multivariate regression tree (MRT) followed the approach described by Borcard et al. (2011) and Lindfield et al. (2016) using the R package *mvpart* (De'ath 2014) with MRTs primarily acting as predictive (versus explanatory) models. Prior to MRT generation, relative abundance data were first Hellinger-transformed, which is an approach well-suited for species abundance datasets, granting lower weights to rare species (Legendre and Gallagher 2001) and multiple zero counts (Rao 1995). Optimal tree size was generated from 100 model runs, with the model selection output based on the highest cross-validated predictive accuracy. The *labdsv* package and *indval* function used to generate subsequent species indicator values from the Dufene and Legendre Index (DLI) (Dufrene and Legendre 1997; Borcard et al. 2011), with the top 10 (maximum) species that recorded a significant difference ($p < 0.05$) listed in order of decreasing DLI values for each MRT leaf output. The subsequent distance-based linear model (DSTLM) and distance-based redundancy analysis (dbRDA) were generated in PERMANOVA+ (Anderson 2008a) as a matching explanatory model, using normalized environmental variables, a Bray-Curtis dissimilarity matrix of *log(x+1)* transformed community abundance data, and based off the modified Aikaike's Information Criterion (AICc) and *BEST* procedure.

Results

A total of 5,583 fish belonging to 36 families were recorded over 107 BRUVS deployments (Figure 3.1). Herbivores, planktivores, and mobile invertivores were the largest components of fish assemblages (Figure 3.2 and Supplementary Materials, Figure S3.1), ranging between 86 – 93% of total abundance and 74 – 82% of species richness at hard-bottom sites, and 77 – 83% abundance and 59 – 79% of species richness at unconsolidated sediment sites, depending on depth. Remaining groups constituted between 0.5 and 4% of total abundance per depth-habitat combination, with the exception of piscivores (8%, 53 – 100 m unconsolidated sediment sites, Figure S3.5B) and generalist macropiscivores (9 – 15% at unconsolidated sediment sites in upper and lower mesophotic zones, Figure 3.8D). We therefore focused analysis on the three prominent functional groups, along with generalist macropiscivores.

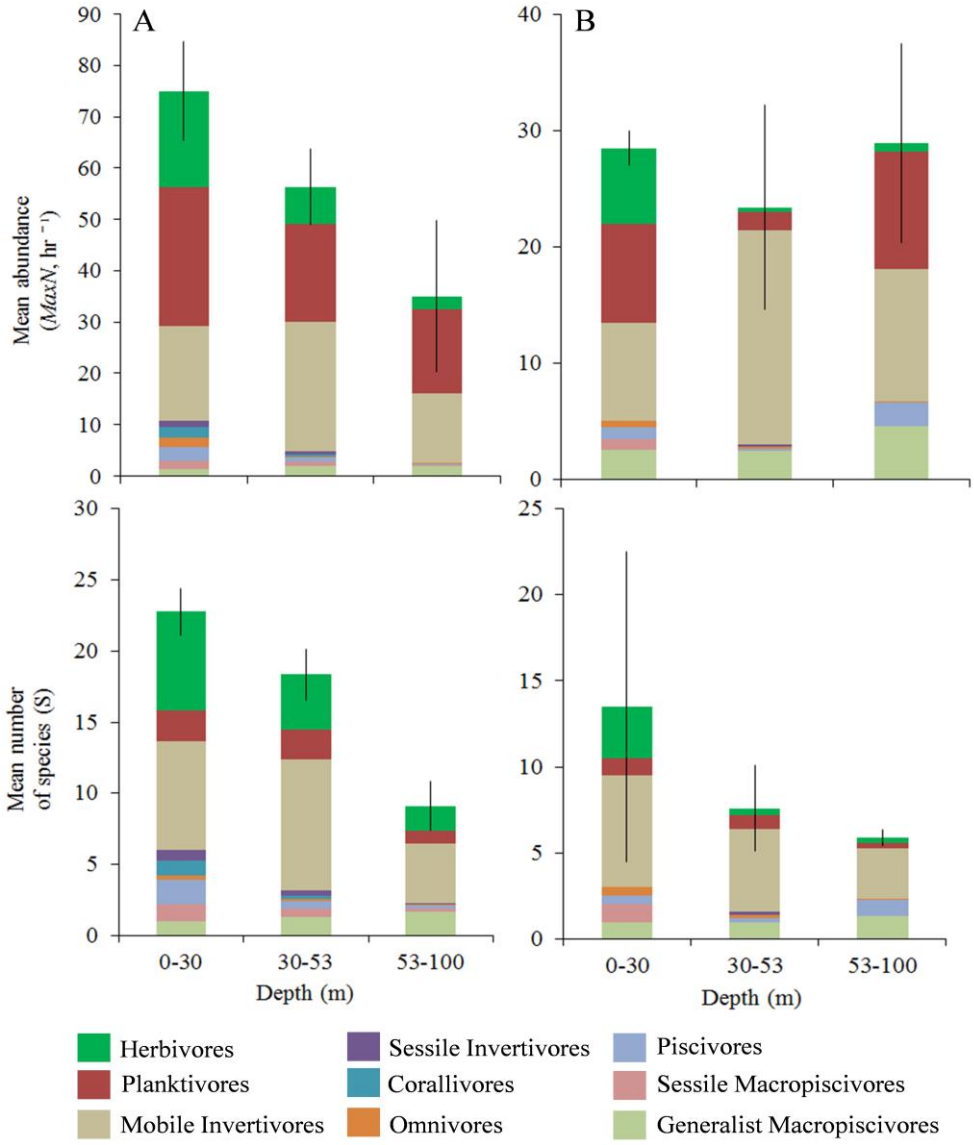


Figure 3.2. Mean trophic group relative abundance (mean MaxN, hr^{-1} ± SE) and species richness (mean number of species, S). A.) Hard-bottom, B.) 100% unconsolidated sediment. Different colors within bars indicate trophic assignments. Note the differing scales between hard-bottom vs. unconsolidated sediment sites.

Univariate Analysis

While community abundance and species richness measures consistently declined with depth (Figures 3.3, 3.4), univariate permuational ANOVAs revealed no significant differences between shallow water and upper mesophotic hard-bottom sites; however, differences (pooled MaxN, all pair-wise tests < 0.01; species richness, all pair-wise tests < 0.001) were noted between those strata and both habitat types in the lower mesophotic zone.

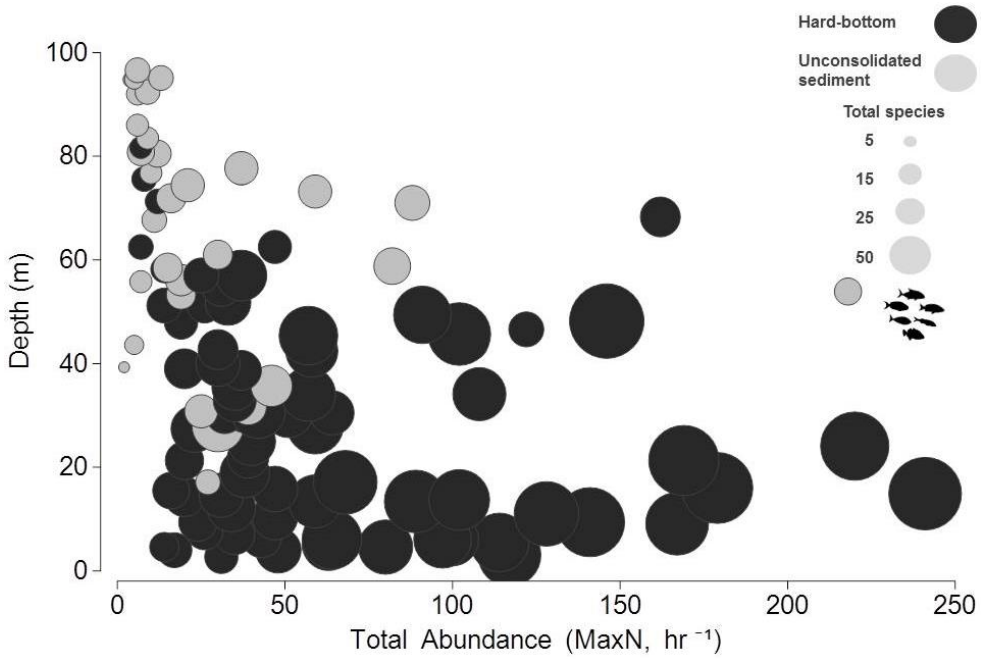


Figure 3.3. *Bubble plot* of total, untransformed relative abundance estimates (MaxN, hr $^{-1}$) in relation to depth and species richness (total species, S).

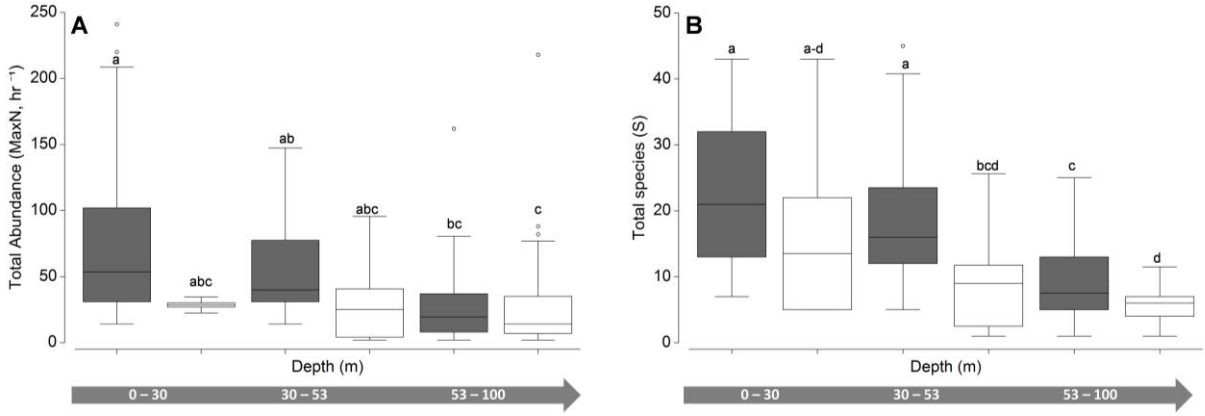


Figure 3.4. Univariate *box plots* of A.) untransformed pooled relative abundance (Total MaxN, hr $^{-1}$) and B.) species richness (total species, S). Columns sharing the same letter do not differ significantly at the 95% confidence level based on PERMANOVA pair-wise tests. Dark boxes indicate hard bottom, white boxes indicate unconsolidated sediment.

Univariate patterns varied within each primary functional group (Figures 3.5, 3.6). Herbivore abundance and richness measures generally declined with depth and when in soft bottom strata (all metrics $p < 0.05$) where herbivores were scarce. In contrast, univariate planktivore abundance and richness tests detected no significant differences among hard-bottom strata, even though planktivores constituted a greater proportion of overall reef fish communities in the lower mesophotic zone irrespective of habitat type (Figure S3.1). Mobile invertivores were represented by more species than any other functional group encountered and were significantly more abundant and species-rich in 30 – 53 m hard-bottom sites than all other assessed strata (all $p < 0.05$, except for sparsely sampled unconsolidated sediment sites in shallow water and upper mesphotic zones). Generalist macropiscivore abundance was significantly higher between shallow water hard-bottom versus lower mesophotic unconsolidated sediment sites; however, there were no differences in species richness between any assessed strata.

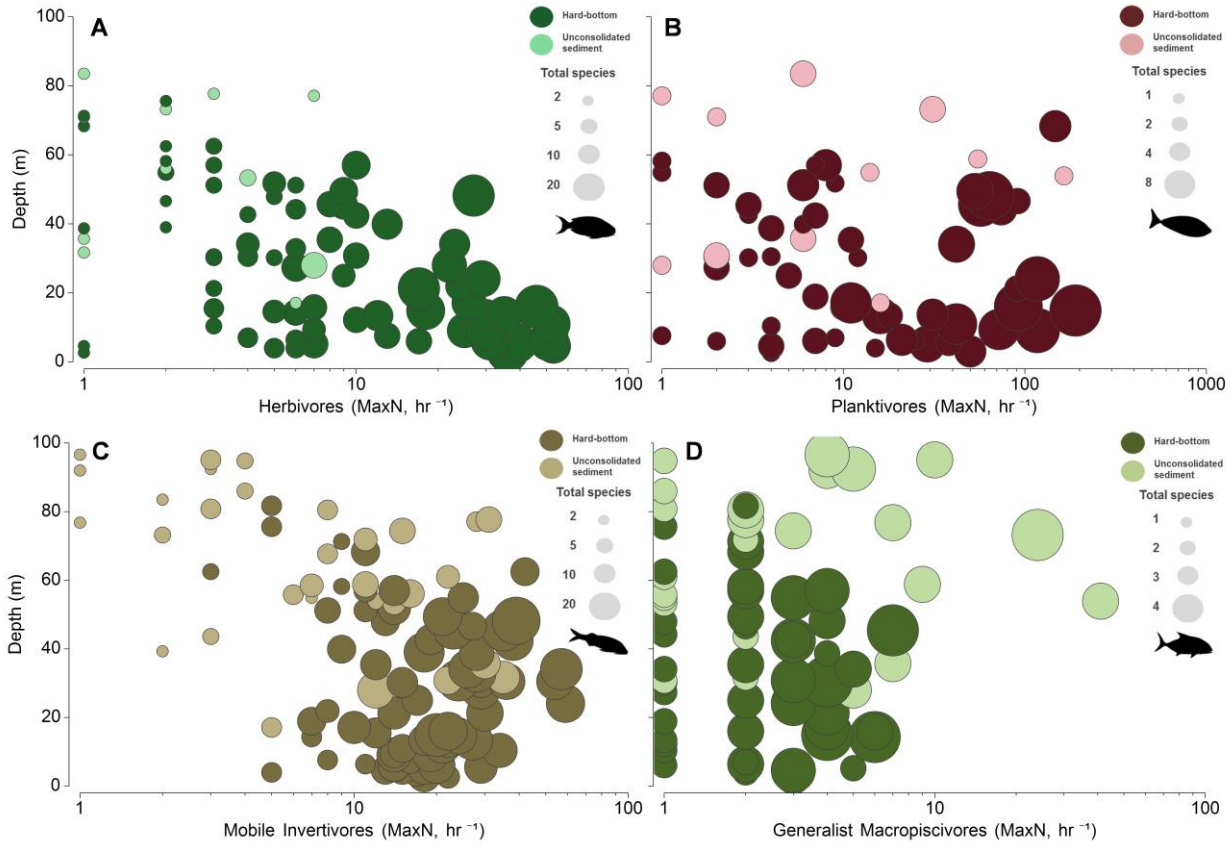


Figure 3.5. *Bubble plots* of untransformed relative abundance (MaxN, hr $^{-1}$) in relation to depth and species richness (total species, S) for (A) herbivores, (B) planktivores, (C) mobile invertivores, and (D) generalist macropiscivores. x-axis abundance estimates displayed on a log scale.

Outputs from less common functional groups analyses (sessile invertivores, corallivores, omnivores, lower level piscivores, sessile macropiscivores) are documented in further detail in Figures S3.4 and S3.5, Supplementary Materials. In brief, sessile invertivores, corallivores, and sessile macropiscivores were most prevalent in 0 – 30 m depths on hard-bottom strata, quickly dropping in abundance and richness between 30 – 53 m and were largely absent in the deepest strata. Omnivores were similarly most prevalent and speciose in shallow water and upper mesophotic zones, but were almost exclusively limited to unconsolidated sediments. Finally, piscivores tended to also show declining richness and abundance with depth in hard bottom strata, but had relatively high richness and abundance at deeper mesophotic soft-bottom strata, largely attributed to relatively high abundance of *Fistularia commersonii* and Synodontidae spp.

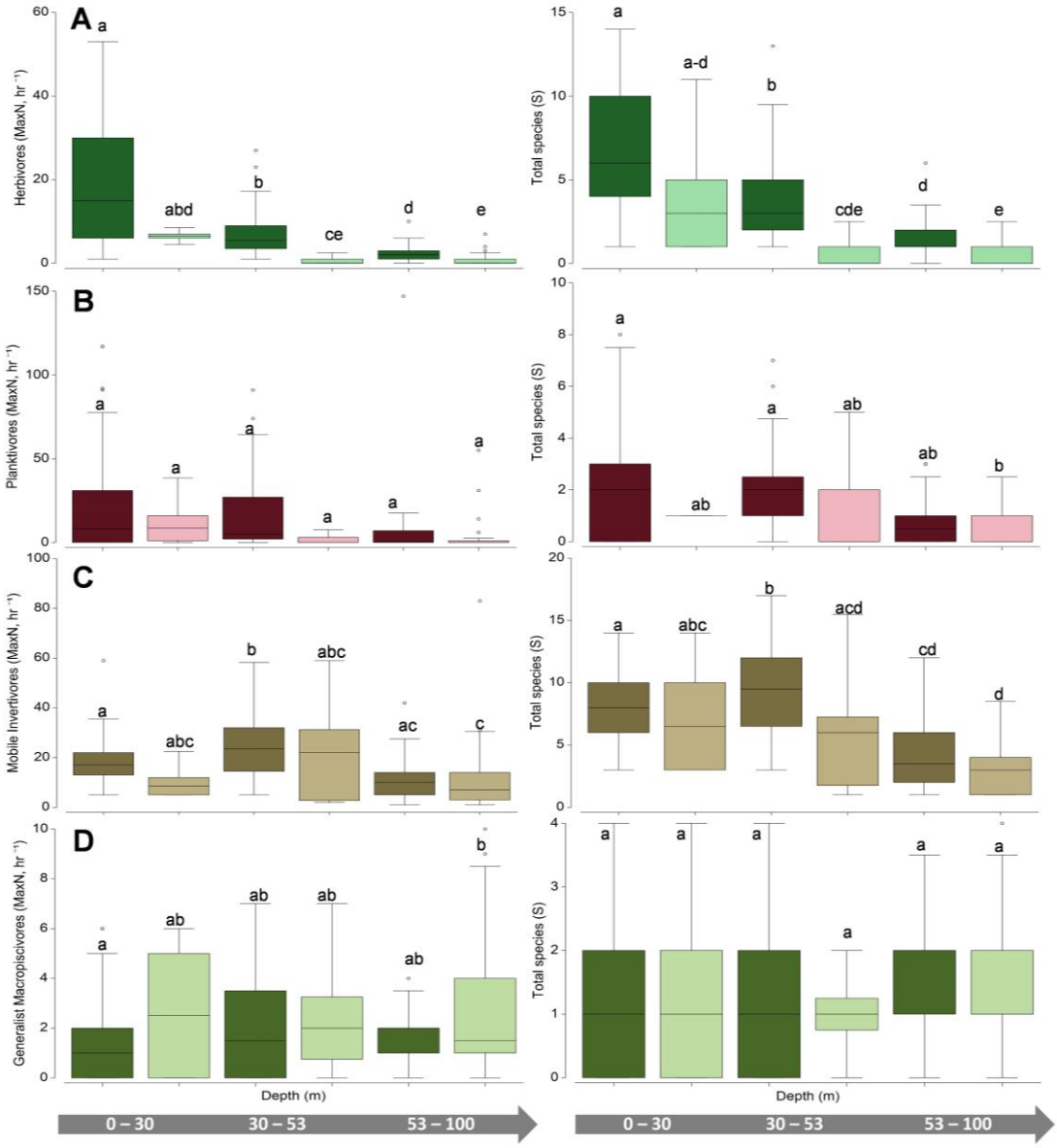


Figure 3.6. Univariate *box plots* of (left) untransformed pooled total abundance (MaxN) and (right) species richness (total species, S) for (A) herbivores (B) planktivores (C) mobile invertivores (D) generalist macropiscivores. Columns sharing the same letter do not differ significantly at the 95% confidence level based on PERMANOVA pair-wise tests. Dark boxes indicate hard bottom, light boxes indicate unconsolidated sediment.

Multivariate Assemblage

The canonical analysis of principal coordinates (CAP; Figure 3.7A) confirmed changes in overall reef fish assemblages among depth and habitat strata (global PERMANOVA, depth Pseudo-F = 3.8827, p = 0.0001; habitat Pseudo-F = 4.4216, p = 0.0001), with $\delta^2 = 0.88$ recorded along the first principal axis and $\delta^2 = 0.63$ along the second principal axis over m = 21 principal coordinate axes, and considerable depth and habitat community separation, albeit with overlaps between site groups. The estimation of misclassification error indicated high allocation success (78%), with 0 – 30 m and 30 – 53 m hard-bottom reef fish assemblages recording the highest percentage of correct assignments (83 – 84%) and the majority of classification errors occurring between the two (Table S3.2).

The mMDS likewise showed a higher degree of community similarity (Figure 3.7B), with several shared species contributing to within-group similarities (Table S3.3), and lower overall SIMPER dissimilarity measures (80.40) between shallow water and upper mesophotic hard-bottom sites versus all compared other strata; however, significant differences in community composition (PERMANOVA pair-wise tests, all p = 0.0001, Table S3.3) were detected between hard-bottom substrates in all three depth zones, along with sites located in lower mesophotic sand flats. When compared to the shallow water zone, hard-bottom substrates in the upper mesophotic zone had higher abundances of several herbivores (e.g. *Acanthurus olivaceus*), planktivores (*Naso hexacanthus*), and mobile invertivores (*Oxycheilinus bimaculatus*, *Parupeneus pleurostigma*), but lower abundances of other planktivores (*Melichthys niger*, *Naso brevirostris*) and mobile invertivores (*Thalassoma duperrey*), with the majority of these species becoming scarce or completely absent beyond 53 m. Additional details on community differences are provided in Table S3.3.

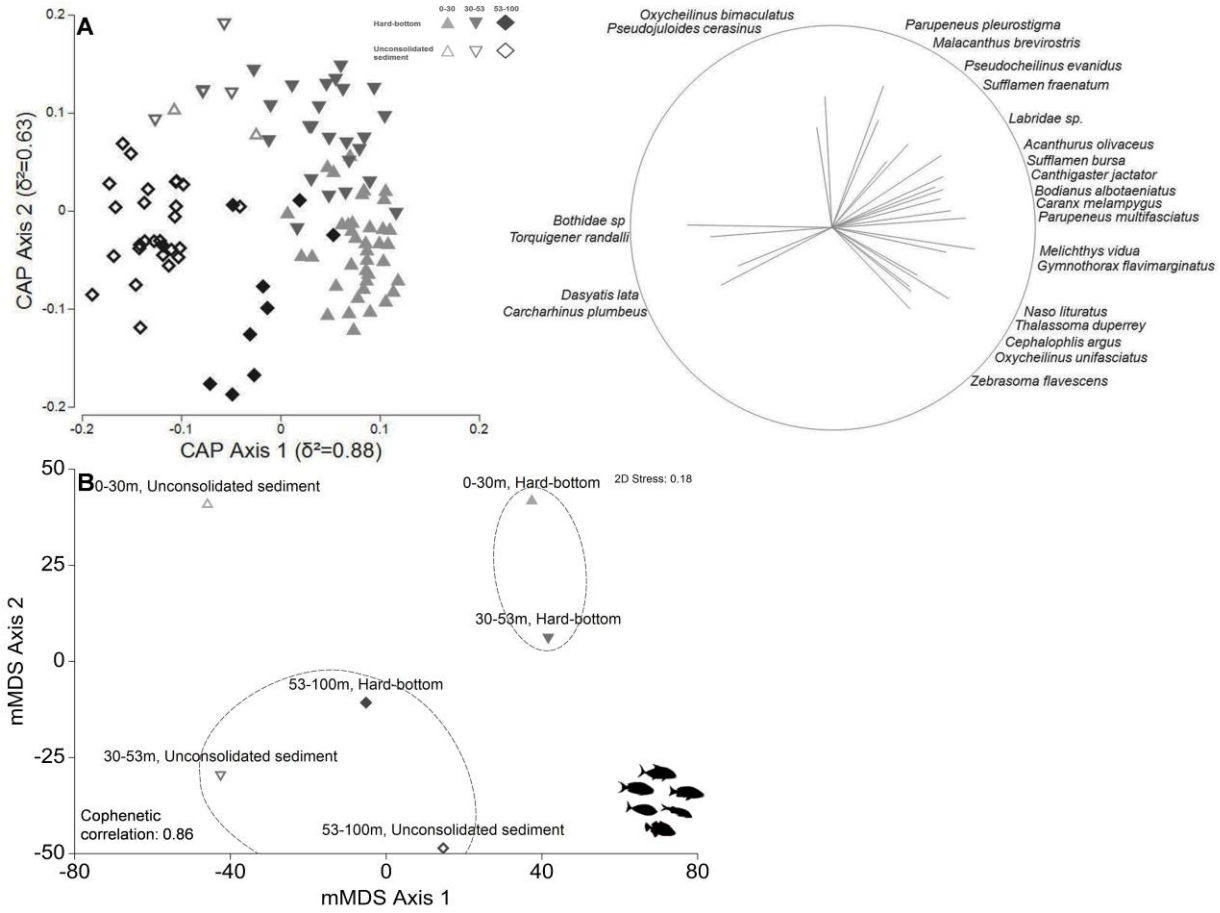


Figure 3.7. A.) Canonical analysis of principal coordinates ordination (CAP) of first two principal axes depicting relationships between reef fish assemblage and depth-habitat categories. Pearson's correlations (>0.4) of fish species listed, with strength indicated by vector length and direction. B.) Metric multidimensional scaling (mMDS) plots of group centroids generated from overall reef assemblage. Dashed lines indicate SIMPROF groups.

Among the four prevalent functional assemblages, herbivores and mobile invertivores were notable for the clustering of hard-bottom, shallow water and upper mesophotic group centroids within respective mMDS SIMPROF ellipses (Figures S3.2A, C) as a result of considerable species overlaps (Figures 3.8A,C). Both retained associated species clusters of shallow water specialists, along with depth-generalists (found between shallow water and upper mesophotic zones, or across all depth zones) in the context of this study;

however, with the exception of *Centropyge potteri*, (which is known to also inhabit 0 – 30 m), no herbivores were found exclusively in mesophotic strata. This contrasted with a number of mobile invertivore species (e.g. *Coris ballieui*, *Parupeneus chrysonemus*, *Iniistius umbrilatus*), of which several were found at higher abundances at lower mesophotic, unconsolidated sediment sites.

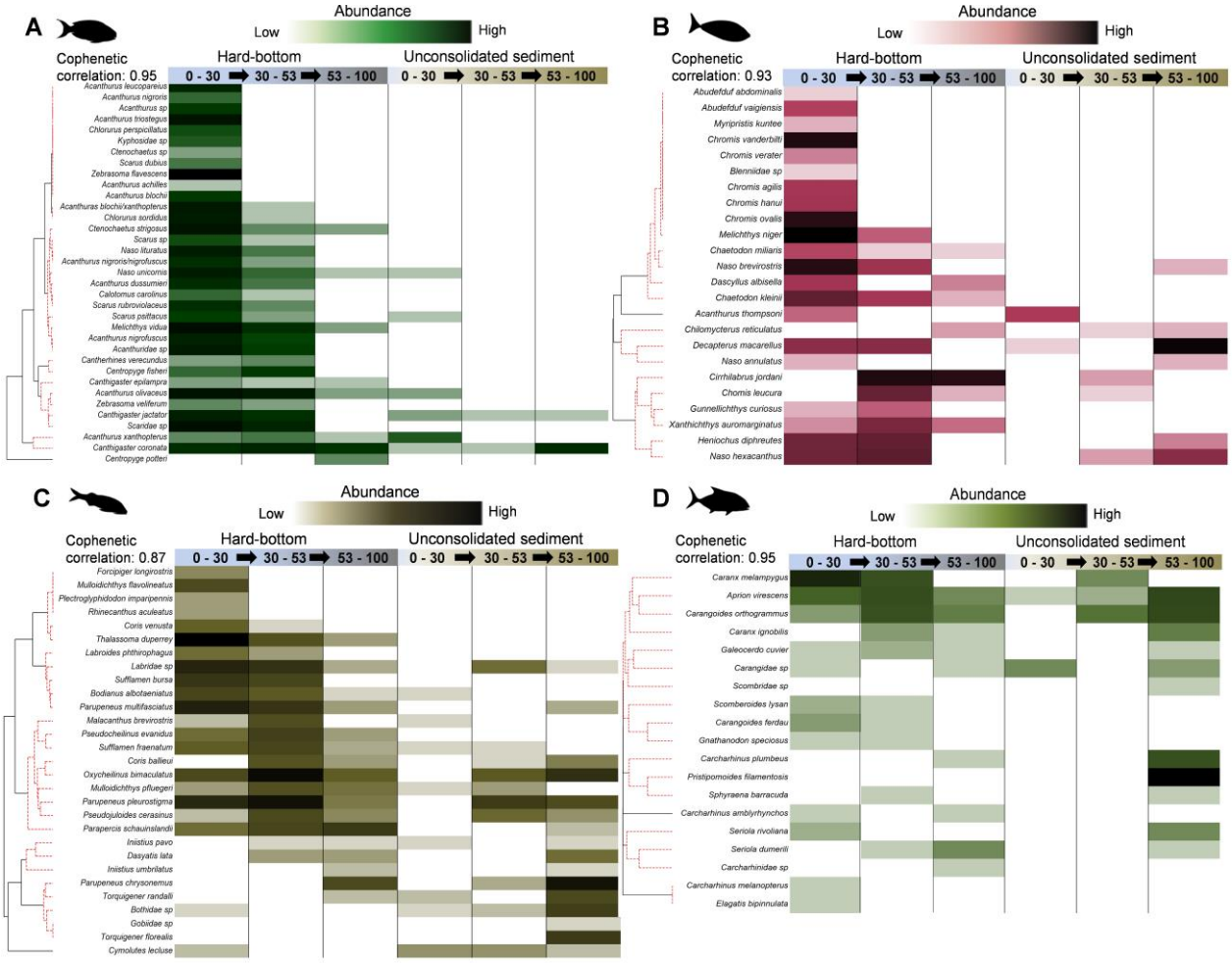


Figure 3.8. *Shade plots* for A.) herbivores, B.) planktivores, C.) mobile invertivores (subset of species recording >20% contributions), D.) generalist macropiscivores. SIMPROF groups depictured along red, dashed lines in y-axis dendrograms.

There were no discernible patterns for planktivores within mMDS SIMPROF groupings (Figure S3.2B), although hard-bottom shallow water and upper mesophotic group centroids had the lowest cophenetic correlation distance (52.8; 45% similarity) in comparison with all other pairings. Similar to mobile invertivores, planktivore communities sampled by BRUVS were characterized by species encountered exclusively between 0 – 30 m (e.g. *Abudefduf abdominais*, *Chromis vanderbilti*), depth generalists (e.g. *Naso brevirostris*, *Melichthys niger*), and mesophotic specialists (e.g. *Cirrhilabrus jordani*, *Chromis leucura*). Like planktivores, generalist macropiscivores had a low cophehetic distance value (37.4; 45% similarity) between shallow water and upper mesophotic hard-bottom centroids, but registered no significant SIMRPOF profiles (Figure S3.2D). While several abundant species were present in multiple strata (e.g. *Carangoides orthogrammus*), others appeared constrained by depth (*Carcharhinus melanopterus*, *Carcharhinus plumbeus*) and/or habitat (e.g. *Pristipomoides filamentosis*). Other fishery targeted generalist macopiscivores are discussed in 'target species' (see below).

Length-based estimates

Only three target species (*Naso hexacanthus*, *Naso brevirostris,* and *Caranx melampygus*) were recorded in sufficient numbers to conduct comparisons of length distributions between shallow water and pooled mesophotic depth strata. Among those species, there were no significant differences in standardized length distributions between shallow water and mesophotic strata, i.e.no indication of skewing or kurtosis biases between depth strata (Langlois et al. 2012), and thus it was appropriate to compare mean lengths. *Naso brevirostris* and *Caranx melampygus* mean lengths were significantly larger in mesophotic compared to shallow depths (Figure 3.9, all $p < 0.001$), contrasting with *Naso hexacanthus*, which were larger in 0 – 30 m ($p < 0.001$).

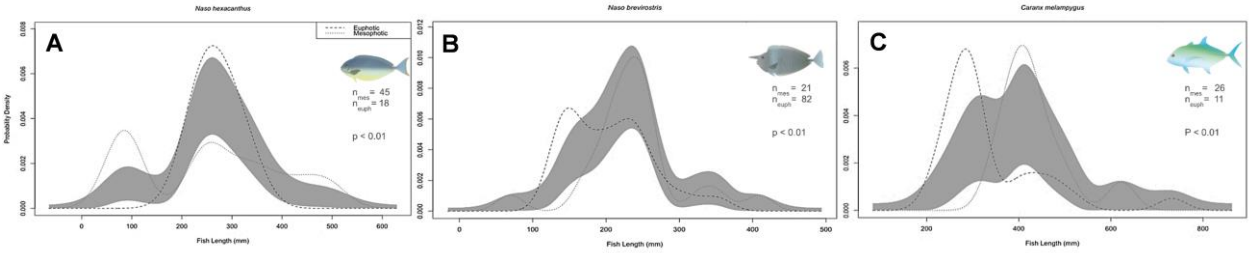


Figure 3.9. Comparison of A.) *Naso hexacanthus*, B.) *Naso brevirostris*, and C.) *Caranx melampygus* kernel density estimate (KDE) probability functions measured at shallow (SPC, 0–30 m) and mesophotic depths (30–100 m) using mean bandwidths. Gray bands indicate one standard error (SE) to either side of the null model, indicating no differences between the KDEs of each depth strata. N, number of fish; p, permutation tests to determine significance between depth-constrained length distributions.

Target species

A total of 1,163 fishes belonging to 31 target species, as identified from MRIP and CML data, were encountered during BRUVS surveys (13 herbivores, 2 planktivores, 6 mobile invertivores, 2 piscivores, 8 generalist macopiscivores; Figure 3.10A, B). Of the six 'fishery depleted' species, only *Acanthurus blochii* was recorded exclusively in the euphotic zone (Figure 3.10C).

Similar to univariate and multivariate trends reported earlier, target herbivorous species were scarce at depths greater than 30 m (Figure 3.10). In contrast, patterns in targeted planktivore abundance varied among species with *Naso brevirostris* more abundant in 0 – 30 m and *Naso hexacanthus* more abundant in deeper water. Generalist macropiscivore depth distributions varied widely between depth-specialists (e.g. *Seriola dumerili*) and generalists (most species). The two fishery-depleted macropiscivores were similarly variable, with *Aprion virescens* occupying multiple depths and habitat strata, whereas *Caranx ignobilis* was exclusively recorded at mesophotic hard-bottom and unconsolidated sediments sites.

Endemism

In total, 32 endemic species were recorded during surveys (Table S3.1), constituting between 18 – 20% of total abundance between 0 – 30 and 30 – 53 m, and 29% in 53 – 100 m, driven largely by increases in abundance of the schooling planktivore *Cirrhilabrus jordani* and mobile invertivore *Parupeneus chrysonemus* in the lower meosphotic. No significant decreases in total abundance of endemics were detected between strata outside of 53 – 100 m unconsolidated sediment habitats (Table S3.3, Figure S.3.3B). However, endemic

richness was highest in shallow waters (18% of overall species richness), declining to 13% in 30 – 53 and 53 – 100 m, with all pair-wise tests showing significant values ($p < 0.05$) among hard-bottom substrates. Endemic communities had significant SIMPROF groupings (Figure S3.3C) and species overlaps (Figure S3.3D) between shallow water and upper mesophotic strata (e.g. *Chaetodon multicinctus*, *Canthigaster jactator*). Finally, 35% of the endemic species were recorded exclusively in $\leq$ 30 m, 26% in > 30 m, with the remaining 39% exhibiting overlapping distributions between shallow water and one or both mesophotic depth zones.

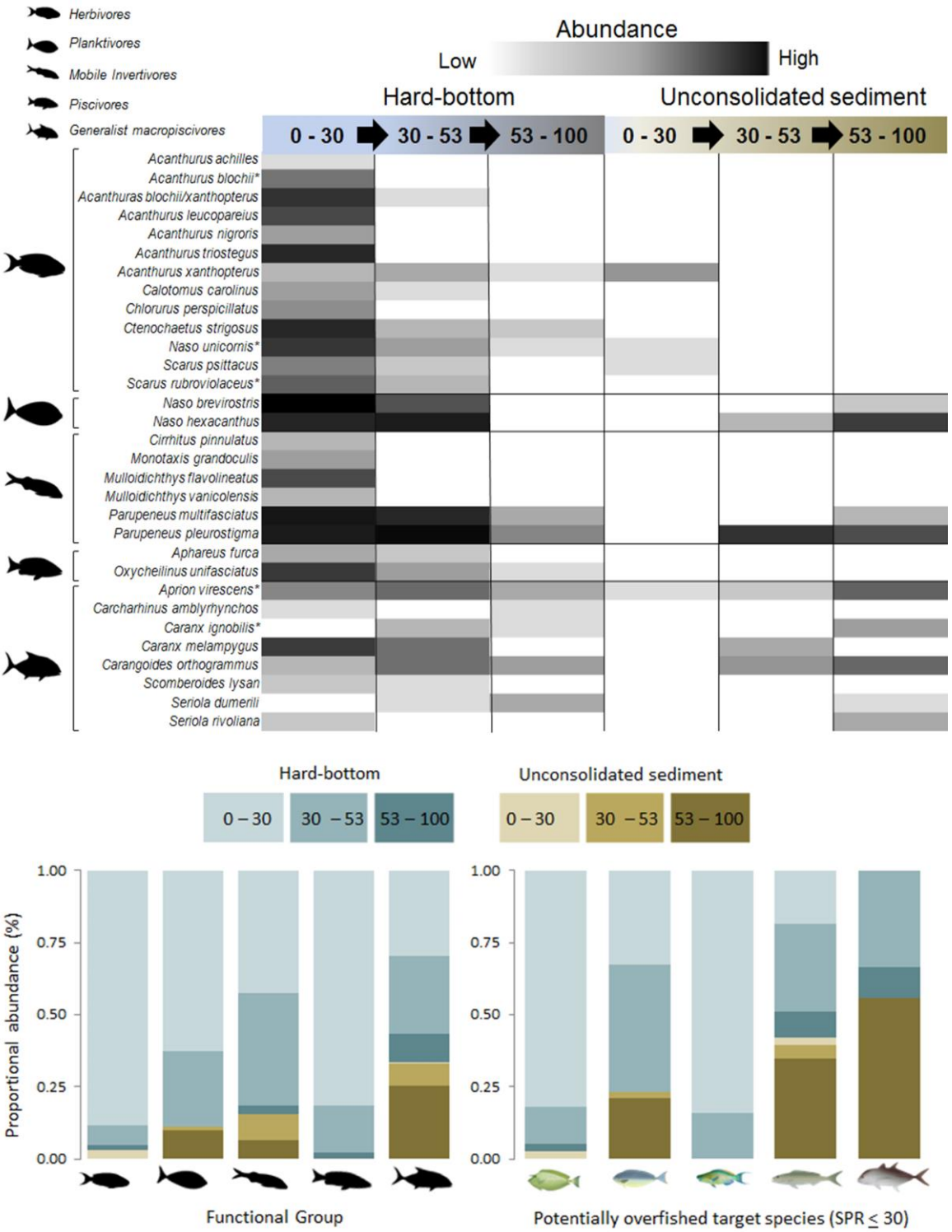


Figure 3.10. A) *Shade plot* of target species subject to extractive (fishing) pressures of ≥450 kg yr^{-1} over a 10 year period (Stamoulis, 2016). Relative abundance ranked from low (light grey) to high (dark grey), and ordered from shallow water to mesophotic depths along hard-bottom substrate and unconsolidated sampling sites. *Indicate species with spawning potential ratios (SPRs) <30 (Nadon, 2015). B.) Proportional relative abundance of functional groups subjected to extractive fishing pressures. Lower right panel: proportional abundance of target species with spawning potential ratio values <30. From left to right: *Naso unicornis*, *Naso hexacanthus*, *Scarus rubroviolaceus*, *Aprion virescens*, and *Caranx ignobilis*.

Habitat Characterization and Environmental Linkages

The principal component analysis (PCA) showed 63% of total variation was explained by the first two principal axes. Increased hard coral cover and habitat complexity between overlapping, hard-bottom shallow water and upper mesophotic sites contrasted against deeper, lower complexity sites hosting increased unconsolidated sediment (sand) cover. Macroalgae were orthogonal to the first principal axis, increasing along the second principal axis in-part as a result of *Halimeda* sp. meadows (≥ 45% biotic cover) encountered in the Maui-Nui sampling region (60% of total sampling sites between 30 – 53 m; 30% of sites between 30 – 100 m; Figure S3.6).

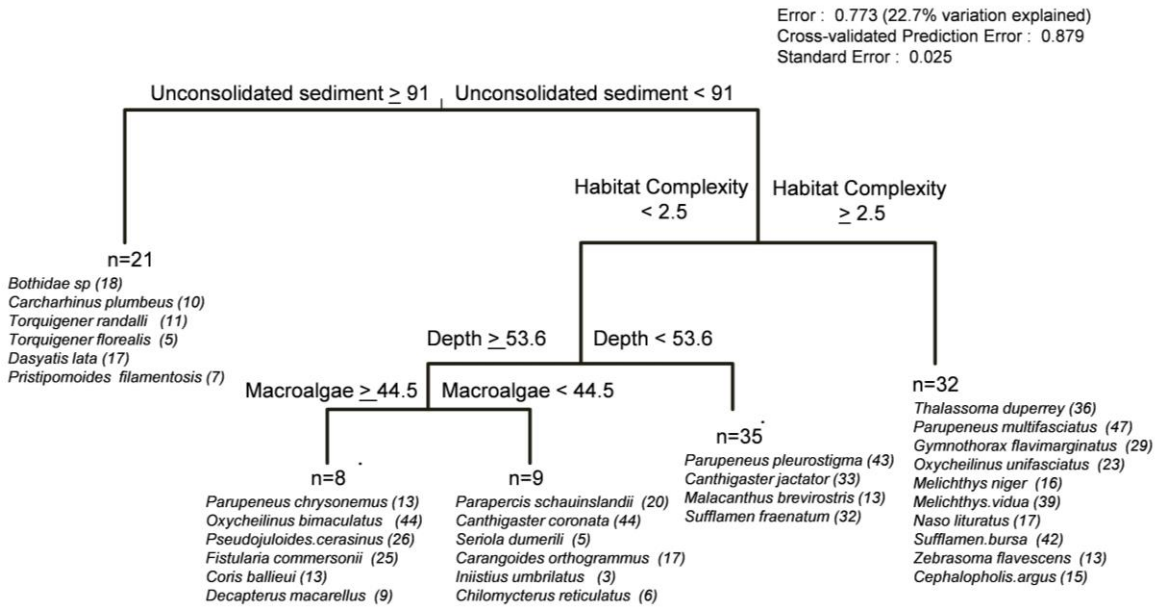


Figure 3.11. Multivariate regression tree illustrating relative abundance of reef fishes in relation to continuous environmental variables. Significant indicator species ($p < 0.05$, maximum number of 10 species per leaf) are listed in order of decreasing DLI values, along with the number of sites where a species was encountered.

Examination of the multivariate regression revealed habitat complexity, depth, and percent cover of unconsolidated sediment and macroalgae to be the principal environmental variables structuring reef fish assemblages (Figure 3.11). The MRT assigned 23% of full model assemblage variation parsed into five separate species groups, with the first major node-split separating a small number of mobile invertivore and generalist macropiscivore species likely to be found at deep, benthic-depauperate sand flats with greater than 91% unconsolidated sediment cover (21 sites). The subsequent habitat complexity node-split at 2.5 aligned with a combination of herbivores (*Melichthys vidua*, *Naso lituratus*, *Zebrasoma flavescens*), the planktivore *Melichthys niger*, several mobile invertivores (*Thalassoma duperrey*, *Parupeneus multifasciatus*, *Sufflamen bursa*), the sessile macropiscivore (moray *Gymnothorax flavimarginatus*), and two piscivorous species (*Cephalopholis argus, oxycheilinus unifasciatus)* indicative of groupings synonymous with more structurally developed, hard-bottom substrates encountered in shallow water and/or upper mesophotic zones (32 sites). Finally, reef fish communities inhabiting lower complexity habitats (< 2.5) were further split at 53.6 meters, with shallow water and upper mesophotic sites (35) largely defined by a small group of mobile invertivores and the herbivore *Cantigaster jactator*, while deeper sites were further delineated by

macroalgal cover largely attributed to *Halimeda* sp. meadows encountered in the Maui-Nui region. Both terminal leaves were largely dominated by mobile invertivores, planktivores, and generalist macropiscivore species. It is important to note that placement of MRT indicator species at a particular tree location does not imply site restriction, as many were found in an array of depths, substrate types, and survey sites resulting in 77% of assemblage variation remaining unexplained; however, DLI species assignments serve as encounter predictors given particular benthic characteristics.

The DISTLM-dbRDA ordination similarly accounted for 23.5% of the total variation with the same environmental variables listed as the MRT, along with the addition of hard-coral as a contributing environmental covariate. Additional details are described in Figure S3.7.

Discussion

This study provides the first *in situ* BRUVS assessment of reef fish communities across shallow water to mesophotic zones in the main Hawaiian Islands. Depth, habitat complexity, macroalgal cover, and unconsolidated sediment acted as influential reef fish assemblage drivers. While a variety of other potential environmental co-contributors, ranging from temperature, hydrodynamics, and sedimentation could also affect the distribution of organisms in mesophotic depths, these remain unaddressed in the scope of this work (Locker et al. 2010; Kahng et al. 2014).

Community shifts similar to patterns observed in other tropical (e.g. Red Sea, Marshall Islands, Puerto Rico, Honduras) and sub-tropical ecosystems, (e.g. South Africa, NWHI), included declines in herbivore abundance with depth, even in mesophotic habitats hosting high levels of macroalgal cover (Thresher and Colin 1986; Feitoza et al. 2005; Brokovich et al. 2010; Bejarano et al. 2014; Kane et al. 2014; Andradi-Brown et al. 2016a; Fukunaga et al. 2016). While planktivore relative abundance and richness measures were relatively similar across depth strata (Figure 3.6B), their proportional abundances was highest in the lower mesophotic zone (Figure S3.1), aligning with depth-based planktivore density and/or biomass peaks recorded in other mesophotic studies (Thresher and Colin 1986; Feitoza et al. 2005; Fukunaga et al. 2016).

The decline of herbivores outside of shallow waters, and increased numbers of mobile invertivores in the upper mesophotic zone, indicate possible shifts in benthic primary productivity sources and compels additional nutrient cycling research between depth and habitat strata (Hilting et al. 2013; Fukunaga et al. 2016). In addition, while isotopic evidence suggests predators remain heavily reliant on resources between 0 – 30 m acting as nutrient conduits to mesophotic depths (Meyer et al. 2001; Wetherbee et al. 2004; Papastamatiou et al. 2006; Hilting et al. 2013; Papastamatiou et al. 2015), marked increases in schooling mobile invertivores (e.g. goatfishes) and planktivores (e.g. *Cirrhilabrus jordani, Decapterus macarellus*) may serve as deep-water prey-bases for predators in the MHI (Smith and Parrish 2002). As with schooling behaviors observed on *Halimeda* meadows (see below), potential prey species were observed seeking shelter in algal canopies or retreating to hard-bottom interstitial spaces during transits by generalist macropiscivores - particularly jacks and *Aprion virescens* - within the BRUVS frame of view (J. Asher, *pers. obs*.).

Of particular interest were mesophotic sand flats and lower-complexity hard-bottom habitats which hosted extensive calcareous *Halimeda* meadows, which generally harbored more limited reef fish communities in

comparison with more structurally complex habitats. The abundance of mobile invertivores (70% of total community), rather than herbivores, was noted in these areas as *Halimeda* are relatively unpalatable to most herbivorous reef fishes (Lewis 1985; Spalding 2012). We observed generalist macropiscivores foraging in these habitats Figure 3.12, B-D), with individuals or small-mixed groups of *Caranx melampygus*, *Carangoides orthogrammus*, *Caranx ignobilis*, and/or *Aprion virescens* seen transiting though *Halimeda* meadows, typically with prey species fleeing or seeking shelter in algal canopies (J. Asher*, pers. obs*). Juvenile tiger sharks (*Galecerdo cuvier*) were also observed transiting along *Halimeda* sp. meadows, indicating possible habitat use as part of their generalist approach to feeding on a wide variety of potential prey items (Werry et al. 2014a). Finally, juvenile bottom-fish *Pristipomoides filamentosis* (9 – 30 cm) were also seen schooling in mesophotic *Halimeda* meadows in the Maui-Nui region in as little as 54 m, suggesting that those habitats may be foraging or refuge areas used by bottom-fish, prior to ontogenic migration into deeper habitats upon maturity.

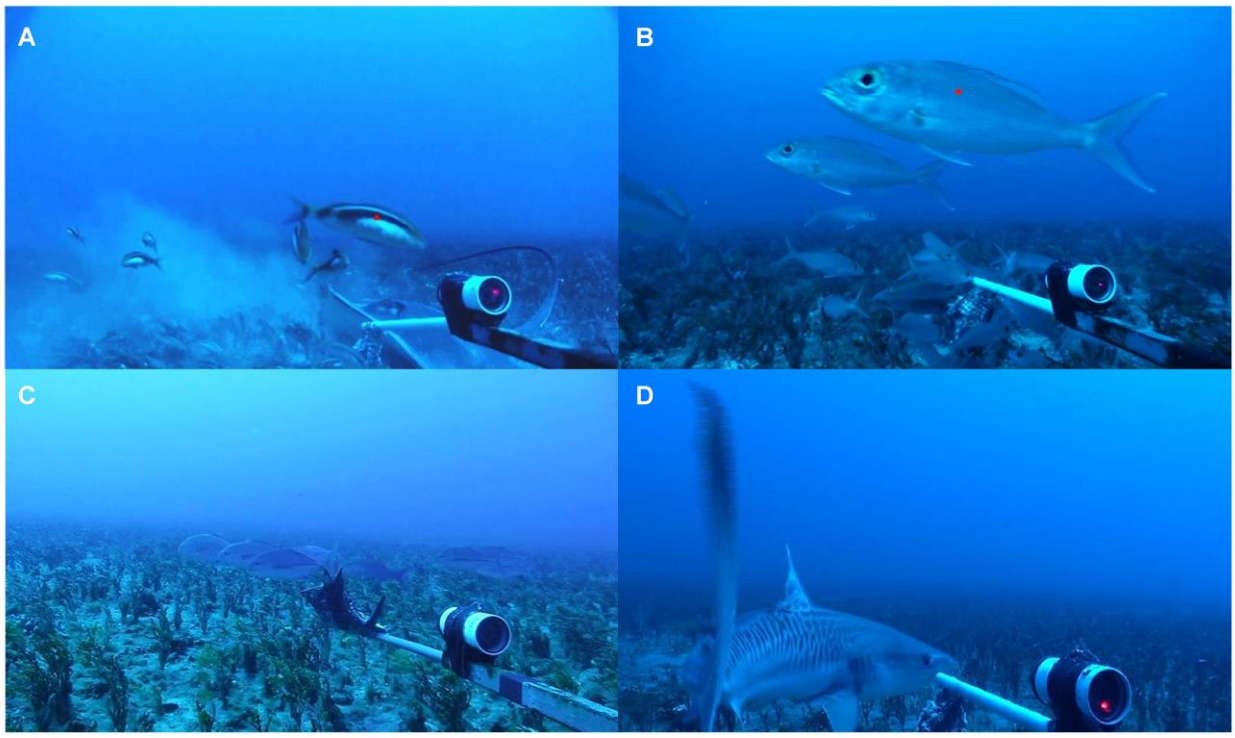


Figure 3.12. Videographic frame-grabs of mesophotic Halimeda sp. meadows sampled in the Maui-Nui complex. A.) School of *Parupeneus chrysonemus* and solitary *Dasyatis lata* feeding on bait bag contents, B.) mixed school of *Caranx melampygus* and *Carangoides orthogrammus*, C.) juvenile *Pristipomoides filamentosis* (bottom-fish), D.) juvenile *Galecerdo cuvier*.

Despite the apparent linkages maintained by depth-generalists, particularly those inhabiting shallow water and upper mesophotic strata, (Tenggardjaja et al. 2014; Papastamatiou et al. 2015), community linkages and species movements between strata are still largely uncharacterized in the MHI. This remains an important focus for future MHI research, particularly for those species subject to high fishing pressures around human population centers. The majority (70%) of 'target' species were encountered in mesophotic depths, including all but one of the species where there is strong evidence of fishery depletion based on shallow water surveys (Figure 3.10), albeit with the majority of species having lower overall mesophotic abundance levels than in 0 – 30 m. Generalist macropiscivores, which remain one of the more susceptible groups to fishing pressures, had ~50% greater abundance on hard-bottom substrates in the upper mesophotic zone compared to shallow water . Higher mesophotic abundances of some groups, and changes in predator communities is a potential

indicator of depth refugia (Thresher and Colin 1986; Bejarano et al. 2014; Andradi-Brown et al. 2016a; Lindfield et al. 2016), particularly for the fishery-depleted target species that were more abundant in mesophotic depths (e.g. *Aprion virescens*, *Caranx ignobilis*, Figures 3.7D and 3.10), or for predatory species with larger mesophotic body sizes (e.g. *Caranx melampygus*, Figure 3.9C). Given that assessments of MHI reef fish stock exploitation rates and annual catch assignments remain largely constrained to fishery-independent, open-circuit diver depths (i.e. $\leq$ 30 m) or fisheries-dependent, commercial catch/recreational survey data obtained from indeterminate depths (Nadon et al. 2015), the use of BRUVS serves as a promising, shallower compliment to the deep-water camera system (BotCam) utilized for Hawaiian bottom fish stock assessments (Merritt et al. 2011). Finally, additional research parsing depth refugia versus ontogeny effects in structuring reef fish communities would be beneficial, as larger-sized mesophotic planktivores (Figures 10B) could be attributed to ontogenic migrations (Andradi-Brown et al. 2016a) and may be less prone to mesophotic predation in lower-complexity habitats that do not provide adequate shelter to more vulnerable size classes.

Mesophotic reef fish community breaks have been proposed at ~ 60 m (Slattery et al. 2011; Fukunaga et al. 2016), with community, functional group, and assessed environmental structural outputs generally supporting this premise. However, community compositions were largely distinct between shallow water and upper mesophotic zones, indicating the potential for depth-based refugia may be limited to depth-generalists and not depth-zone specialists, e.g. specific mobile invertivores and generalist macropiscivores that are equally, if not more abundant in 30 – 53 than in <30 m, with the possibility of refugia further declining when transitioning to more comparably depauperate lower mesophotic communities. While mesophotic reef fish communities may provide meaningful refugia for some species, shallow-water specialists are clearly unlikely to be able to benefit in that way (Fukunaga et al. 2016). Conversely, given that many MHI depth generalists decline when transitioning from shallow water to mesophotic systems seen here and in other studies (Pyle et al. 2016), mesophotic reef fish communities affected by hypothetical biological impacts (e.g. lionfish invasions in the Atlantic) or anthropogenic perturbations (e.g. dredging) may end up reliant on shallow water systems for repopulation. Outside of a small number of species investigations (e.g. *Chromis verater*), the movements of fish larvae between euphotic and mesophotic strata remains largely unknown and remains an important focus for future research (Tenggardjaja et al. 2014).

Mesophotic coral ecosystems in the NWHI appear to be reservoirs of extremely high levels of endemic biodiversity (Kane et al. 2014; Kosaki et al. 2016). In our study, BRUVS showed comparable MHI shallow water and upper mesophotic endemism levels as those documented by underwater visual census surveys in <30 m in the MHI (Randall 1998; DeMartini and Friedlander 2004; Pyle et al. 2016). However, declines in proportionate abundance (excluding two schooling species) and richness (Figure S3.3, B-E) in the lower mesophotic zone conflict with patterns of those seen during technical dive surveys in the NWHI and submersible/technical dive surveys in the MHI. This may be attributed, in part, to these studies targeting specific habitats, e.g. hard-bottom, structurally complex slopes and ledges (Kane et al. 2014; Kosaki et al. 2016) or the *Leptoseris* sp. beds in the Maui-Nui region known to host large, localized endemic populations of fishes. In contrast our MHI mesophotic BRUVS surveys tended to sample mostly lower complexity habitats, e.g. low-lying aggregate *Montipora* reefs, rubble flats, and sand flats, which appear to be the most common habitats in those depths at our study locations.

Results from BRUVS surveys in the Main Hawaiian Islands should be interpreted with several caveats. Largely

as a byproduct of the incomplete bathymetric data, the majority of lower-mesophotic deployments occurred on 100% unconsolidated sediment (27 sites), with only 10 sites sampling hard-bottom habitats (aggregate reef, aggregate patch reefs, consolidated rubble flats). None of our deeper samples were of the (in some places extensive), Maui-Nui *Leptoseris* coral communities which are known to a.) host extensive reef fish populations, and b.) occur in depths beyond our 100 m sampling cutoff (Strasburg et al. 1968; Kahng and Maragos 2006; Costa et al. 2015). As a result, several functional groups (e.g. corallivores) were largely absent in our surveys outside of 53 m, although we know they can be abundant in some habitats.

As with all underwater visual censuses, BRUVS remain subject to possible sampling biases. These include the potential inflation of density estimates due to fish being drawn from outside visible sampling areas, unknown areas of attraction as a byproduct of variable bait plume dispersion, alteration of fish behaviors, competitive exclusion, and/or preferential sampling of predator and scavenger populations with corresponding reductions to other functional groups (Harvey, Cappo et al. 2007; Colton and Swearer 2010; Dorman, Harvey et al. 2012). However, comparisons between baited and unbaited camera stations have shown that while carnivore and scavenger abundances tend to increase in the presence of bait, no commensurate changes are typically detected in herbivore or omnivore abundances (Watson et al. 2005; Harvey et al. 2007). The lack of bait-induced declines among non-carnivorous functional groups could be explained by possible “sheep effects”, whereby species not directly attracted to bait plumes are attracted to the feeding activities of others around BRUVS, or through conspecific social attraction behaviors (Watson et al. 2005; Harvey et al. 2007; Watson et al. 2010; Dorman et al. 2012). Finally, underwater sampling visibility was, in general, much higher than the required BRUVS sampling minimum (7 m), even in mesophotic depths to 100 m. While the authors detected no depth-associated, functional group or species-level behavior alterations as a result of reduced light attenuation in deeper strata, coral reef fishes are known to exhibit behavioral shifts in response to varying light levels, which merits additional consideration for future mesophotic research (Rickel and Genin 2005).

Mesophotic reefs remain infrequently explored throughout the Indo-Pacific region and likely still host numerous undiscovered fish species (Pyle 2001). While shallow water and upper mesophotic reef fish communities are highly connected, these zones have their own distinct functional group assemblages, becoming even more dissimilar in lower depths. In light of anthropogenic and climate-based pressures in shallower waters, coupled with substantial data-gaps for the many reef fish species present in both shallow water and mesophotic habitats, there is a strong need to continue research into depth zone connectivity, along with species and life-stage distributions, in order to develop appropriate and comprehensive coral reef resource management strategies.

Supplementary Materials

Table S.3.1. Fish species categorized to functional group level, recorded during BRUVS surveys in the Main Hawaiian Islands. Depth range (m) denotes depths where a species was encountered during surveys. * indicates maximum species depths indicated in Randall (2007) or Fishbase. (Froese and Pauly 2014). Proportion of sites (%) indicated by depth and habitat strata.

								Hard-bottom			Unconsolidated		
Functional Group	Family	Genus, Species	Endemic?	MRIP/CML Target?	SPR ≤ 30?	Depth range (m)	Max. Depth (m)*	0-30	30-53	53-100	0-30	30-53	53-100
Herbivore	*Acanthuridae*	*A. blochii/xanthopterus*	-	✓	-	3 - 48	91	16.7	4.2	0.0	0.0	0.0	0.0
		Acanthuridae sp	-	-	-	4 - 52	-	50.0	20.8	0.0	0.0	0.0	0.0
		A. achilles	-	✓	-	9	10	3.3	0.0	0.0	0.0	0.0	0.0
		A. blochii	-	✓	✓	6 - 16	15	10.0	0.0	0.0	0.0	0.0	0.0
		A. dussumieri	-	-	-	5 - 49	131	26.7	12.5	0.0	0.0	0.0	0.0
		A. leucopareius	-	✓	-	3 - 16	85	16.7	0.0	0.0	0.0	0.0	0.0
		A. nigrofuscus	-	-	-	3 - 52	25	36.7	12.5	0.0	0.0	0.0	0.0
		A. nigroris	-	✓	-	6 - 11	90	6.7	0.0	0.0	0.0	0.0	0.0
		A. nigroris/nigrofuscus	-	-	-	5 - 48	90	26.7	4.2	0.0	0.0	0.0	0.0
		A. olivaceus	-	-	-	3 - 57	62	73.3	62.5	20.0	50.0	0.0	0.0
		A. triostegus	-	✓	-	3 - 15	90	23.3	0.0	0.0	0.0	0.0	0.0
		A. xanthopterus	-	✓	-	10 - 57	91	6.7	8.3	10.0	50.0	0.0	0.0
		Ctenochaetus sp	-	-	-	14	180	3.3	0.0	0.0	0.0	0.0	0.0
		C. strigosus	✓	✓	-	3 - 46	113	36.7	4.2	10.0	0.0	0.0	0.0
		N. lituratus	-	-	✓	3 - 48	90	46.7	12.5	0.0	0.0	0.0	0.0
		N. unicornis	-	✓	✓	3 - 57	180	30.0	12.5	10.0	50.0	0.0	0.0
		Z. flavescens	-	-	-	3 - 28	81	43.3	0.0	0.0	0.0	0.0	0.0
		Z. veliferum	-	-	-	9 - 48	45	10.0	4.2	0.0	0.0	0.0	0.0
	Balistidae	*M. vidua*	-	-	-	5 - 57	145	86.7	50.0	10.0	0.0	0.0	0.0
	Kyphosidae	*Kyphosidae sp*	-	-	-	6 - 9	20	6.7	0.0	0.0	0.0	0.0	0.0
	Monacanthidae	*C. verecundus*	✓	-	-	25 - 49	92	6.7	4.2	0.0	0.0	0.0	0.0
	Pomacanthidae	*C. fisheri*	-	-	-	25 - 49	95	3.3	20.8	0.0	0.0	0.0	0.0
		C. potteri	✓	-	-	57	138	0.0	0.0	10.0	0.0	0.0	0.0
	Scarinae	*C. carolinus*	-	✓	-	6 - 40	71	13.3	4.2	0.0	0.0	0.0	0.0
		C. perspicillatus	✓	✓	-	6 - 21	71	23.3	0.0	0.0	0.0	0.0	0.0
		C. sordidus	-	-	-	3 - 34	50	40.0	4.2	0.0	0.0	0.0	0.0
		Scarinae sp	-	-	-	3 - 49	-	53.3	25.0	0.0	0.0	0.0	0.0
		S. dubius	✓	-	-	6 - 19	25	10.0	0.0	0.0	0.0	0.0	0.0
		S. psittacus	-	✓		6 - 48	25	23.3	8.3	0.0	50.0	0.0	0.0
		S. rubroviolaceus	-	✓	✓	3 - 49	36	33.3	8.3	0.0	0.0	0.0	0.0
	Tetraodontidae	*C. coronata*	-	-	-	8 - 84	165	36.7	62.5	90.0	50.0	20.0	25.9
		C. epilampra	-	-	-	24 - 63	119	6.7	4.2	10.0	0.0	0.0	0.0
		C. jactator	✓	-	-	3 - 54	89	70.0	37.5	0.0	50.0	20.0	3.7
Mobile Invertivore	*Balistidae*	*B. polylepis*	-	-	-	39 - 48	60	0.0	12.5	0.0	0.0	0.0	0.0
		Balistidae sp	-	-	-	5 - 45	-	3.3	4.2	0.0	0.0	0.0	0.0
		R. aculeatus	-	-	-	8	50	3.3	0.0	0.0	0.0	0.0	0.0
		R. rectangulus	-	-	-	3 - 6	20	23.3	0.0	0.0	0.0	0.0	0.0
		S. bursa	-	-	-	4 - 52	90	86.7	66.7	0.0	0.0	0.0	0.0
		S. fraenatum	-	-	-	6 - 57	183	36.7	70.8	20.0	50.0	20.0	0.0
	Blenniidae	*P. ewaensis*	✓	-	-	12 - 48	55	6.7	12.5	0.0	0.0	0.0	0.0
		P. goslinei	✓	-	-	33 - 48	15	0.0	12.5	0.0	0.0	0.0	0.0
	Bothidae	*Bothidae sp*	-	-	-	14 - 95	686	3.3	0.0	0.0	50.0	20.0	55.6
	Chaetodontidae	*C. ephippium*	-	-	-	3	30	3.3	0.0	0.0	0.0	0.0	0.0
		F. flavissimus	-	-	-	6 - 57	145	23.3	4.2	10.0	0.0	0.0	0.0
		F. longirostris	-	-	-	9 - 21	208	10.0	0.0	0.0	0.0	0.0	0.0
	Cirrhitidae	*Cirrhitidae sp*	-	-	-	21	-	3.3	0.0	0.0	0.0	0.0	0.0
		C. fasciatus	-	-	-	5 - 28	52	10.0	0.0	0.0	0.0	0.0	0.0
		C. pinnulatus	-	✓	-	3 - 9	23	10.0	0.0	0.0	0.0	0.0	0.0
		P. arcatus	-	-	-	6 - 49	91	33.3	16.7	0.0	0.0	0.0	0.0
	Dasyatidae	*D. lata*	-	-	-	34 - 97	357	0.0	12.5	40.0	0.0	0.0	37.0
	Diodontidae	*D. hystrix*	-	-	-	6 - 63	137	10.0	0.0	20.0	50.0	20.0	3.7
	Gobiidae	*Gobiidae sp*	-	-	-	95	-	0.0	0.0	0.0	0.0	0.0	3.7
	Labridae	*B. albotaeniatus*	✓	-	-	3 - 57	200	60.0	45.8	10.0	50.0	0.0	0.0
		C. inermis	-	-	-	13 - 71	30	3.3	4.2	0.0	0.0	60.0	3.7
		C. ballieui	✓	-	-	30 - 78	108	0.0	25.0	20.0	0.0	20.0	7.4
		C. flavovittata	✓	-	-	31	98	0.0	4.2	0.0	0.0	0.0	0.0
		C. gaimard	-	-	-	5 - 48	78	30.0	20.8	0.0	50.0	0.0	0.0
		C. venusta	✓	-	-	6 - 34	10	26.7	4.2	0.0	0.0	0.0	0.0
		C. lecluse	✓	-	-	16 - 59	119	3.3	0.0	0.0	100.0	40.0	3.7
		G. varius	-	-	-	3 - 48	35	30.0	4.2	0.0	0.0	0.0	0.0
		H. ornatissimus	-	-	-	6 - 15	30	13.3	0.0	0.0	0.0	0.0	0.0
		I. aneitensis	-	-	-	31	91	0.0	4.2	0.0	0.0	0.0	0.0
		I. baldwini	-	-	-	42 - 72	132	0.0	8.3	0.0	0.0	0.0	14.8
		I. pavo	-	-	-	28 - 63	100	0.0	4.2	10.0	50.0	0.0	3.7
		I. umbrilatus	✓	-	-	59 - 82	76	0.0	0.0	20.0	0.0	0.0	3.7
		Labridae sp	-	-	-	3 - 76	-	83.3	70.8	20.0	0.0	40.0	3.7
		L. phthirophagus	✓	-	-	9 - 49	122	20.0	12.5	0.0	0.0	0.0	0.0
		M. geoffroy	✓	-	-	15	32	3.3	0.0	0.0	0.0	0.0	0.0
		N. taeniourus	-	-	-	16 - 28	25	3.3	0.0	0.0	50.0	0.0	0.0
		O. bimaculatus	-	-	-	5 - 78	110	26.7	87.5	30.0	0.0	60.0	33.3
		P. evanidus	-	-	-	6 - 68	61	16.7	50.0	20.0	0.0	0.0	0.0
		P. octotaenia	-	-	-	10 - 27	50	20.0	0.0	0.0	0.0	0.0	0.0
		P. cerasinus	-	-	-	9 - 82	61	6.7	58.3	30.0	0.0	60.0	14.8
		S. balteata	✓	-	-	5 - 48	22	13.3	16.7	0.0	0.0	0.0	0.0
		T. ballieui	✓	-	-	5 - 21	60	6.7	0.0	0.0	0.0	0.0	0.0
		T. duperrey	✓	-	-	3 - 57	25	100.0	20.8	10.0	0.0	0.0	0.0
	Lethrinidae	*M. grandoculis*	-	✓		6 - 16	99	10.0	0.0	0.0	0.0	0.0	0.0
	Malacanthidae	*M. brevirostris*	-	-	-	21 - 51	61	3.3	45.8	0.0	50.0	0.0	0.0
	Mullidae	*Mullidae sp*	-	-	-	7 - 46	-	6.7	4.2	0.0	0.0	0.0	0.0
		M. flavolineatus	-	✓	-	6 - 16	76	10.0	0.0	0.0	0.0	0.0	0.0
		M. pfluegeri	-	-	-	15 - 57	110	6.7	29.2	20.0	50.0	20.0	0.0
		M. vanicolensis	-	✓	-	13 - 16	113	6.7	0.0	0.0	0.0	0.0	0.0
		P. chrysonemus	✓	-	-	6 - 77	125	0.0	0.0	10.0	0.0	40.0	22.2
		P. insularis	-	-	-	9 - 21	80	6.7	0.0	0.0	0.0	0.0	0.0
		P. multifasciatus	-	✓	-	3 - 71	140	96.7	62.5	20.0	0.0	0.0	3.7
		P. pleurostigma	-	✓	-	5 - 78	120	43.3	87.5	20.0	0.0	60.0	14.8
	Muraenidae	*E. nebulosa*	-	-	-	5	39	3.3	0.0	0.0	0.0	0.0	0.0
	Myliobatidae	*A. narinari*	-	-	-	17 - 57	97	3.3	4.2	10.0	50.0	0.0	0.0

Table S.3.1 Continued

								Hard-bottom			Unconsolidated		
Functional Group	Family	Genus, Species	Endemic?	MRIP/CML Target?	SPR ≤ 30?	Depth range (m)	Max. Depth (m)*	0-30	30-53	53-100	0-30	30-53	53-100
Mobile Invertivore	*Pinguipedidae*	*P. schauinslandii*	-	-	-	14 - 82	170	10.0	33.3	70.0	0.0	0.0	7.4
	Pomacentridae	*P. imparipennis*	-	-	-	5	15	3.3	0.0	0.0	0.0	0.0	0.0
		S. marginatus	✓	-	-	3 - 28	42	13.3	0.0	0.0	0.0	0.0	0.0
	Tetraodontidae	*A. hispidus*	-	-	-	9 - 31	121	6.7	0.0	0.0	0.0	20.0	0.0
		T. florealis	-	-	-	59 - 74	238	0.0	0.0	0.0	0.0	0.0	18.5
		T. randalli	✓	-	-	17 - 95	296	0.0	0.0	10.0	50.0	0.0	33.3
Planktivore	*Acanthuridae*	*A. thompsoni*	-	-	-	9 - 19	119	10.0	0.0	0.0	50.0	0.0	0.0
		N. annulatus	-	-	-	6 - 73	60	3.3	0.0	0.0	0.0	0.0	3.7
		N. brevirostris	-	✓	-	3 - 71	122	43.3	20.8	0.0	0.0	0.0	3.7
		N. hexacanthus	-	✓	✓	8 - 73	150	26.7	29.2	0.0	0.0	20.0	3.7
	Balistidae	*M. niger*	-	-	-	3 - 52	75	46.7	4.2	0.0	0.0	0.0	0.0
		X. auromarginatus	-	-	-	9 - 57	150	6.7	20.8	10.0	0.0	0.0	0.0
	Blenniidae	*Blenniidae sp*	-	-	-	5	-	3.3	0.0	0.0	0.0	0.0	0.0
	Carangidae	*D. macarellus*	-	-	-	9 - 59	200	6.7	12.5	0.0	50.0	0.0	11.1
	Chaetodontidae	*C. kleinii*	-	-	-	15 - 57	122	13.3	25.0	10.0	0.0	0.0	0.0
		C. miliaris	✓	-	-	15 - 57	250	6.7	4.2	10.0	0.0	0.0	0.0
		H. diphreutes	-	-	-	15 - 84	215	6.7	8.3	0.0	0.0	0.0	3.7
	Diodontidae	*C. reticulatus*	-	-	-	31 - 84	141	0.0	0.0	30.0	0.0	20.0	7.4
	Holocentridae	*M. kuntee*	-	-	-	16	65	3.3	0.0	0.0	0.0	0.0	0.0
	Labridae	*C. jordani*	✓	-	-	31 - 68	186	0.0	29.2	10.0	0.0	20.0	0.0
	Microdesmidae	*G. curiosus*	-	-	-	24 - 51	60	3.3	16.7	0.0	0.0	0.0	0.0
	Pomacentridae	*A. abdominalis*	✓	-	-	13	50	3.3	0.0	0.0	0.0	0.0	0.0
		A. vaigiensis	-	-	-	5 - 11	15	13.3	0.0	0.0	0.0	0.0	0.0
		C. agilis	-	-	-	11 - 17	65	10.0	0.0	0.0	0.0	0.0	0.0
		C. hanui	✓	-	-	13 - 27	50	16.7	0.0	0.0	0.0	0.0	0.0
		C. leucura	-	-	-	31 - 68	118	0.0	29.2	10.0	0.0	20.0	0.0
		C. ovalis	✓	-	-	9 - 27	161	20.0	0.0	0.0	0.0	0.0	0.0
		C. vanderbilti	-	-	-	3 - 21	20	23.3	0.0	0.0	0.0	0.0	0.0
		C. verater	✓	-	-	9	199	3.3	0.0	0.0	0.0	0.0	0.0
		D. albisella	✓	-	-	16 - 57	84	10.0	0.0	10.0	0.0	0.0	0.0
Omnivore	*Monacanthidae*	*A. monoceros*	-	-	-	92	80	0.0	0.0	0.0	0.0	0.0	3.7
		A. scriptus	-	-	-	28 - 63	120	0.0	0.0	10.0	50.0	0.0	3.7
		C. dumerilii	-	-	-	6 - 46	70	16.7	4.2	0.0	0.0	0.0	0.0
		P. aspricaudus	-	-	-	11 - 36	29	3.3	0.0	0.0	0.0	20.0	0.0
	Pomacentridae	*Pomacentridae sp*	-	-	-	4 - 51	-	13.3	12.5	0.0	0.0	0.0	0.0
Corallivore	*Chaetodontidae*	*C. lunulatus*	-	-	-	6 - 52	30	3.3	0.0	0.0	0.0	0.0	0.0
		C. multicinctus	✓	-	-	9 - 46	114	40.0	8.3	0.0	0.0	0.0	0.0
		C. ornatissimus	-	-	-	3 - 49	36	40.0	12.5	0.0	0.0	0.0	0.0
		C. quadrimaculatus	-	-	-	6 - 21	43	13.3	0.0	0.0	0.0	0.0	0.0
		C. unimaculatus	-	-	-	6 - 28	60	26.7	0.0	0.0	0.0	0.0	0.0
	Pomacentridae	*P. johnstonianus*	-	-	-	6 - 17	18	10.0	0.0	0.0	0.0	0.0	0.0
Piscivore	*Aulostomidae*	*A. chinensis*	-	-	-	9 - 24	124	20.0	0.0	0.0	0.0	0.0	0.0
	Cirrhitidae	*P. forsteri*	-	-	-	15 - 31	35	6.7	4.2	0.0	0.0	0.0	0.0
	Fistulariidae	*F. commersonii*	-	-	-	4 - 81	89	30.0	4.2	10.0	0.0	20.0	48.1
	Labridae	*O. unifasciatus*	-	✓	-	3 - 57	160	56.7	20.8	10.0	0.0	0.0	0.0
	Lutjanidae	*A. furca*	-	✓	-	9 - 46	122	10.0	4.2	0.0	0.0	0.0	0.0
		Lutjanidae sp	-	-	-	86 - 92	-	0.0	0.0	0.0	0.0	0.0	7.4
		L. fulvus	-	-	-	4 - 21	75	23.3	0.0	0.0	0.0	0.0	0.0
		L. kasmira	-	-	-	9 - 21	265	6.7	0.0	0.0	0.0	0.0	0.0
	Mullidae	*P. cyclostomus*	-	-	-	6 - 77	125	16.7	16.7	0.0	50.0	0.0	3.7
	Serranidae	*C. argus*	-	-	-	3 - 17	40	50.0	0.0	0.0	0.0	0.0	0.0
	Synodontidae	*Synodontidae sp*	-	-	-	59 - 81	-	0.0	0.0	0.0	0.0	0.0	22.2
		T. myops	-	-	-	59	400	0.0	0.0	0.0	0.0	0.0	3.7
Sessile Invertivore	*Chaetodontidae*	*C. auriga*	-	-	-	5 - 49	61	33.3	12.5	0.0	0.0	0.0	0.0
		C. fremblii	✓	-	-	19 - 28	128	6.7	0.0	0.0	0.0	0.0	0.0
		C. lunula	-	-	-	6 - 52	158	20.0	8.3	0.0	0.0	0.0	0.0
	Ostraciidae	*L. diaphana*	-	-	-	97	124	0.0	0.0	0.0	0.0	0.0	3.7
		L. fornasini	-	-	-	36	132	0.0	0.0	0.0	0.0	20.0	0.0
		Ostraciidae sp	-	-	-	5	-	3.3	0.0	0.0	0.0	0.0	0.0
	Pomacanthidae	*A. arcuatus*	✓	-	-	17	91	3.3	0.0	0.0	0.0	0.0	0.0
	Zanclidae	*Z. cornutus*	-	-	-	3 - 57	182	26.7	20.8	10.0	0.0	0.0	0.0
Sessile Macropiscivore	*Muraenidae*	*G. flavimarginatus*	-	-	-	3 - 52	150	73.3	25.0	0.0	50.0	0.0	0.0
		Gymnothorax sp	-	-	-	3 - 24	-	16.7	0.0	0.0	0.0	0.0	0.0
		G. javanicus	-	-	-	45	46	0.0	4.2	0.0	0.0	0.0	0.0
		G. meleagris	-	-	-	4 - 57	50	10.0	0.0	10.0	0.0	0.0	0.0
		G. undulatus	-	-	-	3 - 52	110	43.3	29.2	0.0	50.0	0.0	0.0
		Muraenidae sp	-	-	-	44	44	0.0	4.2	0.0	0.0	0.0	0.0
		S. okinawae	-	-	-	11	Unknown	3.3	0.0	0.0	0.0	0.0	0.0
		S. tigrina	-	-	-	6	25	3.3	0.0	0.0	0.0	0.0	0.0
	Ophichthidae	*M. magnificus*	✓	-	-	68	262	0.0	0.0	10.0	0.0	0.0	0.0
Generalist Macropiscivore	*Carangidae*	*Carangidae sp*	-	-	-	5 - 97	-	3.3	0.0	10.0	50.0	0.0	7.4
		A. ciliaris	-	-	-	59	100	0.0	0.0	0.0	0.0	0.0	3.7
		C. ferdau	-	-	-	14 - 31	60	3.3	4.2	0.0	0.0	0.0	0.0
		C. orthogrammus	-	✓	-	17 - 97	168	6.7	25.0	40.0	0.0	40.0	11.1
		C. ignobilis	-	✓	✓	31 - 81	188	0.0	12.5	10.0	0.0	0.0	14.8
		C. melampygus	-	✓	-	3 - 47	230	63.3	29.2	0.0	0.0	40.0	0.0
		E. bipinnulata	-	-	-	15	150	3.3	0.0	0.0	0.0	0.0	0.0
		G. speciosus	-	-	-	14 - 42	162	3.3	4.2	0.0	0.0	0.0	0.0
		S. lysan	-	✓	-	3 - 31	100	6.7	4.2	0.0	0.0	0.0	0.0
		S. dumerili	-	✓	-	43 - 92	385	0.0	4.2	30.0	0.0	0.0	3.7
		S. rivoliana	-	✓	-	21 - 92	245	3.3	0.0	0.0	0.0	0.0	7.4
	Carcharhinidae	*Carcharhinidae sp*	-	-	-	57	-	0.0	0.0	10.0	0.0	0.0	0.0
		C. amblyrhynchos	-	✓	-	24 - 68	275	3.3	0.0	10.0	0.0	0.0	0.0
		C. melanopterus	-	-	-	15	75	3.3	0.0	0.0	0.0	0.0	0.0
		C. plumbeus	-	-	-	55 - 95	280	0.0	0.0	10.0	0.0	0.0	33.3
		G. cuvier	-	-	-	5 - 56	350	3.3	8.3	10.0	0.0	0.0	3.7
	Lutjanidae	*A. virescens*	-	✓	-	13 - 95	180	26.7	33.3	40.0	50.0	20.0	22.2
		P. filamentosis	-	-	-	54 - 95	360	0.0	0.0	0.0	0.0	0.0	25.9
	Scombridae	*Scombridae sp*	-	-	-	55	-	0.0	0.0	0.0	0.0	0.0	3.7
	Sphyraenidae	*S. barracuda*	-	-	-	30 - 54	100	0.0	4.2	0.0	0.0	0.0	3.7

Table S.3.2. Canonical Analysis of Principal Coordinates (CAP), leave-one-out allocation test of depth and habitat groupings for overall assemblage composition.

Substrate		**Hard-bottom**			**Unconsolidated sediment**				
	Depth (m)	**0 - 30**	**30 - 53**	**53 - 100**	**0 - 30**	**30 - 53**	**53 - 100**	Total	%correct
Hard-bottom	**0 - 30**	32	6	0	0	0	0	38	84.211
	30 - 53	3	20	1	0	0	0	24	83.333
	53 - 100	1	1	7	0	0	1	10	70
Unconsolidated sediment	**0 - 30**	1	0	0	0	1	0	2	0
	30 - 53	0	1	0	1	2	1	5	40
	53 - 100	0	1	2	0	2	21	26	80.769

Table S.3.3. Main species driving within-group similarities and between-group dissimilarities (both 70% contribution, maximum of 10 species listed) based on B-C similarity and dissimilarity comparisons of depth and habitat strata in the MHI .Note: hard-bottom habitats, (all depths) and unconsolidated sediment sites between 53 – 100 m presented. PERMANOVA pair-wise comparisons highlighted **in bold** are statistically different (pair-wise PERMANOVA; minimum p < 0.05).

Hard-bottom, Euphotic (0 - 30 m) Average similarity: 24.70					
Species	Functional Group	Av.Sim	Sim/SD	Contrib%	Cum.%
Thalassoma duperrey	Mobile Invertivore	3.76	1.02	15.23	15.23
Parupeneus multifasciatus	Mobile Invertivore	1.99	0.91	8.04	23.27
Labridae sp	Mobile Invertivore	1.64	0.72	6.62	29.89
Melichthys vidua	Herbivore	1.56	0.82	6.3	36.19
Sufflamen bursa	Mobile Invertivore	1.48	0.81	6	42.19
Canthigaster jactator	Herbivore	1.16	0.59	4.7	46.89
Acanthurus olivaceus	Herbivore	1.13	0.62	4.59	51.48
Gymnothorax flavimarginatus	Sessile Macropiscivore	0.82	0.65	3.33	54.81
Melichthys niger	Planktivore	0.76	0.34	3.07	57.88
Caranx melampygus	Generalist Macropiscivore	0.74	0.5	3	60.87
Hard-bottom, Upper mesophotic (30 - 53 m) Average similarity: 31.55					
Oxycheilinus bimaculatus	Mobile Invertivore	5.66	1.3	17.93	17.93
Parupeneus pleurostigma	Mobile Invertivore	4.2	1.33	13.31	31.24
Labridae sp	Mobile Invertivore	2.02	0.88	6.41	37.64
Sufflamen fraenatum	Mobile Invertivore	2	0.87	6.33	43.98
Acanthurus olivaceus	Herbivore	1.73	0.69	5.48	49.46
Sufflamen bursa	Mobile Invertivore	1.7	0.8	5.38	54.83
Canthigaster coronata	Herbivore	1.65	0.72	5.23	60.06
Parupeneus multifasciatus	Mobile Invertivore	1.62	0.73	5.14	65.2
Pseudojuloides cerasinus	Mobile Invertivore	1.38	0.65	4.38	69.58
Pseudocheilinus evanidus	Mobile Invertivore	1.01	0.5	3.21	72.79
Hard-bottom, Lower mesophotic (53 - 100 m) Average similarity: 23.50					
Parapercis schauinslandii	Mobile Invertivore	9.12	0.82	38.79	38.79
Canthigaster coronata	Herbivore	7.43	1.24	31.63	70.42
Unconsolidated sediment, Lower mesophotic (53 - 100 m) Average similarity: 17.68					
Bothidae sp	Mobile Invertivore	5.15	0.59	29.12	29.12
Fistularia commersonii	Piscivore	2.33	0.51	13.17	42.29
Oxycheilinus bimaculatus	Mobile Invertivore	1.45	0.29	8.21	50.49
Dasyatis lata	Mobile Invertivore	1.3	0.37	7.33	57.83
Torquigener randalli	Mobile Invertivore	1.24	0.31	7.03	64.86
Pristipomoides filamentosis	Generalist Macropiscivore	1.03	0.25	5.81	70.67

Hard-bottom: Euphotic vs. Upper mesophotic Average dissimilarity: 80.40, **p = 0.0001**					
Species	Functional Group	Av. Diss	Diss/SD	Contrib%	Cum.%
Oxycheilinus bimaculatus	Mobile Invertivore	3.33	1.36	4.14	4.14
Thalassoma duperrey	Mobile Invertivore	3.07	1.30	3.82	7.96
Parupeneus pleurostigma	Mobile Invertivore	2.78	1.37	3.46	11.41
Melichthys niger	Planktivore	1.96	0.70	2.43	13.85
Labridae sp	Mobile Invertivore	1.80	0.96	2.24	16.08
Parupeneus multifasciatus	Mobile Invertivore	1.79	1.11	2.23	18.32
Naso brevirostris	Planktivore	1.70	0.73	2.11	20.43
Acanthurus olivaceus	Herbivore	1.53	1.09	1.90	22.33
Melichthys vidua	Herbivore	1.43	1.12	1.77	24.10
Naso hexacanthus	Planktivore	1.42	0.74	1.77	25.87
Hard-bottom: Euphotic vs. Lower mesophotic Average dissimilarity: 92.58, **p = 0.0001**					
Thalassoma duperrey	Mobile Invertivore	4.27	1.28	4.61	4.61
Parapercis schauinslandii	Mobile Invertivore	4.07	1.14	4.40	9.01
Parupeneus multifasciatus	Mobile Invertivore	2.52	1.04	2.72	11.73
Labridae sp	Mobile Invertivore	2.44	0.82	2.64	14.37
Melichthys niger	Planktivore	2.29	0.67	2.47	16.85
Canthigaster coronata	Herbivore	2.23	1.23	2.41	19.26
Melichthys vidua	Herbivore	2.09	1.11	2.25	21.51
Oxycheilinus bimaculatus	Mobile Invertivore	2.06	0.73	2.22	23.73
Sufflamen bursa	Mobile Invertivore	1.97	1.12	2.13	25.86
Acanthurus olivaceus	Herbivore	1.84	0.91	1.98	27.85
Hard-bottom: Upper vs. Lower mesophotic Average dissimilarity: 82.98, **p = 0.0001**					
Oxycheilinus bimaculatus	Mobile Invertivore	4.98	1.31	6.00	6.00
Parupeneus pleurostigma	Mobile Invertivore	4.36	1.42	5.25	11.25
Parapercis schauinslandii	Mobile Invertivore	4.11	1.19	4.95	16.20
Cirrhilabrus jordani	Planktivore	3.20	0.55	3.86	20.06
Labridae sp	Mobile Invertivore	2.59	1.06	3.12	23.18
Parupeneus multifasciatus	Mobile Invertivore	2.38	1.17	2.87	26.05
Acanthurus olivaceus	Herbivore	2.29	1.06	2.76	28.82
Sufflamen fraenatum	Mobile Invertivore	2.27	1.10	2.74	31.56
Sufflamen bursa	Mobile Invertivore	2.17	1.16	2.62	34.17
Pseudocheilinus evanidus	Mobile Invertivore	2.15	0.85	2.59	36.76
Lower mesophotic: Hard-bottom vs. Unconsolidated sediment Average dissimilarity: 90.17, **p = 0.0001**					
Parapercis schauinslandii	Mobile Invertivore	8.7	1.18	9.64	9.64
Canthigaster coronata	Herbivore	5.16	1.3	5.72	15.37
Oxycheilinus bimaculatus	Mobile Invertivore	4.81	0.81	5.33	20.7
Bothidae sp	Mobile Invertivore	4.64	0.88	5.15	25.85
Parupeneus chrysonemus	Mobile Invertivore	4.13	0.6	4.58	30.43
Fistularia commersonii	Piscivore	3.47	0.79	3.84	34.27
Pristipomoides filamentosis	Generalist Macropiscivore	2.93	0.52	3.25	37.52
Torquigener randalli	Mobile Invertivore	2.81	0.65	3.11	40.64
Aprion virescens	Generalist Macropiscivore	2.53	0.78	2.8	43.44
Carangoides orthogrammus	Generalist Macropiscivore	2.51	0.66	2.79	46.22

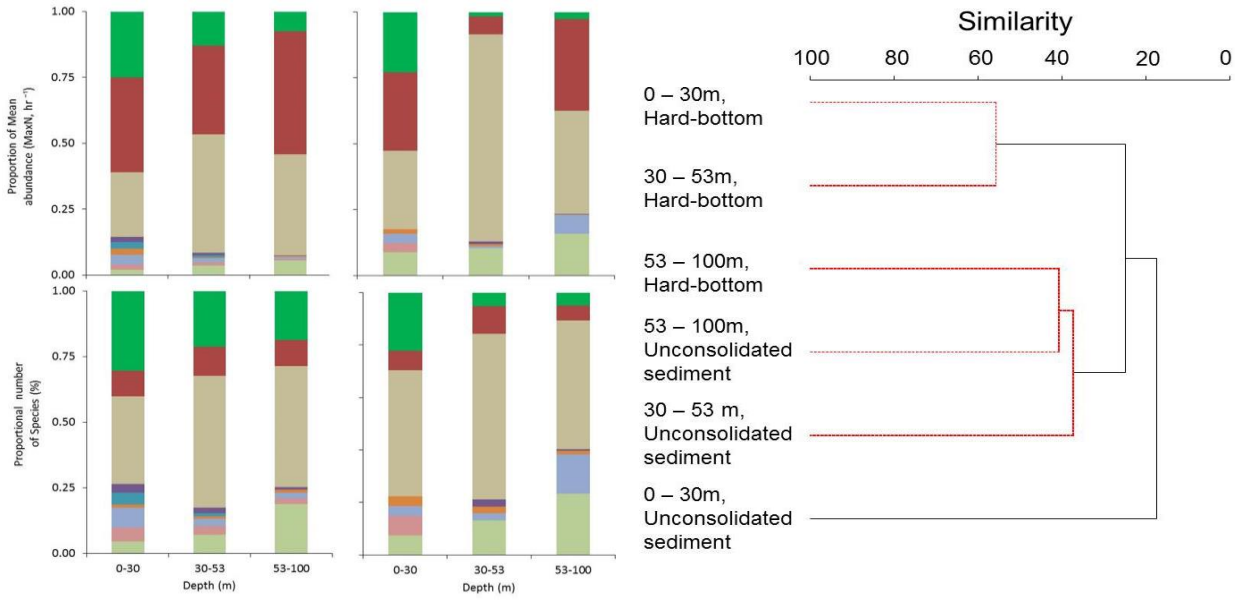


Figure S.3.1. Fish community weighted by A.) relative abundance and B.) total species (S). Percentage of each trophic group was calculated by summing all fish identified within each BRUVS replicate and shallow water-mesophotic depth bands. C.) Cluster analysis showing the Bray-Curtis similarity of reef fish communities (relative abundance, MaxN) along shallow water-mesophotic depth and habitat strata in the Main Hawaiian Islands. Dotted red lines indicate SIMPROF groupings.

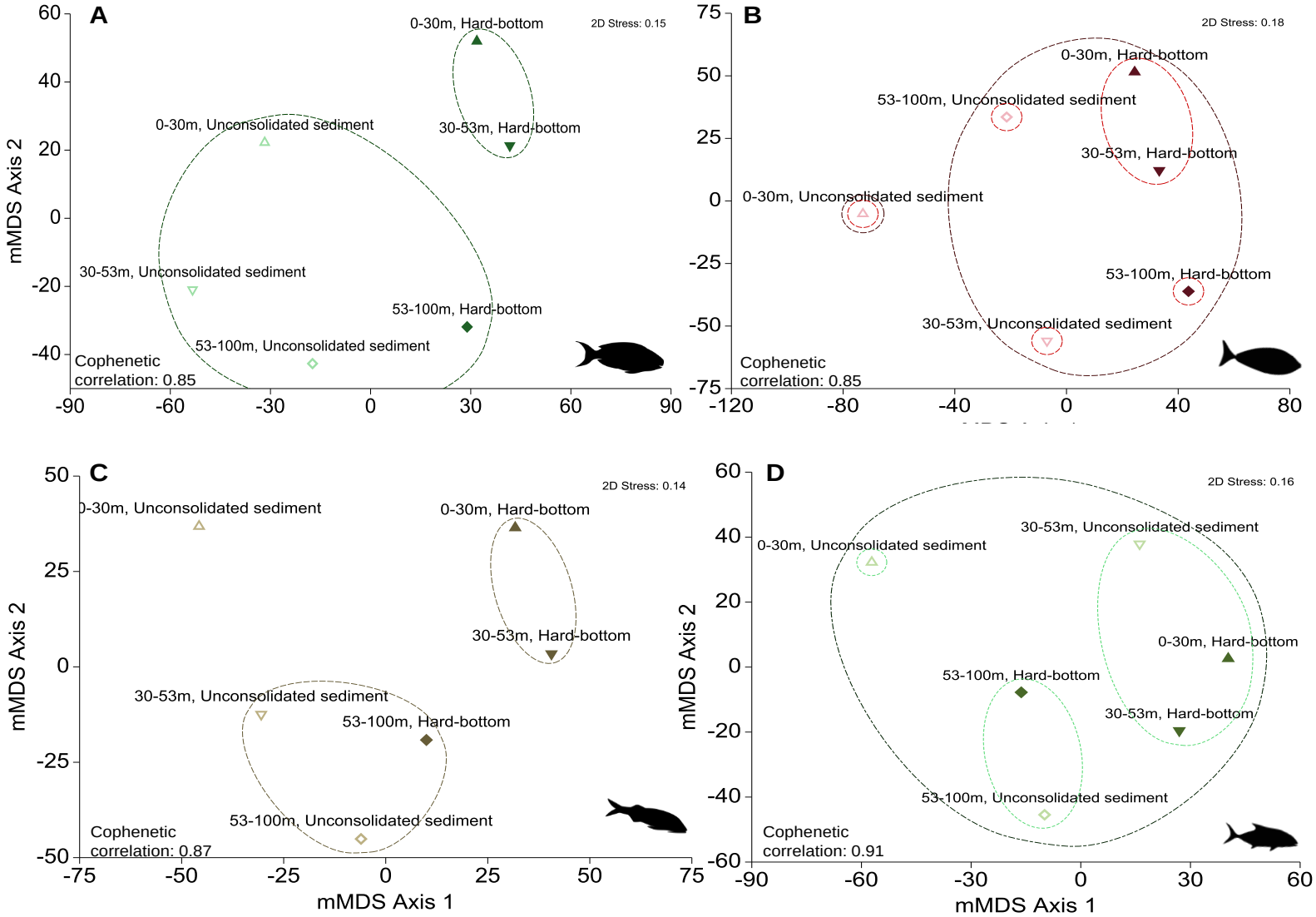


Figure S.3.2. Metric multidimensional scaling (mMDS) plots of group centroids generated from A.) herbivores B.) planktivores C.) mobile invertivores and D.) generalist macropisicvores by depth and habitat categorization. Dark colored dashed lines indicate SIMPROF groups for all groups. Light-colored dashed lines indicate 45% similarity ellipses for planktivores and generalist macropiscivores.

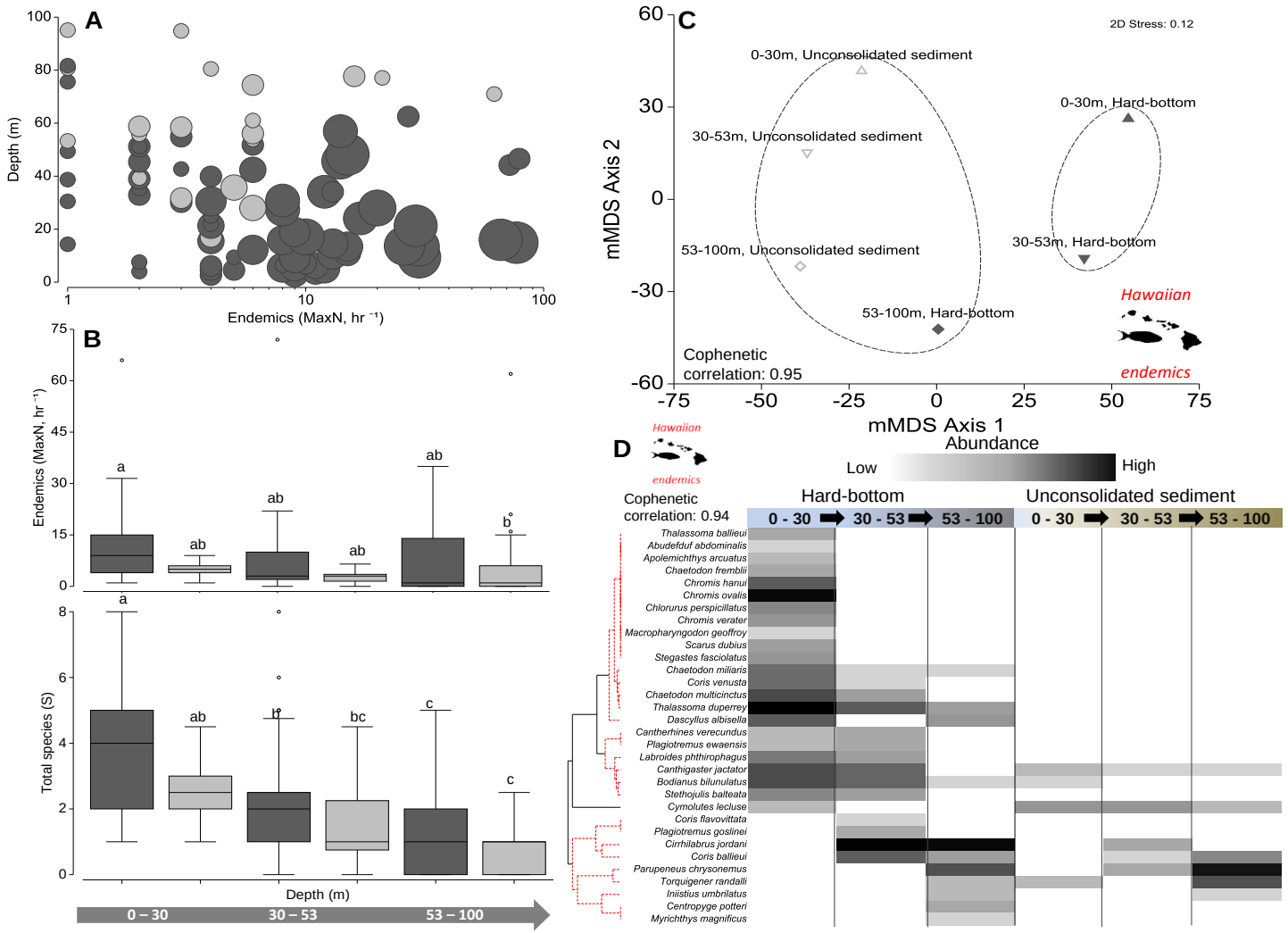


Figure S.3.3. A.) *Bubble plot* of untransformed relative abundance (MaxN, hr^{-1}) in relation to depth and species richness (total species, S) for Hawaiian endemics. X-axis displayed on a log scale. B.) Univariate *box plots* of untransformed pooled total abundance (MaxN, hr^{-1}) and species richness (total species, S) for endemics. Columns sharing the same letter do not differ significantly at the 95% confidence level based on PERMANOVA pair-wise tests. Dark boxes indicate hard bottom, light boxes indicate unconsolidated sediment. C.) Metric multidimensional scaling (mMDS) plot of endemics by depth and habitat categorization. Dashed lines indicate 50% similarity ellipses. D.) Endemic species recording $\geq$ 20% contributions. SIMPROF groups depictured along red, dashed lines in dendrogram.

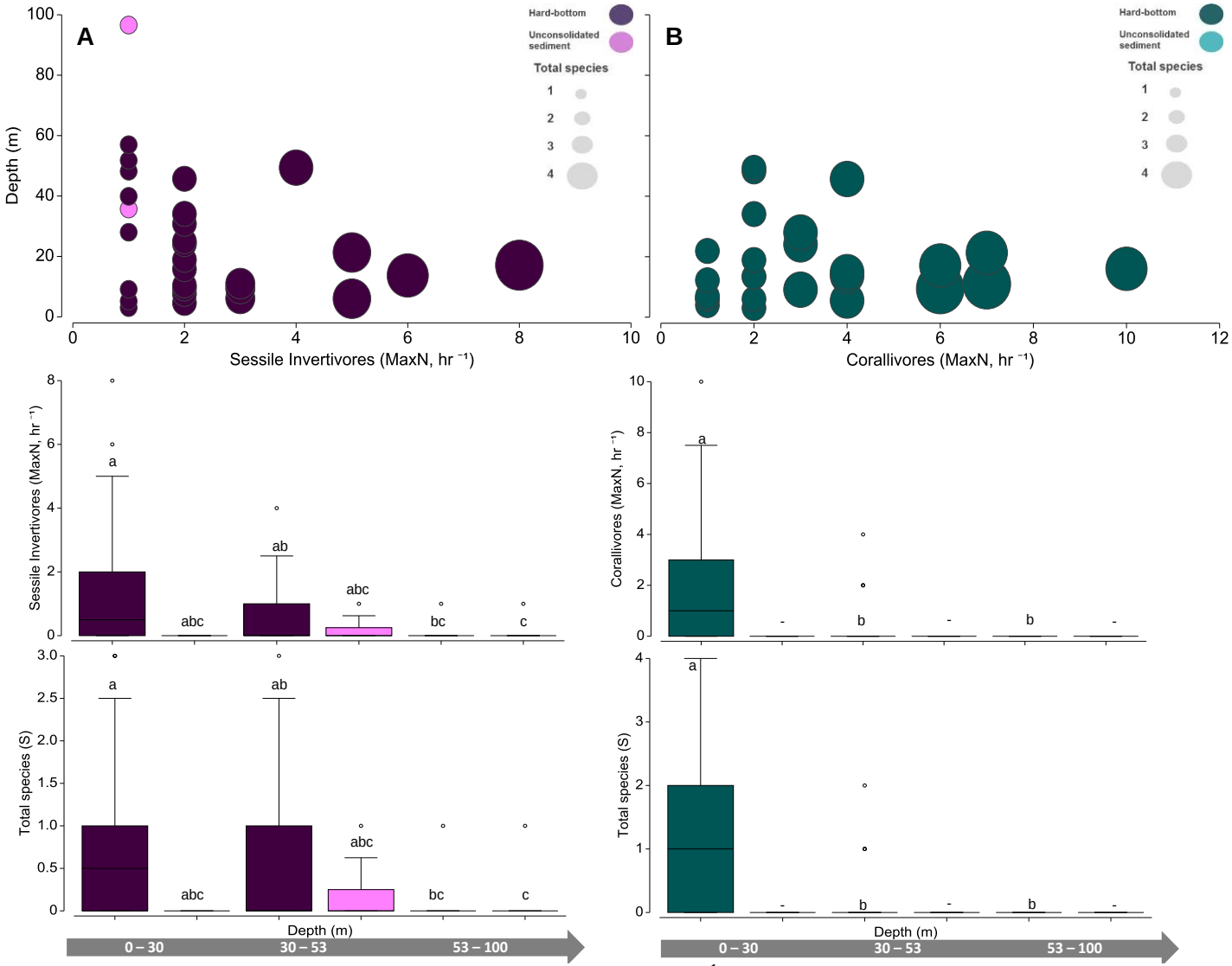


Figure S.3.4. *Bubble* and *box plots* of untransformed pooled total abundance (MaxN, hr^{-1}) and total species (S) for A.) sessile invertivores B.) corallivores. Columns sharing the same letter do not differ significantly at the 95% confidence level based on PERMANOVA pair-wise tests. Dark boxes indicate hard bottom, light boxes indicate unconsolidated sediment.

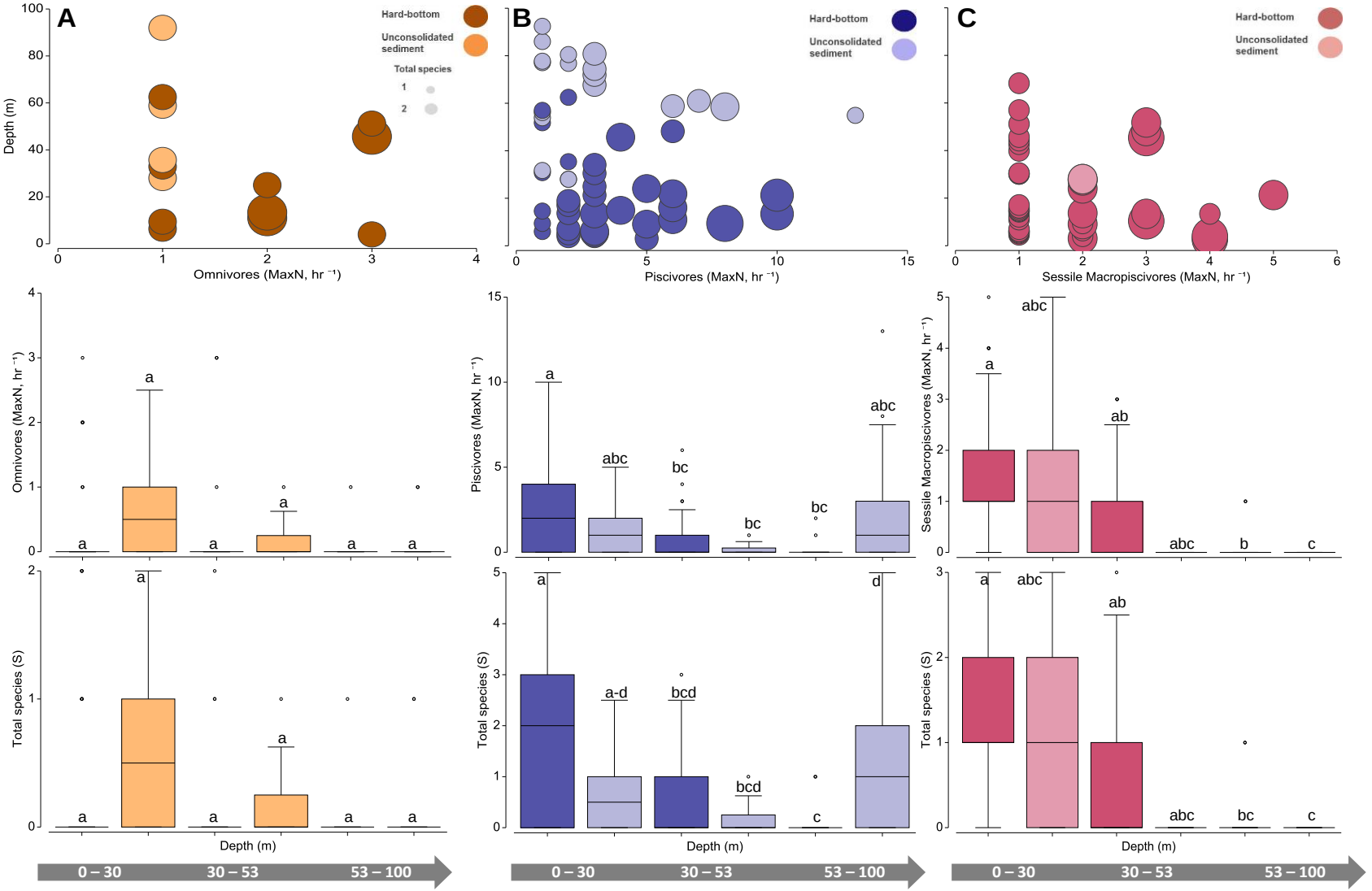


Figure S.3.5 *Bubble* and *box plots* of untransformed pooled total abundance (MaxN, hr^{-1}) and total species (S) for A.) omnivores B.) piscivores C.) sessile macropiscivores. Columns sharing the same letter do not differ significantly at the 95% confidence level based on PERMANOVA pair-wise tests . Dark boxes indicate hard bottom, light boxes indicate unconsolidated sediment.

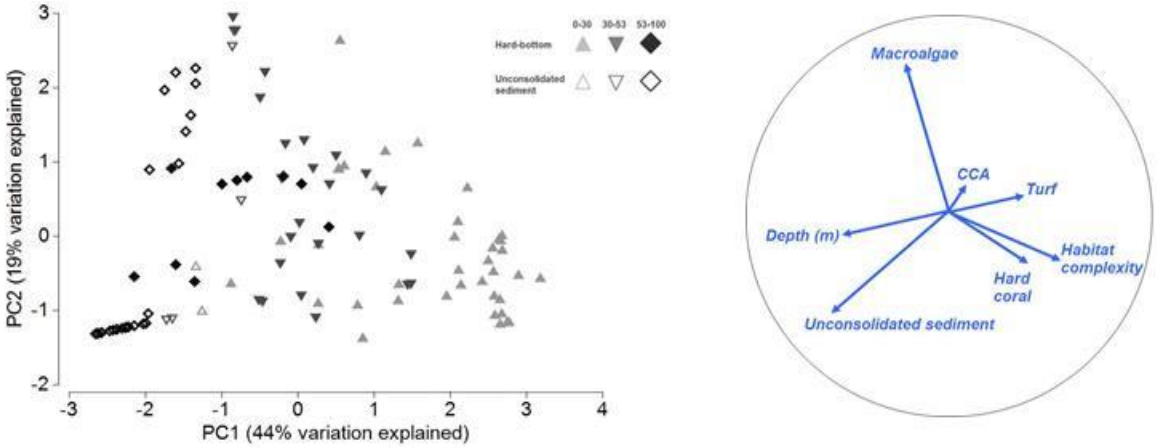


Figure S.3.6. Principal components analysis (PCA) of habitat composition in the Main Hawaiian Islands. Data plotted as individual BRUV replicates, with symbols indicating depth and habitat type. Correlation of variables designated by vector length and direction.

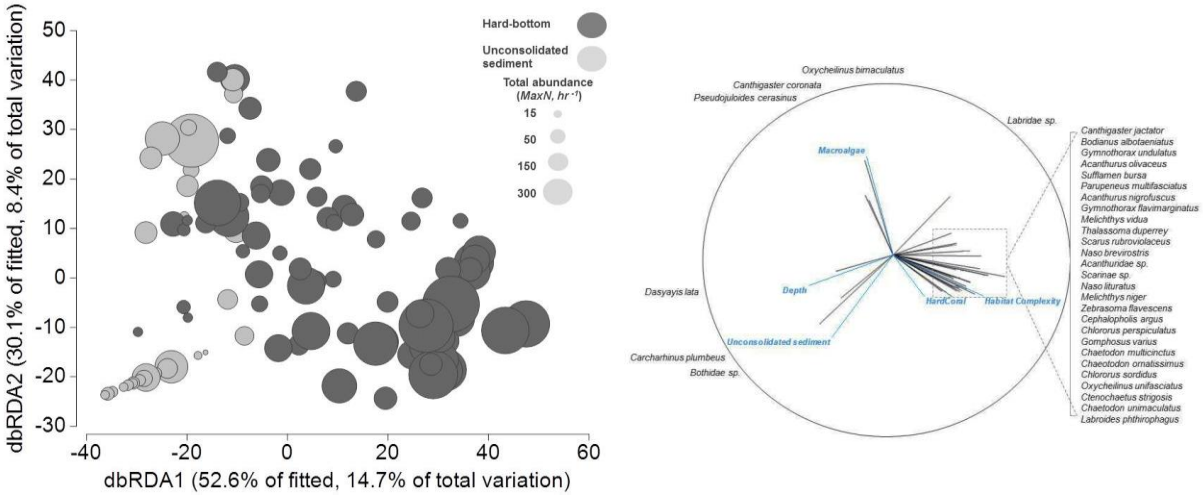


Figure S.3.7. Distance-based redundancy analysis (dbRDA) of total reef fish abundance. The left panel illustrates the relationship between environmental variables along the first and second axes to the overall reef fish assemblage. Bubbles are shaded and scaled to reflect total abundance at each site and habitat type. The right panel shows the strength and direction of environmental variables, along with prominent species recording Pearson's r values $\geq$ 0.4.

Species which recorded Pearson's r values $\geq$ 0.4 were asymmetrically distributed and provided fewer discriminatory patterns than the multivariate regression tree, with the majority of abundances aligning with overlaps between 0 – 30 and 30 – 53 m hard-bottom habitats with increased habitat complexity/coral cover, and a smaller proportion attributed to areas of increased macroalgae (primarily *Halimeda* sp.) cover and deeper areas of unconsolidated sediment.

Chapter 4 – An assessment of mobile predator populations along shallow and mesophotic depth gradients in the Hawaiian Archipelago

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 (Friedlander and DeMartini 2002; Baum et al. 2003; Baum and Myers 2004; Myers et al. 2007; Dulvy et al. 2008; Ward-Paige et al. 2010b; Nadon et al. 2012). 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 (Nadon et al. 2012) 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 (Friedlander and Dalzell 2004; Randall 2007; Santos et al. 2011; Nadon et al. 2015). 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) (Friedlander and DeMartini 2002; Williams et al. 2011a).

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 (Friedlander and DeMartini 2002; Holzwarth et al. 2006; Williams et al. 2011a). However, these groups are also known to inhabit considerably deeper 'mesophotic' strata of 30 – 150 m or more, where information on predator movements and habitat use remains severely understudied(Pickard 2013; Bejarano et al. 2014; Papastamatiou et al. 2015). For example, tiger sharks (*Galeocerdo cuvier*) and Galapagos sharks (*Carcharhinus galapagensis*) have been documented to depths greater than 200 m(Holland et al. 1999; Meyer et al. 2010a; Nakamura et al. 2011; Fitzpatrick et al. 2012; Werry et al. 2014b), while whitetip reef sharks (*Triaenodon obesus*) have been recorded down to 330 m (Randall 1977). 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 (Ralston et al. 1986; Chave and Mundy 1994; Randall 2007). Mesophotic coral reefs (herein denoted as 'MCEs') and other mesophotic ecosystems ≥ 30 m may be partially shielded from environmental and anthropogenic influences impacting shallow water coral reefs between 0 – 30 m, and may serve as population reservoirs for predator species targeted by fishers in shallower depths (Bongaerts et al. 2010; Bejarano et al. 2014; Papastamatiou et al. 2015; Lindfield et al. 2016). However, while mesophotic predator research has increased over the past two decades through the use of advanced sampling technologies, e.g. closed-circuit rebreather underwater visual surveys or acoustic/satellite tracking, predator assessments in Pacific mesophotic ecosystems remain largely unassessed in comparison with their shallower counterparts (Meyer et al. 2010b; Bridge et al. 2013; Kahng et al. 2014; Papastamatiou et al. 2015).

Given the documented evidence for higher roving predator abundance and/or biomass estimates in deeper waters around high-density human populations (Lindfield et al. 2016), sparsely populated or remote areas (Parrish et al. 2008; Bejarano et al. 2014), and the noted rarity or absence of several reef-associated shark species (e.g. sandbar sharks, *Carcharhinus plumbeus* and *Galeocerdo cuvier*) during diver surveys (Dale et al. 2011), it's feasible that open-circuit underwater visual censuses may be missing the bulk of their populations if surveys remain constrained to depths less than 30 m. Therefore, there is a clear need to expansion research into deeper coral reef habitats in order to better understand patterns in distributions of roving predator in the Hawaiian Archipelago and elsewhere.

Baited remote underwater stereo-video systems (stereo-BRUVs; herein denoted as 'BRUVS' as in previous chapters) 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 (Zintzen et al. 2012; Moore et al. 2013; Sackett et al. 2014), 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 (Brooks et al. 2011; Goetze and Fullwood 2013; Espinoza et al. 2014; Rizzari et al. 2014; Santana-Garcon et al. 2014; Malcolm et al. 2015).

Here, we present results of roving predator BRUVS surveys across the Hawaiian Archipelago covering depths down to 100 m. Research objectives included the: a.) comparison of relative abundances and length-based distributions of major species contributing to roving predator assemblages across shallow and mesophotic depth strata in the MHI and NWHI; and b.) investigation of mesophotic habitats, which remain largely inaccessible to underwater visual censuses on open-circuit scuba, as possible 'depth refugia' (defined as areas protected from shallow water disturbances that may serve as potential reproductive population reservoirs) for MHI roving predator species considered rare in 0 – 30 m depths (Bongaerts et al. 2010; Pinheiro et al. 2016).

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 archipelagos in the world. The archipelago includes the Main Hawaiian Islands (MHI), which are geologically young, high-islands subjected to heavy population and fishing pressures (Friedlander and DeMartini 2002), 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 and subsequent expansion of the Papahānaumokuākea Marine National Monument (PMNM) in 2007 and 2016 respectively. Because of their management status and their remoteness, access is almost entirely limited to research and management groups and traditional Native Hawaiian practitioners.

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 (French Frigate Shoals, Lisianski, Pearl and Hermes Reef, Midway Atoll) were conducted during two NOAA research expeditions in May and September 2014 (Figure 4.1, top panel). 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 (Ayotte et al. 2015b; Williams et al. 2015), 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 backscatter data products produced by the University of Hawaii, School of Earth and Ocean Sciences (SOEST), Hawaii Mapping Research Group (Main Hawaiian Islands Multibeam Bathymetry and Backscatter Synthesis, http://www.soest.hawaii.edu/HMRG/multibeam/). Grid cells were constrained within a 100 m contour line using data derivatives from SOEST HMRG 50 m bathymetry and topography grid cells, and stratified into three predetermined, near "equally spaced" depth bins (30 – 53 m, 53 – 76 m, 76 – 100 m). Because the primary goal was to compare among hard-bottom habitats, grid cells containing backscatter values with > 35% unconsolidated sediment (sand; obtained from SOEST HMRG 60 m backscatter grid cells) 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.

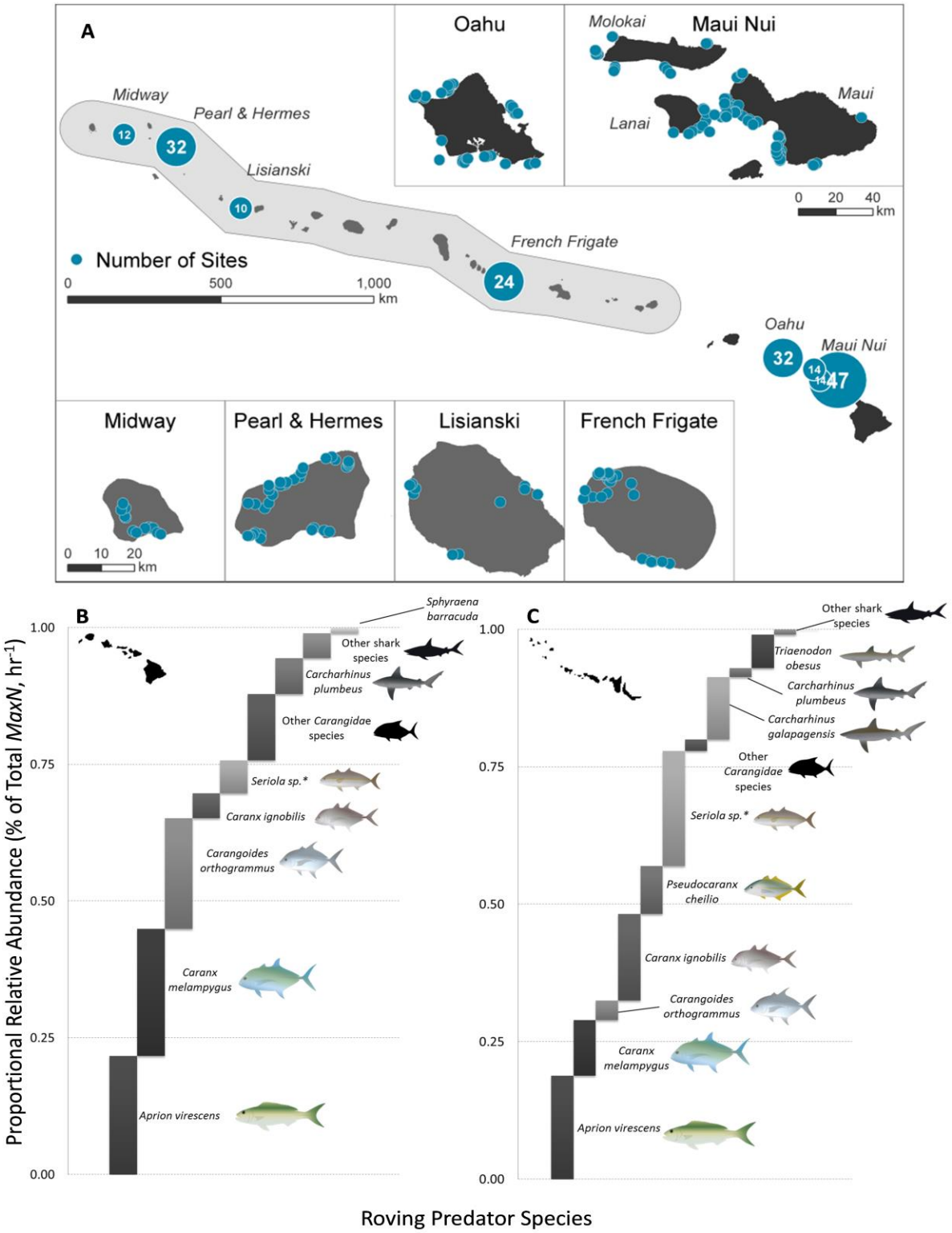


Figure 4.1. A.) Map indicating stereo-BRUVs sampling locations across the Hawaiian Archipelago, with the NWHI highlighted in grey shade. Upper right panel: Shaded black areas indicate island outlines for the MHI (Oahu, Maui, Molokai, Lanai). Lower panel: islands and atolls sampled in the NWHI, with shaded areas indicating 100 m depth contours. B.) Stagged *bar plots* of the proportional relative abundance (% of total MaxN, hr^{-1}) of pooled predator assemblages in the MHI and C.) NWHI. * Indicates numerical abundance of *Seriola dumerili, Seriola rivoliana, and Seriola sp.* (excluding *Seriola lalandi*) pooled.

Table 4.1. 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
	Subtotal	72	35	107
Northwestern Hawaiian Islands	0-30	27	-	27
	30-53	19	3	22
	53-100	23	6	29
	Subtotal	69	9	78
	Total surveys	**141**	**44**	**185**

Stereo-video collection and data processing

The BRUVS used in this study followed the design of Harvey *et al.* (Harvey and Shortis 1995; Harvey and Shortis 1998; Harvey et al. 2002b), and were constructed from a pair of high definition Sony handheld video cameras with a wide-angle lens adaptor, held in waterproof housing and mounted on a base bar 0.7 m apart, inwardly converged at 8^{o}. Prior to and following each research mission, each BRUVS was calibrated using CAL^{TM} software according to protocols described elsewhere (Harvey and Shortis 1995; Harvey and Shortis 1998; Seager 2008; Harvey et al. 2013a). 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.

Upon 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-Stereo^{TM} videographic software (Seager 2008). 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" (Priede et al. 1994; Ellis and Demartini 1995; Willis and Babcock 2000a; Willis et al. 2000b; Cappo et al. 2003; Cappo et al. 2004) 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 (Harvey et al. 2010). All MaxN and fork-length data were compiled and cataloged according to the National Fisheries Information System (FIS) Information Portal practices (Pacific Islands Fisheries Science Center 2015).

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. A subtotal of 107 baited sites in the MHI, and 78 sites in the NWHI were sampled (185 pooled deployments; Figure

4.1, top panel). Outputs from efforts by region and depth strata are listed in Table 4.1.

Target groups

Analysis of BRUVS surveys was focused on high-level roving predators, with selections based on assignments as described in Friedlander and DeMartini (2002), Holzwarth *et al*. (2006), Parrish et al (2008), and Williams *et al*. (2011). These included 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 flat (100% unconsolidated sediment) (Chave and Mundy 1994). 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 (Wilson et al. 2007). Finally, percent cover of hard coral, soft coral, macroalgae, turf algae, crustose coralline algae, and sand was visually-estimated from video imagery using the NOAA PIFSC CREP fish team benthic classification protocol (Heenan 2014).

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). The decision to combine 53 – 76 m and 76 – 100 m abundance estimates *post-hoc* into a single level (lower mesophotic) came as a result of the reduced number of MHI hard-bottom mesophotic sites encountered below 53 m, with upper/lower mesophotic depth stratification aligning with coral reef fish assemblage structures observed in the MHI (Asher, unpublished data) and reported elsewhere (Pinheiro et al. 2016; Rosa et al. 2016). A third *post-hoc*, two-level fixed factor was added (Habitat; hard-bottom, unconsolidated sediment), as coral reef roving predators were commonly sighted in 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) because of small sample sizes.

Statistical analyses

Multivariate roving predator assemblage analysis was conducted on a zero-adjusted Bray-Curtis (B-C) (Clarke et al. 2006) dissimilarity matrix using square root transformed relative abundance data using PRIMER v7.0.11 with the PERMANOVA+ add on software (Anderson 2008a; Clarke and Gorley 2015).

Segregated regional and depth-inferred differences between roving predator population aggregates were first obtained through the bootstrapping function (Efron 1982; Manly 2006), and visualized as a metric multidimensional scaling (mMDS) (Cox and Cox 2000) ordination with bootstrap regions set to 95% confidence intervals (plotted as ellipses), a Kruskal stress formula set to 1, and minimum stress assigned to 0.01. A successive Hierarchical Cluster Analysis (Rousseeuw 1987)was calculated from distanced-dissimilarities between group centroids (region x depth x habitat) in order to visualize potential effect sizes and their interactions, 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 $r \geq 0.8$ can be interpreted as a strong representation of the original centroid dataset (Rohlf and Wooten 1988).

Changes to MHI and NWHI roving predator assemblages were evaluated along the continuous depth gradient within each respective region using a canonical analysis of principal coordinates (CAP). Subsequent CAPs were used to examine the efficacy of *a priori* MHI and NWHI depth group assignments through "leave-one-out" cross validation and allocation of observations to groups (Anderson and Robinson 2003; Anderson and Willis 2003). Finally, Person's rank correlations of individual species recording > 0.35 were superimposed (as vectors) with the resultant CAP axes within each respective region as additional exploratory measures(Anderson 2008a).

Variation in assemblage structure between regions, depth strata, and habitat types were further tested using a Permutational Multivariate Analysis of Variance (PERMANOVA) as this is a robust test for examining correlations within potential heterogeneous variances (Anderson and Walsh 2013). 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 within and between factor levels, with Monte Carlo p-values used for cases with fewer than 30 unique permutations (Anderson 2008a). 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 shade plot/heat map (Wilkinson and Friendly 2009) was constructed to further delineate abundance distributions of individual species 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 (Rousseeuw 1987) using group average clustering and a Type III similarity profile (SIMPROF) analysis (Clarke et al. 2008) with 9999 permutations. A Similarity Percentages, Species Contributions (SIMPER) test(Clarke 1993; Clarke and Warwick 2001) was then 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 distance 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 lalandi*, which had distinctly different characteristics than other members of the *Seriola* genus, were rarely encountered and were excluded from pooling.

Finally, changes to the relative abundance of individual species identified in SIMPER were modeled along continuous depth gradients using R statistical software (version 3.3.0) following the approach used by Fukunaga *et al*. (2016), generating non-parametric quantile regression splines through the rq() function in the *quantreg* package (Anderson 2008b; R Core Team 2016).

Length-based estimates

Differences in length distributions for those species identified in SIMPER output were compared between respective regions (MHI, NWHI) and depth strata (shallow [0 – 30 m], mesophotic [pooled 30 – 100 m strata]) using untransformed raw length data (no zeros) across model factors and the non-parametric Kolmogorov-Smirnov test (Massey Jr 1951), with data pooled from all mesophotic depths due to insufficient target species length measurements in upper or mesophotic strata alone. 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.

Habitat Characterization

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, a Kruskal stress formula set to 1, and minimum stress assigned to 0.01. In order to further gauge the ecological relationships between shallow water and upper and lower mesophotic zones, a Principal Component Analysis (PCA) (Wold et al. 1987; Jolliffe 2002) was performed on normalized environmental variables separately for the MHI and NWHI.

Finally, linkages between normalized, Euclidean-distance based environmental matrices and roving predator assemblage (abundance) matrices in the MHI and NWHI were explored using distance-based linear modeling (DISTLM) in PERMANOVA+ (Anderson 2004; Anderson 2008a) , with the most parsimonious model constructed using modified Akaike's Information Criterion (AICc) and *BEST* procedures. DISTLM allows for the testing of variation within predator assemblages to be explained through multiple environmental predictor variables, generating the most parsimonious models from the lowest AIC values. Distance-based redundancy analyses (dbRDA) were then used to construct constrained ordinations from *BEST* fitted values from the MHI and NWHI, using linear combinations of environmental variables which best explained the variation within roving predator assemblages belonging to each respective region (Anderson 2008a).

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), while 425 roving predators were recorded over 78 BRUVS sites in the NWHI (5.45 ± 0.84, Table 4.2). 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; Figure 4.1B, C). 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 4.2), with *Caranx melampygus* dominating shallow water abundances (51%, Figure 4.2A) and *Carangoides orthogrammus* remaining prevalent in mesophotic depths (27%, Figure 4.2B). 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%, Figure 4.2C), and *Seriola sp*† comprising the major group (28%) in mesophotic habitats (Figure 4.2D). Finally, sharks formed 12% and 20% of MHI and NWHI roving predator abundances respectively (Table 4.2, Figure 4.2). 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 of encounters. Neither species were sampled by BRUVS in the MHI.

Roving predator assemblages differed between regions and depth strata (Global PERMANOVA, both p = 0.0001, Table 4.3). The relationship between roving predator assemblage structures and continuous depth gradients among the 107 surveys in the MHI ($\delta^2 = 0.35$, m = 4 principal coordinate axes, Supplementary Materials, Figure S.4.1A) and 78 surveys in the NWHI ($\delta^2 = 0.55$, m = 3 principal coordinate axes, Figure S.4.1B) confirmed a high degree of community overlaps between depths, particularly between 0 – 30 and 30 – 53 m (Figure 4.3A, Supplementary Materials, Table S.4.2). When examining the efficacy and cross validation of depth-zone assignments within the MHI and NWHI, 63% and 97% of assignments in the lower mesophotic zone were correctly made in the MHI and NWHI respectively, with misclassification errors largely driven by assignment switches (i.e. assemblage overlaps) between shallow water and upper mesophotic groups (Supplementary Table S.4.1, Figure S.4.1C, D), with MHI patterns being particularly susceptible to leave-one-out allocation errors due to the greater number of zero sightings or singleton predator observations during BRUVS surveys.

Upon assessing the unbalanced sampling of hard-bottom vs. unconsolidated sediment sites, assemblage patterns between group centroids largely mirrored as previously described (Figure 4.3B) with outliers attributed to small sample sizes for those strata (MHI unconsolidated sediment: n=2, 0 – 30 m and NWHI: n=3, 30 – 53 m). Interactive effects were disproportionately driven by intra- and inter-regional differences highlighted in successive pair-wise tests (Supplementary Material, Table S.4.2).

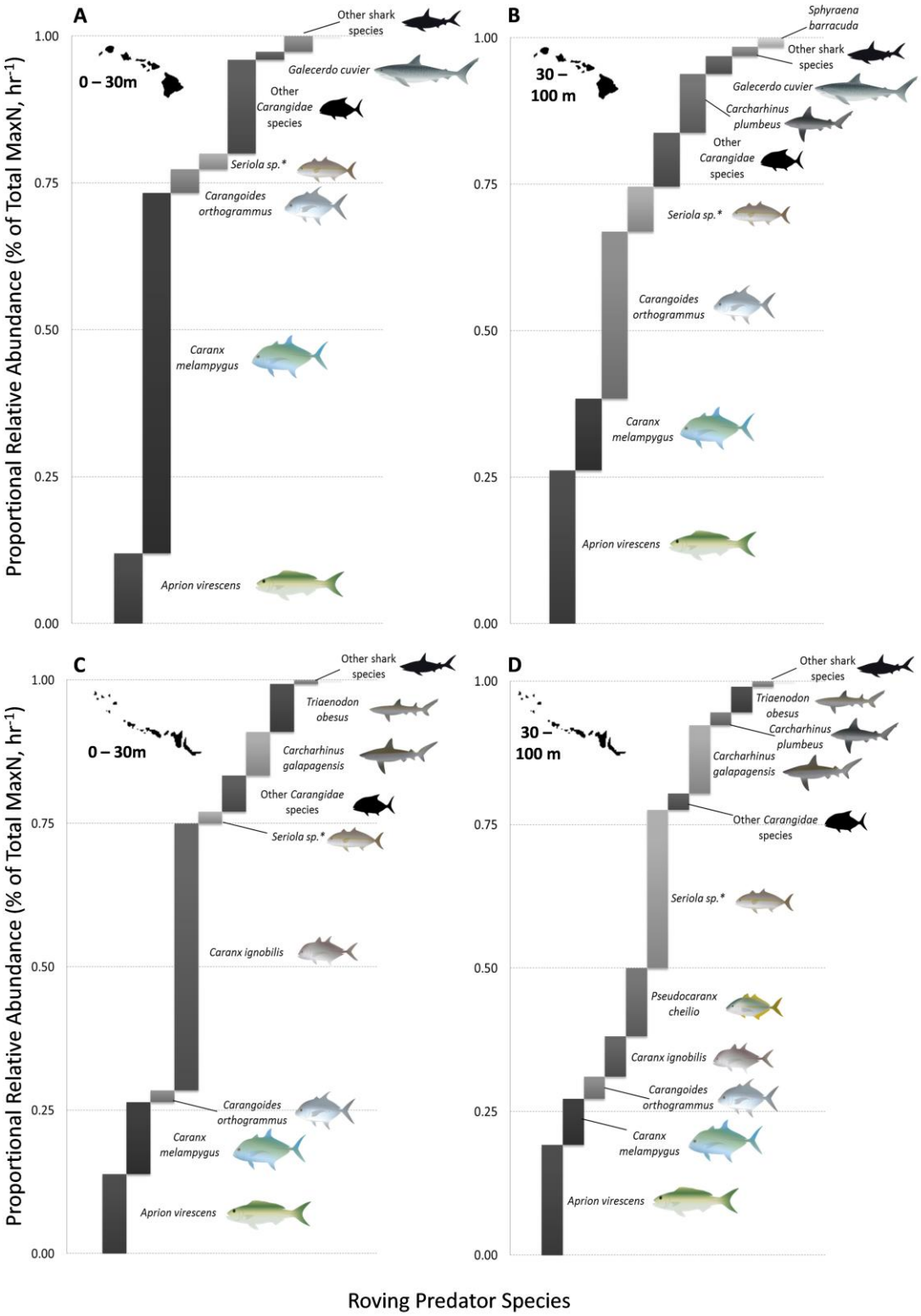


Figure 4.2. Staggered *bar plots* of the A.) Shallow and B.) Mesophotic proportional relative abundance (% of total MaxN, hr^{-1}) of pooled predator assemblages in the MHI. C.) Shallow and D.) Mesophotic proportional relative abundance of pooled predator assemblages in the NWHI.

Table 4.2. Average abundance (mean MaxN), standard error (SE), and NWHI:MHI abundance ratios for roving predator species sampled in the Hawaiian Archipelago. % Drops indicate the percentage number of BRUVS deployments where a species or group is observed. FFS: French Frigate shoals, LIS: Lisianski, PHR: Pearl and Hermes Reef, MID: Midway. * *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)	Islands	n	Mean *MaxN*	% Drops	Min. depth (m)	Max.depth (m)	Islands	NWHI:MHI
Barracuda (*Sphyraenidae*)														
Sphyraena barracuda	Great barracuda	2	0.02±0.01	1.9	30.2	53.9	Molokai	-	-	-	-	-	-	-
Snappers (*Lutjanidae*)														
Aprion virescens	Green jobfish	43	0.41±0.11	26.2	13.4	94.8	All	80	1.03±0.16	73.1	2.7	100.0	All	2.51
Jacks (*Carangidae*)														
Main species														
Carangoides orthogrammus	Island jack	40	0.37±0.13	15.9	17.1	96.6	Maui, Lanai, Oahu	15	0.19±0.08	9.0	5.5	50.3	FFS, LIS, PHR	0.51
Caranx melampygus	Bluefin trevally	46	0.43±0.09	26.2	3.0	46.6	All	43	0.55±0.14	34.6	2.7	50.3	All	1.28
Caranx ignobilis	Giant trevally	9	0.08±0.03	7.5	30.8	80.8	Maui, Molokai, Oahu	67	0.86±0.29	28.2	2.7	50.3	All	10.75
Pseudocaranx cheilio	Thick-lipped jack	-	-	-	-	-	-	37	0.47±0.31	10.3	40.5	100.0	PHR, MID	-
Seriola dumerili	Greater amberjack	6	0.06±0.03	4.7	42.7	92.0	Molokai, Oahu	55	0.71±0.39	14.1	23.5	93.3	FFS, LIS, PHR	11.83
Seriola rivoliana	Almaco jack	6	0.06±0.03	2.8	21.3	92.0	Molokai, Oahu	27	0.35±0.17	16.7	24.7	100.0	LIS, PHR, MID	5.83
Unidentified *Seriola sp.**		-	-	-	-	-	-	7	0.09±0.04	7.7	60.4	-	FFS, LIS, PHR	-
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	-	Oahu	-	-	-	-	-	-	-
Carangoides ferdau	Barred jack	4	0.04±0.03	1.9	14.3	30.5	Maui, Oahu	1	0.01±0.01	1.3	37.8	-	FFS	0.25
Elagatis bipinnulata	Rainbow runner	1	0.01±0.01	0.9	14.9	-	Lanai	-	-	-	-	-	-	-
Gnathanodon speciosus	Yellow trevally	2	0.02±0.01	1.9	14.3	42.4	Maui, Oahu	-	-	-	-	-	`	-
Scomberoides lysan	Queenfish	3	0.03±0.02	2.8	3.05	30.5	Lanai, Maui, Oahu	-	-	-	-	-	-	-
Seriola lalandi	Yellowtail amberjack	-	-	-	-	-	-	5	0.06±0.03	2.6	65.5	85.3	LIS, PHR	-
Unidentified Carangidae		9	0.08±0.04	4.7	4.6	96.6	Maui, Oahu	3	0.04±0.03	2.6	43.6	55.8	FFS, PHR	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	All	-
Carcharhinus plumbeus	Sandbar shark	13	0.12±0.05	8.4	54.9	95.1	Maui, Molokai, Oahu	7	0.09±0.03	9.0	55.8	93.3	FFS, LIS, PHR	0.75
Triaenodon obesus	Whitetip reef shark	-	-	-	-	-	-	26	0.14±0.05	25.6	5.8	61.6	All	-
Other species														
Galeocerdo cuvier	Tiger shark	5	0.05±0.02	4.7	4.6	55.8	Maui, Molokai, Oahu	1	0.01±0.01	1.3	86.6	-	PHR	0.20
Carcharhinus amblyrhynchos	Grey reef shark	2	0.02±0.01	1.9	24.1	68.3	Maui, Oahu	1	0.01±0.01	1.3	73.2	-	FFS	0.50
Carcharhinus melanopterus	Blacktip reef shark	1	0.01±0.01	0.9	14.9	-	Lanai	-	-	-	-	-	-	-
Unidentified shark		1	0.01±0.01	0.9	57.0	-	Oahu	2	0.03±0.02	2.6	38.1	73.2	FFS, LIS	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

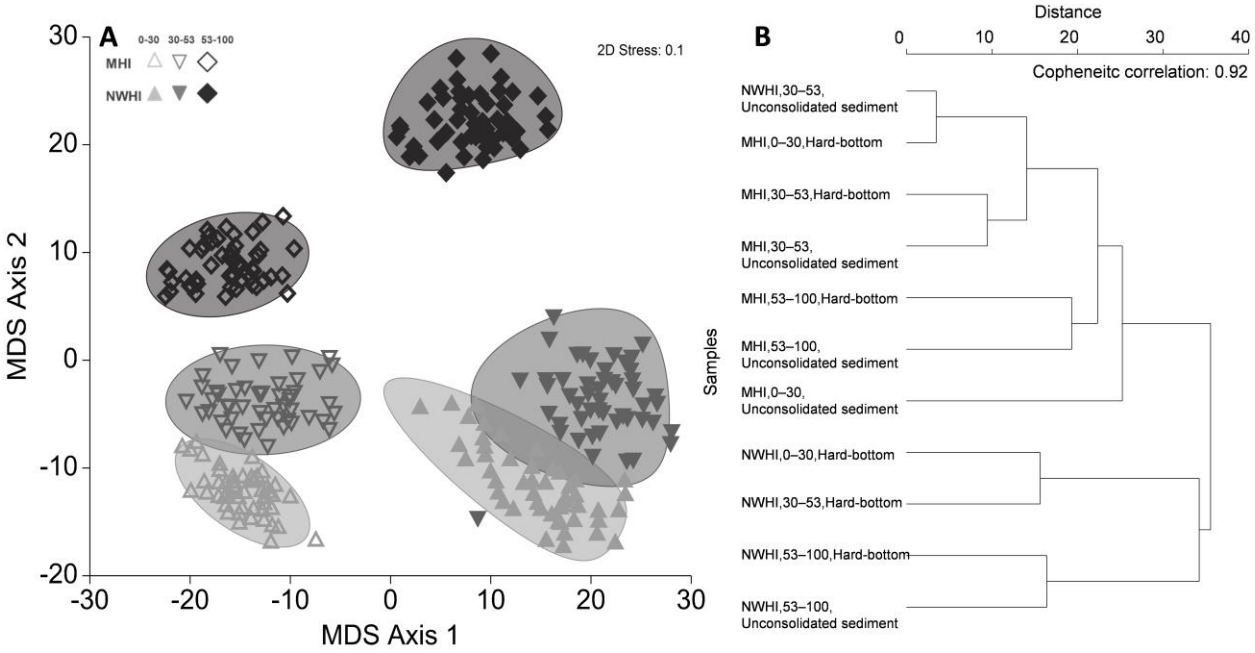


Figure 4.3. *Bootstrap resampling plot*, 50 bootstraps per group. Square root transformed, zero-adjusted Bray Curtis roving predator abundance data (MaxN, hr^{-1}) by Region (MHI, NWHI) x Depth Strata (SPC; upper and lower mesophotic), plotted metric multi-dimensional scaling (mMDS). Shaded bootstrap regions, which represent measurements of centroid error: 95% confidence ellipses, averages based on m = 10 dimensional metric MDS (rho = 0.985). Open symbols represent MHI sites, closed symbols represent NWHI sites. Light grey = shallow water (0 – 30 m), medium grey = upper mesophotic (30 – 53 m), dark grey = lower mesophotic (53 – 100 m). B.) *Hierarchical cluster analysis dendrogram* of group centroids f by Region (MHI, NWHI), Depth (0 – 30 m, 30 – 53 m, 53 – 100 m), and Habitat (Hard-bottom, unconsolidated sediment). Note the absence of NWHI unconsolidated sampling sites between 0 – 30 m. Cophenetic correlation = 0.92.

Finally, the prominent species identified in SIMPER similarity/dissimilarity measures and shade plot outputs (Figure 4.4) largely drove assemblage differences between regions and depth strata. These included *Aprion virescens*, *Caranx melampygus*, *Carangoides orthogrammus*, *Caranx ignobilis*, *Triaenodon obesus*, *Carcharhinus galapagensis, Pseudocaranx cheilio*, *Seriola sp*.[†], and *Carcharhinus plumbeus*. Comparable with MHI CAP outputs, *Caranx melampygus* appeared aligned with shallow and upper mesophotic sites, while *Carangoides orthogrammus* and *Aprion virescens* were encountered in higher abundances in upper and lower mesophotic zones (Figure 4.4, Supplementary Material, Figure S.4.1C, lower panel). *Caranx melampygus* presented a similar pattern in the NWHI, with *Carangoides orthogrammus*, *Caranx ignobilis, and Triaenodon obesus* likewise remaining more prevalent in shallow and upper mesophotic zones. In contrast, *Aprion virescens* and *Carcharhinus galapagensis* remained more broadly distributed between depth strata, although greater abundances were noted for both species in mesophotic depths. Finally, *Seriola sp*.[†], *Pseudocaranx cheilio*, *and Carcharhinus plumbeus* remained prevalent in the upper and/or lower mesophotic zones, being near-absent from shallow-water strata (Figure 4.4, Supplementary Material, Figure S.4.1D, lower panel).

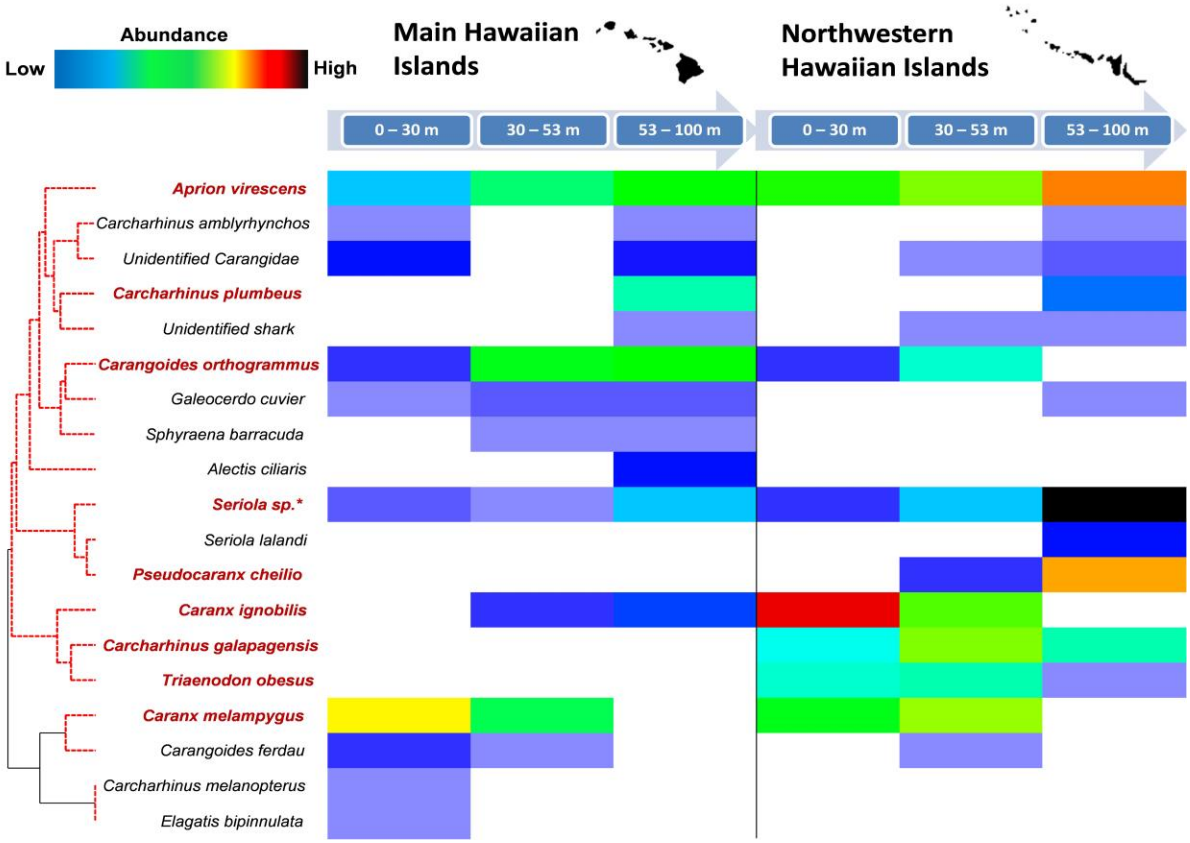


Figure 4.4. *Shade plot* showing regional (MHI, NWHI) and depth distributions of all roving predator species. Raw species relative abundance values (MaxN, hr^{-1}: color ramped blocks) were square root transformed to down-weight more abundant species. Y-axis (roving predator resemblance): position of standardized MaxN, hr^{-1} 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. Species identified in SIMPER highlighted in red. b.) X-axis: Sites grouped according to region (MHI, NWHI) and depth strata, aligned from left to right.

Roving Predator Abundances: Univariate analysis

Aprion virescens were homogeneously dispersed ($p > 0.05$) across all depth and habitat strata (Tables 4.3 – 4.4; Figure 4.5, 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 S.4.2).

Caranx ignobilis and *Seriola sp*[†] (both $p = 0.0001$, Table 4.3) were an order of magnitude more abundant in the NWHI (Table 4.2). In particular, only small numbers of *Caranx ignobilis* were encountered between 30 – 100 m (upper and lower mesophotic zones) in the MHI (Tables 4.3 – 4.4, Supplementary Material Table S.4.2, and Figure 4.5 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 S.4.2). 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 4.3 – 4.4, Figure 4.5 center). Following the inclusion of pooled habitats, retests for region and depth remained significant (both $p = 0.0001$), 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 4.3 – 4.4), although no differences were detected between mesophotic zones (Supplementary Materials, Table S.4.2).

Table 4.3. 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 exceeds 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)	

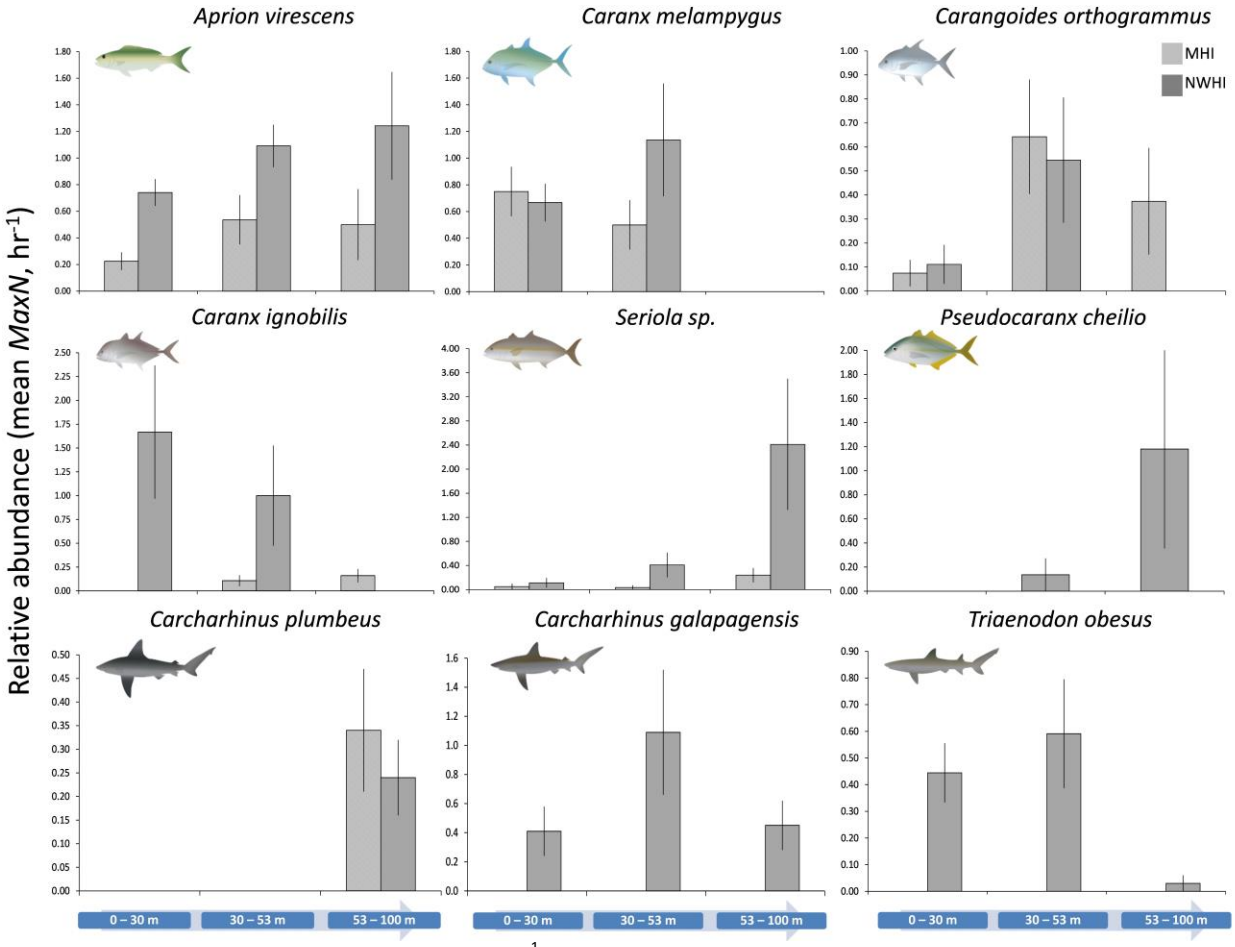


Figure 4.5. Mean relative abundance (Mean MaxN, hr^{-1} ±SE) of roving predator species identified in SIMPER analyses across regions and depth strata (habitats pooled). Depth is ordered in increasing intervals, with all habitats pooled. Light grey = MHI, dark grey = NWHI. Note the differences in scales along the y-axis.

The most commonly encountered shark in the MHI - *Carcharhinus plumbeus* - were recorded exclusively in the lower mesophotic zone (Figure 4.5, bottom left), with nearly 4 times the number of sightings occurring on unconsolidated sediment compared to hard-bottom substrate with a similar general pattern evident in the NWHI (Table 4.4). Regional abundances were homogenous and non-significant when pooled habitats were compared between regions ($p > 0.05$, Supplementary Materials, Table S.4.2). Finally, the two species of shark only recorded in the NWHI - *Carcharhinus galapagensis* and *Triaenodon obesus* - similarly had peak abundances between 30 – 53 m, were present in 0 – 30 m, and uncommon in 53 – 100 m. Despite *Carcharhinus galapagensis* abundance peaking in the upper mesophotic zone (Table 4.3 and Figure 4.5, bottom center), there were no significant depth differences even when habitats were pooled. Similarly, *Triaenodon obesus* was most frequently encountered in the upper mesophotic zone (Figure 4.5, lower right), with significant differences between depth strata ($p < 0.01$, Table 4.4); 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 S.4.2). Results from univariate species-level regression spline models, with depth presented as a continuous variable for each species identified in SIMPER by region, corresponded with previously described patterns. A graphical summary

can be found in Supplementary Materials, Figure S.4.2.

Table 4.4. 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

Aprion virescens (519 ± 40 and 626 ± 13 mm) and *Caranx melampygus* (367 ± 19 and 507 ± 24, Table 4.5 and Figure 4.6) were significantly smaller (both species, $p = 0.0014$) in the MHI than in the NWHI. While there were no differences relating to depth strata for *Aprion virescens* ($p = 0.5412$, Table 4.6) in either region, *Caranx melampygus* mean size was 29% larger at MHI mesophotic sites than at shallow-water sites in < 30m (435 ± 23 versus 337 ± 23 mm, $p = 0.0007$). In addition, *Caranx ignobilis* mean size was 26% smaller in the MHI (650 ± 36 mm) than in the NWHI (878 ± 30 mm, $p < 0.01$, Tables 4.5 and 4.6, Figure 4.6), primarily driven by larger individuals in the NWHI observed in mesophotic strata. Finally, *Carcharhinus galapagensis* mean size was 45% larger in mesophotic depths compared to shallow in the NWHI (1361 ± 43; 934 ± 15 mm), 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 4.5. 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 4.6. 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

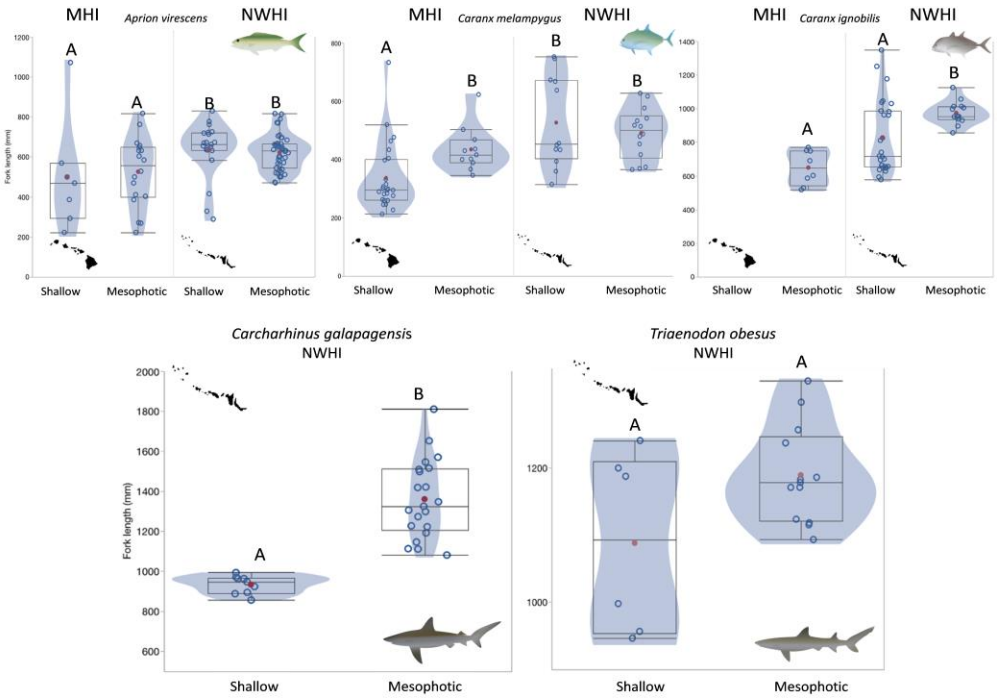


Figure 4.6. *Box and whisker plots* indicating fork-length size distributions for *Aprion virescens*, *Caranx melampygus*, *Caranx ignobilis*, *Carcharhinus galapagensis*, and *Triaenodon obesus*. Whiskers indicate minimum and maximum values, the box specifies the lower interquartile range, and the solid 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 PCA ordinations in the MHI and NWHI (Figure S.4.3, A-C). However, DISTLM-dbRDA linkages between discriminant MHI roving predators (Pearson's r $\geq$ 0.25, *Caranx melampygus*, *Carcharhinus plumbeus*, *Seriola sp*†) and environmental variables were weakly correlated, with only 10.5% of the total variation accounted for by depth, % turf algae, and habitat complexity (Figure S.4.3D). While several NWHI species aligned with areas of greater habitat complexity (e.g. *Carcharhinus galapagensis*, *Caranx ignobilis*), and depth (*Seriola sp*., *Carcharhinus plumbeus*), DISTLM-dbRDA linkages remained weak with only 18.6% of the variation explained by % hard coral, % macroalgae, habitat complexity, and depth. More detail is given in Supplementary Materials, Figures S.4.3C, D.

Discussion

For assessing predator populations, BRUVS offer several potential benefits over shallow water diver surveys. Aside from removing depth constraints associated with open-circuit scuba and potential bias due to different responses of fishes to divers in different locations, i.e. predator avoidance in populated areas and attraction in remote areas (Thresher and Gunn 1986; Bozec et al. 2011; Lindfield et al. 2014), and reducing concerns associated with diver instantaneous versus non-instantaneous predator counts (Ward-Paige et al. 2010b), archived video can be used to extract data on other species or to verify the authenticity of predator identifications and length measurements (Cappo et al. 2006a). Like all field survey methods, BRUVS have limitations including deployment challenges in vertical habitats, variable bait plume areas (Cappo et al. 2004; Stobart et al. 2007), and the potential for competitive exclusion of some species (Willis and Babcock 2000a; Bailey and Priede 2002; Stobart et al. 2007). However, for roving reef predators that are often rare or absent during underwater visual censuses, BRUVS may provide a better community-wide representation of assemblage composition (Willis and Babcock 2000a; Cappo et al. 2004; Brooks et al. 2011).

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 4.2), 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 (Friedlander and DeMartini 2002), although reported belt-derived ratios for *Caranx ignobilis* alone were considerably higher than 10:1.

Sharks can be patchily distributed over fine spatial scales (Heupel et al. 2006; Grubbs et al. 2007), and while BRUVS sampled more shark species than are typically encountered by open-circuit scuba divers, several were potentially underrepresented (or were not recorded at all) in this study. This likely came as a result of 1.) sparse sampling or exclusion of some habitat types (e.g. backreef and lagoons were not sampled) and/or several Hawaiian islands, 2.) constraints due to limited seasonal and day-time only BRUVS deployments; and 3.) one-hour BRUVS soak time limits. For example, only a single blacktip reef

shark was sighted during MHI surveys (*Carcharhinus melanopterus*, shallow water observation at Lanai, Figure 4.7A), but localized aggregations of that species are known to occur, e.g. at Pelekane Bay on the Big Island, MHI (Hoover and Gold 2006). In addition, a single mesophotic blacktip shark (*Carcharhinus limbatus*) sighting occurred outside of the one-hour BRUVS sampling period on Oahu (Figure 4.7B) and while both species can be found in low numbers in the both the MHI and NWHI, their absence during this study suggests future BRUVS sampling could be improved, at minimum, by expanding surveys to include additional islands in the Hawaiian Archipelago, increasing the number of sites at each island, and incorporating backreef/lagoonal environs into future designs (Dale et al. 2010; Dale et al. 2011).

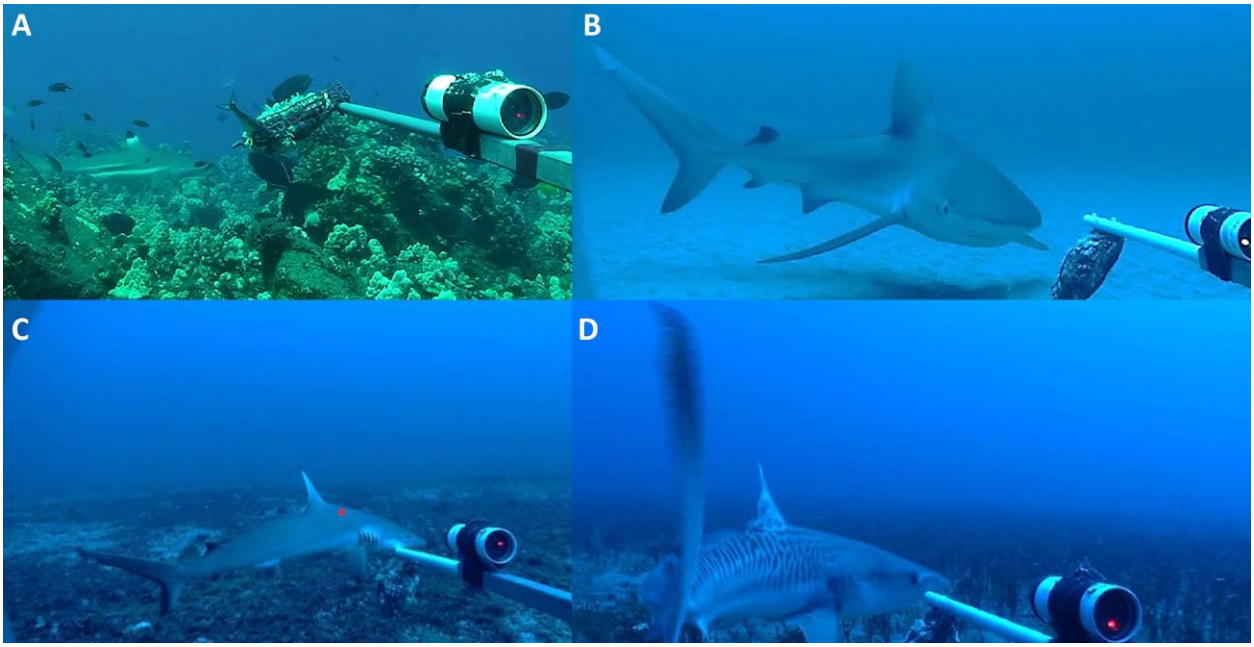


Figure 4.7. A.) *Carcharhinus melanopterus*, Lanai. B.) *Carcharhinus limbatus*, Oahu. Mesophotic sighting outside of 1-hour BRUVS sampling period C.) C*archarhinus amblyrhynchos*, Maui. D.) Juvenile *Galeocerdo cuvier*, Maui.

Similarly, no *Carcharhinus galapagensis* or *Triaenodon obesus* were sampled during MHI BRUVS surveys, and only two *Carcharhinus amblyrhynchos* were recorded (one mesophotic site off of the Maui town of Lahaina (Figure4. 7C), and one shallow water site off of the south shore of Oahu). While Galapagos sharks were once deemed abundant in the MHI and are noted for frequent sightings and seasonal movements in certain areas (e.g. north shore of Oahu), they remain spatially restricted around islands hosting high human population densities, with historic catch-rates low in comparison with sandbar, tiger, and grey reef sharks.(Tester 1969; Wetherbee et al. 1994; Wetherbee et al. 1996; Papastamatiou et al. 2006; Meyer et al. 2009b; Dale et al. 2010). In addition, while divers may encounter grey reef or white tip reef sharks more frequently than other species in the MHI, they appear relatively uncommon and/or patchily distributed outside of localized populations. These include grey reef shark aggregations around Molokini, Niihau, and Ka'ula Rock in the MHI and Necker and French Frigate Shoals in the NWHI, and historic white tip reef shark sightings along Oahu's western, southern, and eastern shorelines, along with South Maui, Molokini, and the Kona coast of the Big Island (Wetherbee et al. 1997; Papastamatiou et al. 2006; Whitney et al. 2012). When combining the absence of both species in the MHI irrespective of surveyed depths or habitats, scant grey reef and blacktip reef shark sightings, common bycatch rates observed for commercial and recreational fisheries across the state's coastal waters, and the 5-fold

difference in pooled shark abundances between MHI and NWHI (Table 4.2), these collectively serve as additional evidence towards reduced reef-shark baselines around populated areas (Wetherbee et al. 1997; Nadon et al. 2012; Whitney et al. 2012; Filous et al. 2017).

The majority of MHI BRUV sightings occurred in mesophotic depths. Aside from *Carcharhinus plumbeus* and a single *Carcharhinus amblyrhynchos*, these consisted exclusively of mature or small-bodied (≤ 2m) female tiger sharks, *Galeocerdo cuvier* (Figure 4.7D), which may be indicative of migratory patterns documented from the NWHI to the MHI linked to the September – November pupping season, or possible evidence of sex segregation (Meyer et al. 2009a; Papastamatiou et al. 2013). While additional environmental effects (thermal, available food resources) may explain the increased mesophotic presence seen here, interpretations based on small BRUVS sample sizes should be treated with caution, as tiger sharks are depth-generalists that may be considerably more abundant (comprising up to 20% of all sharks captured during longline surveys in the NWHI) than accounted for in this study (Holland et al. 1999; Dale et al. 2011).

Overlaps between shallow water and upper mesophotic zone roving predator communities, coupled with a partial separation of lower mesophotic zone assemblages, was seen in both the MHI and NWHI, albeit with divergent species and depth distributions driving interzone connectivity. In the NWHI, *Aprion virescens* remained more broadly distributed 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 (Meyer et al. 2001), competition with more abundant species in the lower mesophotic zone (e.g. *Seriola sp*†, *Carcharhinus plumbeus*), and/or the reduced density of preferred prey in deeper depths. While isotopic analyses indicate *Carcharhinus galapagensis* primarily forage in shallow water, their movements in mesophotic depths may be underestimated, and runs contrary to longline studies which captured the majority of *Carcharhinus galapagensis* between 40 – 45m (Wetherbee et al. 1996; Meyer et al. 2010b; Papastamatiou et al. 2015). The prevalence of smaller *Carcharhinus galapagensis* and *Caranx ignobilis* in < 30 m depths suggests possible body size and depth segregation, potential avoidance of intra- or inter-specific predation pressures (Compagno 2001) in deeper waters despite documented juvenile Galapagos shark movements in mesophotic depths thought to be tied to diel, vertical migration patterns, and no evidence of NWHI shallow water nursery areas as seen elsewhere(Kato and Carvallo 1967; Wetherbee et al. 1996; Papastamatiou et al. 2006). Predator alignments with thermocline position (Thresher and Colin 1986), and increases in mesophotic fish densities (i.e. prey availability) between 50 – 60 m (Fukunaga et al. 2016; Lindfield et al. 2016) 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 predator escort and foraging interactions between seals and *Aprion virescens*, sharks, and jacks occurring between 60 – 80 m, suggesting predator depth adjustments may be coupled to seal foraging in some cases (Parrish 2006; Parrish et al. 2008). The general absence of predator movements in > 100 m depths or interisland transits (Meyer et al. 2007a; Meyer et al. 2007b; Parrish et al. 2008; Papastamatiou et al. 2015) are indicative of predatory spatial residency, and BRUVS surveys appear able

to capture overall depth-range demographics for these aforementioned species in the NWHI. This also seems to be confirmed with historic bait station and submersible surveys in bottom fish depths (286 – 657 m), where sightings of sharks, *Aprion virescens, Caranx ignobilis*, *Caranx melampygus*, and *Carangoides orthogrammus* were rare, but *Pseudocaranx cheilio* and *Seriola sp*[†] were commonly detected (Kelley and Ikehara 2006; Moore et al. 2013; Sackett et al. 2014). 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 expanded investigations into *Carangidae* diel, lunar, and seasonal migrations (e.g. with *Caranx ignobilis*) (Meyer et al. 2007a), and nutrient transport potential between depth zones (Papastamatiou et al. 2015).

Large-bodied snappers, jacks and sharks are susceptible to fishing activities in the MHI, and changes in abundance and/or biomass may be indicative of extraction pressures (Jennings and Polunin 1996; Williams et al. 2011a; Weijerman et al. 2013; Lindfield et al. 2016). Mesophotic habitats may act as depth-refuges for species considered particularly vulnerable to fishing (Riegl and Piller 2003; Bejarano et al. 2014; Lindfield et al. 2016), and evidence from this study remains suggestive of potential depth insulation for several predators in the MHI, mirroring patterns seen elsewhere (Thresher and Colin 1986; Feitoza et al. 2005; Bongaerts et al. 2010; Pinheiro et al. 2016). In particular, *Caranx melampygus* was one of the primary species responsible for shallow-upper mesophotic zone overlaps in the MHI, with relatively similar numbers recorded between zones; however, overall mean fork-lengths were smaller in < 30 m than at mesophotic sites or at sites in the NWHI. *Carangoides orthogrammus* were 6 – 15 times more abundant in the upper mesophotic zone than in diver depths, and *Caranx ignobilis* were only recorded in mesophotic zones in the MHI. In contrast, inferences on MHI shark population parameters are limited by low number of encounters during this study. Sightings of *Carcharhinus plumbeus* align with previous research, which have shown sandbar sharks to be the most common shark species in the MHI, that they are primarily captured in 60 – 90 m depths (although they may diurnally migrate to shallower depths of 18 – 20 m at night, and depth-segregate by age and sex) , and that they are less abundant than several other shark species at location in the NWHI (McElroy et al. 2006; Papastamatiou et al. 2006). However, in this study, mean abundance (0.12 ± 0.05 vs. 0.09 ± 0.03) and encounter rate (8.4% vs. 9%) were similar between regions (Table 2, which coupled with comparable longline catch-rates at French Frigate Shoals (Dale et al. 2011), suggests that sandbar sharks may not be as uncommon in the NWHI as previously suspected.

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, FiguresS.3A -C). However, environmental linkages with roving predator assemblages were tenuous at best (Supplementary Materials, Figures S.3D, E), 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 , the assessed species presented here (except for whitetip reef sharks) are known to utilize shallow water sandy habitats (Uchida and Uchiyama 1986; Smith and Parrish 2002; Wetherbee et al. 2004; Holzwarth et al. 2006; Meyer et al. 2007a; Meyer et al. 2007b) and were similarly encountered on mesophotic sand flats during the course of this study. In addition, *Caranx melampygus*, *Caranx ignobilis*, *Aprion virescens*, and *Seriola sp*[†] were all observed feeding in areas of unconsolidated sediment (J. Asher, pers. obs.); however, while several studies indicate the presence of high predator biomass over sand flats in comparison with other functional groups, the frequency and ecological effects of sand flat usage as foraging grounds, seasonal aggregation sites, refugia, or as transitional habitats (i.e. as corridors between areas hosting higher complexity, hard-bottom substrates) remains largely unaccounted for (Friedlander et al. 2007; Papastamatiou et al. 2011; Filous et al. 2017). 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 are clearly present in the deeper, underexplored unconsolidated sediment habitats in the MHI.

In conclusion, roving predator research has been heavily reliant on underwater visual censuses, along with a smaller number of fishery independent remote underwater video surveys, tracking studies, and limited fishery-dependent or extractive surveys (Dale et al. 2011). 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 beyond open-circuit SCUBA depths.

Supplementary Materials

Table S.4.1. Canonical analysis of Principal Coordinates (CAP), leave-one-out Allocation of Observations to depth groups in the MHI and NWHI.

Original group (MHI)	0-30	30-53	53-100	Total	% Correct
0-30	18	20	2	40	45
30-53	9	10	10	29	34.5
53-100	0	14	24	38	63.2
Original group (NWHI)	0-30	30-53	53-100	Total	% Correct
0-30	14	7	6	27	51.85
30-53	9	7	6	22	31.82
53-100	0	1	28	29	96.55

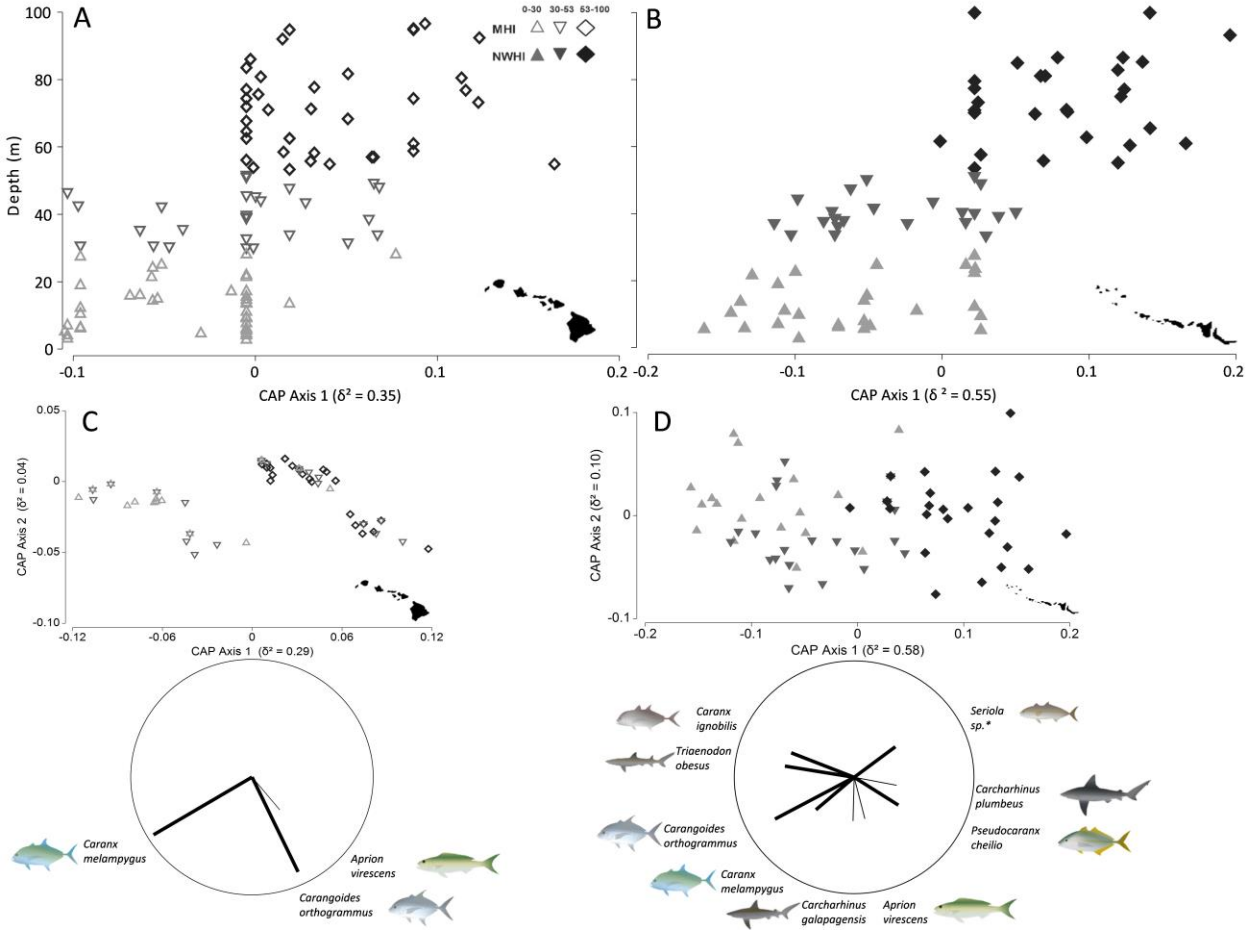


Figure S.4.1. Canonical analysis of Principal Coordinates (CAP) illustrating the structure of roving predators in the MHI (A) and (B) NWHI and depth. Analysis was based on zero-adjusted Bray-Curtis resemblance matrix calculated from square root transformed roving predator abundance (MaxN, hr^{-1}). Open symbols represent MHI sites, closed symbols represent NWHI sites. Light grey triangles = shallow water (0 – 30 m), medium grey, inverted triangles = upper mesophotic (30 – 50 m), dark grey diamonds = lower mesophotic (53 – 100 m). Canonical analysis of Principal Coordinates (CAP) illustrating the structure of roving predators in the MHI (C) and (D) NWHI according to *a priori* depth and habitat categories. Right-hand panels display vector overlays of Pearson's rank correlation of individual predator species with the CAP axes by region. Light back lines, lengths $\geq$ 0.35. Dark black lines, lengths $\geq$ 0.40.

Table S.4.2. Pair-wise PERMANOVA comparisons for aggregate roving predator populations and select species. Monte Carlo values presented when the number of permutations are ≤ 50.

All Roving Predators (Pooled)				
MHI, Depth only	t	P(perm)	No. Perms	P(MC)
0-30 vs 30-53 m	1.6525	0.0503	9954	-
0-30 vs 53-100 m	2.9604	**0.0001**	9950	-
30-53 vs 53-100 m	1.8372	**0.0054**	9943	-
NWHI, Depth only				
0-30 vs 30-53 m	1.2580	0.1938	9956	-
0-30 vs 53-100 m	3.4002	**0.0001**	9953	-
30-53 vs 53-100 m	2.6145	**0.0001**	9940	-
MHI, NWHI				
0-30 m	4.3199	**0.0001**	9961	-
30-53 m	3.0275	**0.0001**	9943	-
53-100 m	3.0147	**0.0001**	9940	-
MHI, Depth, Habitat				
0-30 m, Hard vs unconsolidated	1.3760	0.1373	108	-
30-53 m, Hard vs unconsolidated	0.5526	0.8137	4802	-
53-100 m, Hard vs unconsolidated	1.4682	0.0523	9891	-
NWHI, Depth, Habitat				
0-30 m, Hard vs unconsolidated	-	-	-	-
30-53 m, Hard vs unconsolidated	1.7225	**0.0131**	1348	-
53-100 m, Hard vs unconsolidated	0.9037	0.5735	9091	-
MHI, NWHI, Hard-bottom				
0-30 m	4.3773	**0.0001**	9963	-
30-53 m	3.2704	**0.0001**	9936	-
53-100 m	1.8523	**0.0046**	9938	-
MHI, NWHI, Unconsolidated				
0-30 m	-	-	-	-
30-53 m	0.6636	0.7764	41	0.6734
53-100 m	1.9719	**0.0023**	7614	-
MHI, Depth, Hard-bottom				
0-30 vs 30-53 m	1.6720	**0.0468**	9955	-
0-30 vs 53-100 m	2.6502	**0.0005**	9240	-
30-53 vs 53-100 m	1.2381	0.1969	9895	-
MHI, Depth, Unconsolidated				
0-30 vs 30-53 m	0.9830	0.3339	16	0.4244
0-30 vs 53-100 m	0.8573	0.5824	140	-
30-53 vs 53-100 m	1.4154	0.0587	5004	-
NWHI Depth, Hard-bottom				
0-30 vs 30-53 m	1.5115	0.0621	9958	-
0-30 vs 53-100 m	2.7869	**0.0001**	9950	-
30-53 vs 53-100 m	2.6736	**0.0001**	9946	-
NWHI Depth, Unconsolidated				
0-30 vs 30-53 m	-	-	-	-
0-30 vs 53-100 m	-	-	-	-
30-53 vs 53-100 m	1.2773	0.1349	63	-

Carangoides orthogrammus				
MHI, Depth	t	P(perm)	No. Perms	P(MC)
0-30 vs 30-53 m	2.7649	**0.0079**	34	**0.0082**
0-30 vs 53-100 m	1.7491	0.095	42	0.0797
30-53 vs 53-100 m	0.7986	0.4744	83	-
NWHI, Depth				
0-30 vs 30-53 m	1.7091	0.1049	30	0.0964
MHI, NWHI				
0-30 m	0.3961	0.9414	9	0.6955
30-53 m	0.2772	0.8126	107	-
Caranx ignobilis				
MHI, Depth				
30-53 vs 53-100 m	0.4535	0.761	16	0.6432
NWHI, Depth				
0-30 vs. 30-53 m	1.1716	0.252	805	-
MHI, NWHI				
30-53 m	2.2566	**0.0389**	38	**0.0303**
*Seriola sp**				
MHI, Depth				
0-30 vs 30-53 m	0.1154	1	4	0.9246
0-30 vs 53-100 m	1.6798	0.1426	24	0.0972
30-53 vs 53-100 m	1.4419	0.1728	20	0.149
NWHI, Depth				
0-30 vs 30-53 m	1.5207	0.1681	30	0.1315
0-30 vs 53-100 m	4.0926	**0.0003**	1065	-
30-53 vs 53-100 m	2.4797	**0.0128**	1807	-
MHI, NWHI	`			
0-30 m	0.8547	0.5541	6	0.4024
30-53 m	2.2232	0.0575	20	**0.0307**
53-100 m	3.9797	**0.0002**	1908	-
Pseudocaranx cheilio				
NWHI, Depth				
30-53, 53-100 m	1.5644	0.1001	60	-
Carcharhinus plumbeus				
MHI, NWHI				
53-100 m	0.2718	0.832	23	0.798
Triaenodon obesus				
NWHI, Depth				
0-30 vs 30-53 m	0.5550	0.5702	96	-
0-30 vs 53-100 m	3.2475	**0.0028**	22	**0.002**
30-53 vs 53-100 m	3.2726	**0.0021**	42	**0.0022**

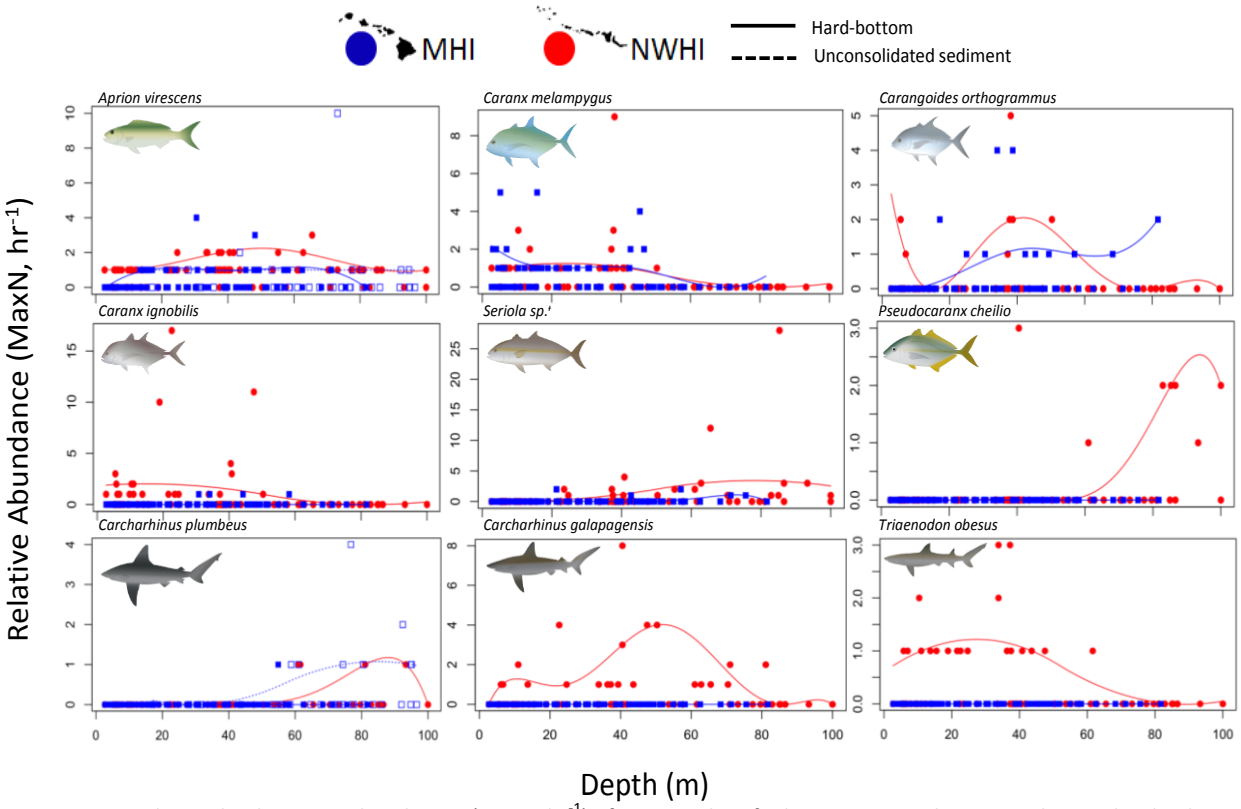


Figure S.4.2. Relationship between abundances (MaxN, hr^{-1}) of species identified in SIMPER analysis according to depth. The regression spline model for the 85th percentile is shown.

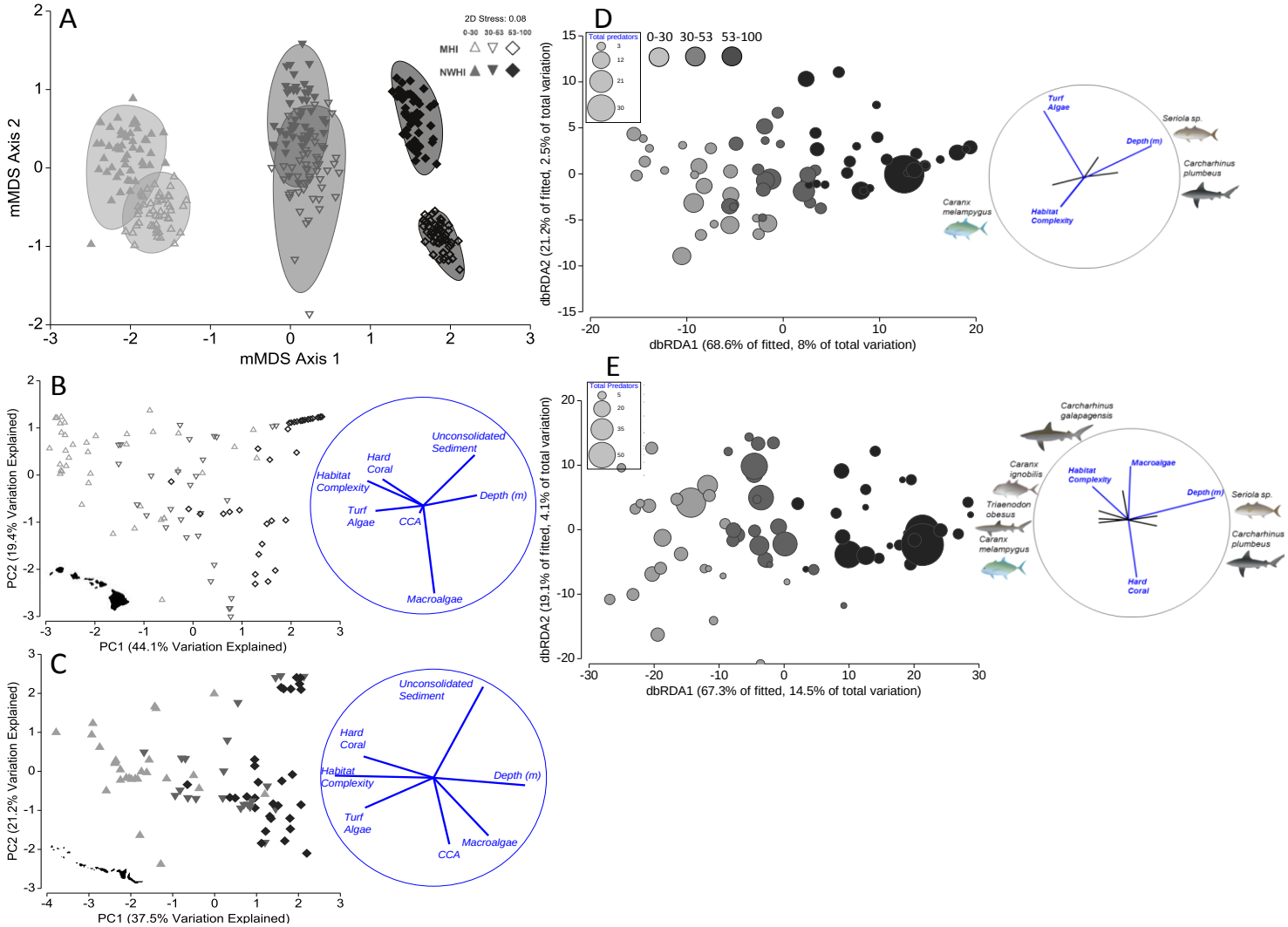


Figure S.4.3. A.) Bootstrap resampling, 50 bootstraps per group. Normalized environmental data, transformed into a Euclidean distance matrix Region (MHI, NWHI) x Depth Strata (shallow; upper and lower mesophotic), plotted mMDS. Shaded bootstrap regions, which represent measurements of centroid error: 95% confidence intervals, averages based on m = 4 dimensional metric MDS (rho = 0.994). B.) Principal Component Analysis (PCA) of normalized environmental variables plotted for the MHI and C.) NWHI. Individual samples representing sites binned into regional (MHI, NWHI) and depth groups (shallow water; upper and lower mesophotic). Correlations of habitat variables specified by vector direction and length. D.) Distance-based redundancy analyses (dbRDA) on roving predator assemblage abundances for the MHI and E.) NWHI. *Bubbles* are scaled to represent total predator relative abundances at each site.

Environmental habitat variables were similar between the MHI and NWHI (Figure S.4A), as evidenced by the overlap of 95% confidence interval ellipses between the shallow water and upper mesophotic zones between regions. However, variable separation in the lower mesophotic zones was attributed (in part) to asymmetric sampling of hard-bottom versus unconsolidated sediment sites substrate types (i.e. disproportionate number of sand flat sites surveyed in the MHI), coupled with changes to biotic cover (e.g. diminished coral cover) and declining habitat complexity with depth.

The Principal Component Analyses (PCA), which assesses covariance along benthic functional groups for all pooled survey sites across the MHI (Figure S.4B) and NWHI (Figure S.4C), explained over 63.5% and 58.7% of the variation along the first two principal components respectively. Coral cover, habitat complexity, and turf algae were aligned along the first principal axis and tended to be higher in shallow water coinciding with shifts from aggregate reef, spur-and-groove, and boulder habitats to lower lying aggregate and patch reefs, rubble flats, or sand flats as depth increased. Macroalgae and crustose coralline algae cover were aligned with the second principal component and largely driven by previously described changes in sampled habitats when moving from shallow to mesophotic depths, along with shifts in increased unconsolidated sediment percent cover.

While 89.8% (MHI; Figure S.4D) and 86.4% (NWHI, Figure S.4E) of the fitted DistLM-dbRDA models were explained along the first two axes, only 10.5% and 18.6% of the total variation could be explained within each respective region. In the MHI, habitat complexity, depth, and % turf algae were identified as the main environmental contributory variables by the relationships between dbRDA coordinate axes and orthonormal X variables and three species (*Caranx melampygus*, *Carcharhinus plumbeus*, and *Seriola sp.;* Figure S.3D) being weakly correlated (Pearson correlation > 0.25), with assemblage vectors indicative of strength and direction. In particular *Caranx melampygus* was aligned with areas of increased habitat complexity, while *Seriola sp*. and *Carcharhinus plumbeus* were unsurprisingly correlated with increasing depth.

In the NWHI, % hard coral, % macroalgae, habitat complexity, and depth acted as principal, contributory variables. Seven species were correlated in patterns largely as previously described, with alignments noted for *Caranx ignobilis* and *Carcharhinus galapagensis* in shallower water in more complex environments, and the influence of depth on increased numbers of *Seriola sp*. and *Carcharhinus plumbeus* in mesophotic depths.

Chapter 5 – Is seeing believing? Diver and video-based censuses reveal inconsistencies with predator estimates between regions

Abstract

Coral reef research programs in Hawaii primarily use diver-based underwater visual censuses in ≤ 30 m to assess shark and jack populations between the Main and Northwestern Hawaiian Islands. As a probable consequence of survey biases, results from some methods imply remarkably top-heavy trophic pyramids that potentially inflate the scale of difference between remote and populated regions. Other data limitations include the absence of information on deeper habitats > 30 m, which can harbor large portions of predator populations. In order to better assess the scale of differences between the Main Hawaiian Islands (MHI) and the Northwestern Hawaiian Islands (NWHI), we compared shallow water roving predator abundances and estimated predator length-frequencies between two diver-based visual assessment methods (stationary point count, towed diver) and two remote video sampling techniques (unbaited RUVS, BRUVS). We also surveyed deeper water (30 – 100 m, 'mesophotic') roving predator assemblages using RUVS and BRUVS. As with diver-based visual assessments, RUVS and BRUVS sampled considerably higher numbers of roving predators in the NWHI compared to the MHI, with patterns generally consistent between video methods. However, the NWHI:MHI scales of difference for both video survey types tended to be substantially lower than for diver surveys. For example, NWHI:MHI ratios of densities for the snapper *Aprion virescens* ranged from 62:1 from SPC and 24:1 for towed diver surveys, to 5:1 for RUVS and 3:1 for BRUVS. Similarly, reef shark NWHI:MHI ratios ranged from 142:1 for SPC and 76:1 for towed diver, to 20:1 for RUVS and 11:1 for BRUVS. The largest discrepancies were recorded for the giant trevally *Caranx ignobilis,* where NWHI:MHI abundance ratios varied by over two orders of magnitude between diver SPC and all other methods. Although our results corroborate substantially higher roving predator densities in the NWHI, this study demonstrates that application of different methods can result in strikingly dissimilar predator estimates. Inflated predator abundances in remote areas coupled with underrepresentation in populated areas remained a concern with diver-based estimates. In contrast, lower encounter rates/higher variances and unknown areas of attraction remained concerning for RUVS and BRUVS respectively. Continued assessments among survey techniques, coupled with the expansion of surveys into mesophotic depths, remain vital to improving understanding of predator populations and providing information that is properly aligned with management and conservation needs.

Introduction

In the absence of robust fishery dependent data, underwater visual diver censuses on open-circuit SCUBA remain the primary means for obtaining information on the abundance, biomass, and species richness of large-bodied, roving coral reef predators in the Hawaiian Archipelago. Several methods, including belt-transect, stationary point counts (SPC) and towed-diver surveys are widely used to compare predator populations inhabiting ≤ 30 m habitats (herein denoted as 'shallow water') between the remote Northwestern Hawaiian Islands (NWHI), and the populated, heavily fished Main Hawaiian Islands (MHI) (Friedlander and DeMartini 2002; DeMartini and Friedlander 2004; Williams et al. 2011b; Nadon et al. 2012).

However, diver visual censuses remain subject to a number of biases including: (1) different responses

of target-fishes to the presence of divers, including diver avoidance in areas where fishing occurs, and inflation of abundance estimates in remote areas due to diver attraction (Chapman 1974; Chapman 1976; Chapman 1986; Kulbicki 1998; Parrish and Boland 2004; Cole et al. 2007; Watson and Harvey 2007; Graham et al. 2010; Dickens et al. 2011; Lindfield et al. 2014; Gray et al. 2016). In addition, the more commonly used diver censuses have a tendency to overestimate highly mobile species (most sharks and jacks), and the extent of that overestimation depends on the precise method and survey area dimensions used (Sandin et al. 2008a; Friedlander et al. 2010; Ward-Paige et al. 2010a; McCauley et al. 2012; Rizzari et al. 2014). Finally, differences among observers, particularly when it comes to estimating the size of large roving piscivores, can be a substantial source of survey error, although one that can be reduced by appropriate training and among observer comparisons (Bell et al. 1985; Yulianto et al. 2015); and (2) divers on SCUBA are largely limited to relatively shallow water ($\leq$ 30 m), whereas roving predators can be highly abundant in deeper habitats down to 100 m and beyond (Meyer et al. 2010b; Nakamura et al. 2011; Papastamatiou et al. 2015; Fukunaga et al. 2016; Asher et al. 2017). Therefore, diver censuses only survey a small portion of populations potentially affected most by fishing pressures.

To date, diver-based studies have consistently shown large differences in predator densities between populated versus unpopulated areas in the Pacific (Ayling and Choat 2008; Nadon et al. 2012); however, pronounced discrepancies in the scale of those differences depend on the assessment method used (Dale et al. 2010; Graham et al. 2010; Ward-Paige et al. 2010b; McCauley et al. 2012; Ruppert et al. 2013; Rizzari et al. 2014). In the case of the NWHI versus MHI, scales of regional differences between predator abundance, density, and/or biomass estimates can also vary according to the type of survey (Friedlander and DeMartini 2002; Holzwarth et al. 2006; Nadon et al. 2012). For example, belt-transect survey data indicated that NWHI:MHI roving predator biomass was 70 times higher in the NWHI, whereas point count predator biomass was over 50 times higher, signaling a general alignment between methods. In contrast, towed-diver surveys yielded predator density estimates for the most common roving predators in the NWHI – *Aprion virescens*, *Caranx ignobilis*, *Caranx melampygus* – that were 11 – 90 times lower than densities derived from belt transect surveys (Friedlander and DeMartini 2002; Richards et al. 2011; Williams et al. 2011b).

We address this issue in the Hawaiian Archipelago by comparing results from four survey techniques (diver SPC, towed-diver, unbaited and baited video surveys), specifically comparing the different methods' estimates of differences in relative abundance and size between populated and remote parts of the archipelago.

The main analysis objective was to quantify the extent of sub-regional level differences in predator abundance ratios in $\leq$ 30 m depending on survey method, and incorporating deeper (30 – 100 m) RUVS and BRUVS data to compare against shallow-water datasets. Secondary goals included assessments of predator size distributions between methods in shallow water, along with an informal evaluation of the species encountered by the different methods.

Methods

Survey area

The Hawaiian Archipelago is separated into two distinct sub-regions: the populated MHI (Hawaii to Niihau) and the NWHI (French Frigate Shoals to Kure Atoll). There are considerable human population density differences and associated impacts to reefs in the MHI; however, all are close to large population centers (Williams et al. 2011b). In contrast, the remote NWHI have been closed to fishing with the establishment of the Marine Refuge in 2005, with subsequent protections added with the creation and expansion of the Papahānaumokuākea Marine National Monument (PMNM) in 2007 and 2016 respectively.

Sampling Procedures

Diver SPC surveys conducted by the NOAA Pacific Islands Fisheries Science Center (PIFSC), Ecosystem Sciences Division, Coral Reef Ecosystem Program (CREP) are small-scale censuses used to tally all conspicuous diurnally-active species, including large-bodied roving predators as part of the Pacific Reef Assessment and Monitoring Program (Figure 5.1). However, because they don't cover large reef areas, small scale surveys may potentially be unsuited to sampling rare or patchily distributed species (Richards et al. 2011; Rizzari et al. 2014). Consequently, towed-diver surveys are used to compliment SPC surveys by targeting large-bodied, wide-ranging fishes $\geq$ 500 mm in length over large distances (Holzwarth et al. 2006; Brainard et al. 2008; Richards et al. 2011). Two alternative approaches which had never previously been compared in the Hawaiian Archipelago are unbaited and baited remote underwater stereo-video systems (stereo-RUVs, herein denoted as 'RUVS'; stereo-BRUVS, herein denoted as 'BRUVS', as in previous chapters). BRUVS are often preferred for predator surveys, although BRUVS may underestimate predator populations in very high density areas as a result of count saturation within space-limited fields of view (Willis and Babcock 2000a; Cappo et al. 2004; Watson et al. 2005; Watson and Harvey 2007; Wraith 2007; Stobart et al. 2015). In contrast, RUVS are rarely used in comparison with BRUVS due to higher among-site variability and reduced sampling power, especially in areas where predators are scarce. Both RUVS and BRUVS can also survey deep habitats that are areas inaccessible to SPC and towed-divers, thereby sampling predator populations outside operable depths accessible with open-circuit SCUBA. However, the comparability of RUVS and BRUVS with diver-based predator assessments, and their ability to discriminate regional scales of difference remain unknown.

All SPC, towed-diver, RUV, and BRUV surveys were conducted in the Hawaiian Archipelago in accordance with well-established protocols, and are briefly described below (Heenan 2014; Ayotte et al. 2015a; McCoy 2017). Diver SPC surveys last approximately 25 – 30 minutes each, and were randomly located within $\leq$ 30 m hard-bottom habitats, with pairs of diver recording the number, size, and species of fishes within adjacent, 15 m diameter cylinders along a 30 m transect line. SPC counts followed a two-stage process where divers spent the first 5 minutes building a list of species present within their cylinders, followed by a count phase whereby divers work successively through their species lists, recording numbers and size of each taxa in a series of rapid visual sweeps of their cylinders. In cases where these

groups were present during the initial 5 minute species enumeration period but not present during subsequent instantaneous sweeps, divers recorded their best estimates for numbers and sizes at the time they were first observed (and these are considered 'non-instantaneous' observations). Divers also recorded the number and sizes of any species that enters the cylinder for the first time after the species enumeration period. Depending on the period at which species were first observed, observations were classified as different observation types. However, for this analysis, all observation types were pooled into total counts per SPC.

During towed-diver surveys, a diver pair included one collecting data on benthos, and one recording numbers, size and species of all fishes larger than 500 mm total length within a 10-m belt centered on the diver and up to 10 m ahead of the diver. Each towed diver survey lasts 50 minutes, in which time divers were pulled 2.2 km average distance, with survey lengths and locations derived from a tracking GPS and layback algorithm. Towed diver surveys were haphazardly located with the broad goal of being as widely spread as possible around each sampling location (e.g. island), and were typically in ~15 m of water (Richards et al. 2011). Diver SPC and towed-diver surveys were collected during routine NOAA and PMNM monitoring cruises from 2010 – 2016. For all methods, survey operations were conducted at four of the MHI (Oahu, Molokai, Lanai, and Maui) and three atolls in the NWHI (French Frigate Shoals, Pearl and Hermes Reef, Midway). While SPC and towed-diver surveys were completed at other locations, those were excluded from analysis so that we only used data from the same subset of islands for all methods. All RUV and BRUV surveys were completed from 2012 – 2014.

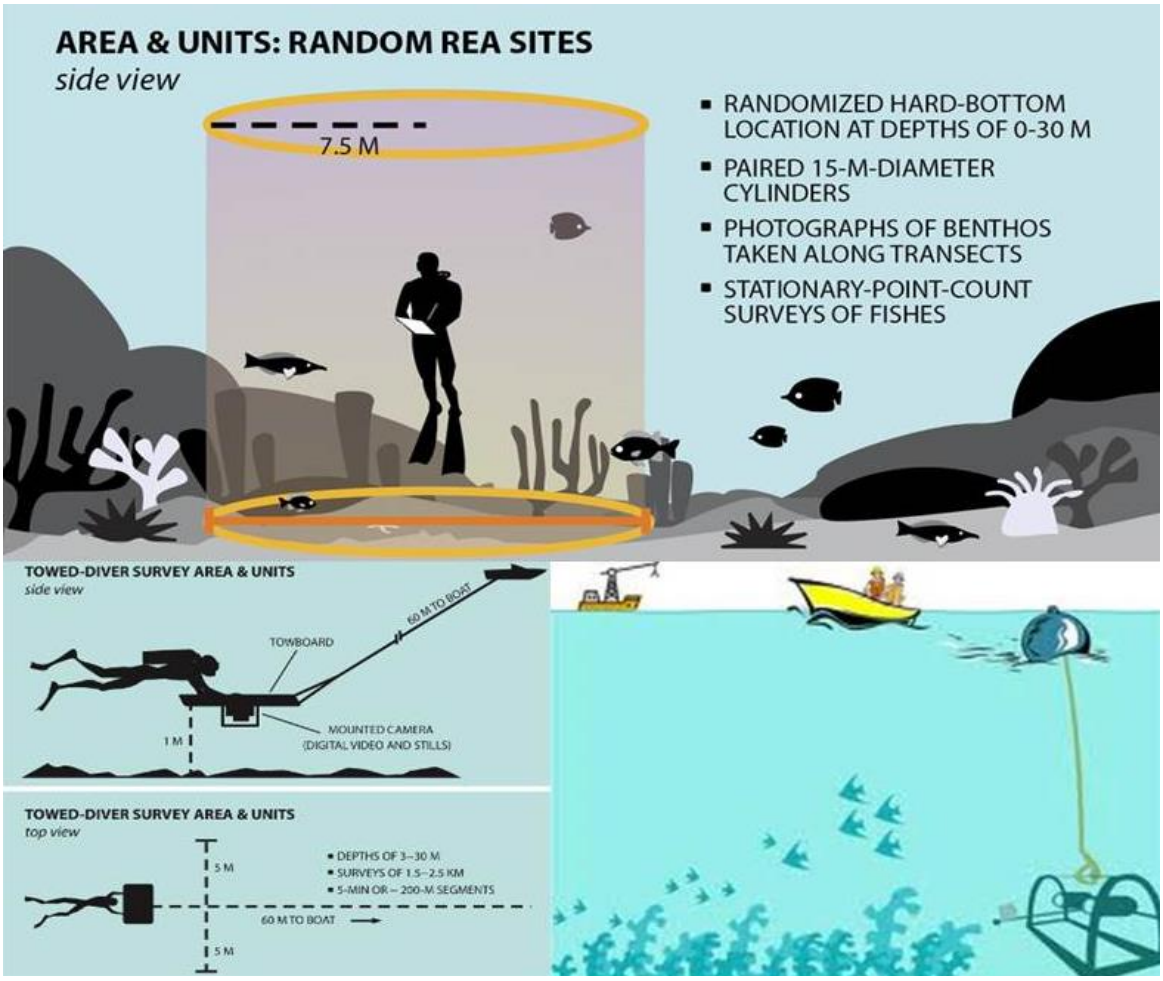


Figure 5.1. Illustrations of methods assessed in this study. Top panel: diver stationary point count (SPC). Lower left panel: towed-diver survey. Bottom right panel: RUVS and BRUVS surveys. All graphics generated by NOAA.

RUVS and BRUVS are operationally identical remote stereo-video surveys, other than that BRUVS are baited – using 800 g of Japanese sanma (*Cololabris saira*) pulped into a wire mesh based 1.2 meters in front of the stereo-cameras, while RUVS were deployed without bait bags. Shallow-water RUVS surveys were randomly assigned to a subset of previously surveyed SPC sites (MHI: 2012, NWHI: 2014), with a minimum of 20 minutes between divers exiting the water and RUVS being deployed. Similarly, BRUVS were deployed at a subset of RUVS shallow water and mesophotic sites, with a minimum of 20 minutes between RUVS recoveries and BRUVS deployments. Each RUVS or BRUVS was deployed for a 60-minute sampling duration, and utilized paired Sony handycams calibrated using the CAL™ software package (www.seagis.com.au; Seager 2008) before and after each data collection effort following standard protocols (Harvey and Shortis 1998; Shortis and Harvey 1998). Following research cruises, stereo-video files were reviewed, with predator species annotated to the lowest possible taxonomic level using EventMeasure-Stereo™ (Seager 2008).

To increase consistency among surveys, we only utilized towed-diver, SPC, RUV, and BRUV surveys in hard-bottom forereef or slope habitats. In total, we analyzed data from 588 SPC sites, 243 towed-diver surveys, 65 RUVS, and 39 BRUVS survey sites between 0 – 30 m in the MHI, and 325 SPC, 166 towed-

diver, 39 RUVS, and 27 BRUVS survey sites in the NWHI. An additional 100 RUVS and 33 BRUVS were examined in mesophotic depths in the MHI, and 79 RUVS and 42 BRUVS in mesophotic depths in the NWHI (Figure 5.2).

Target species

We focused on large-bodied roving as described in Friedlander et al. (2002), Hozwarth (2006), Williams (2011), and Nadon (2012). These included all shark (Carcharhinidae) and non-plantivorous jacks (Carangidae), along with the snapper *Aprion virescens.*

We assessed relative abundance ratios for several shark groupings: 1.) all sharks (Galapagos *Carcharhinus galapagensis*, grey reef *Carcharhinus amblyrhynchos,* blacktip reef *Carcharhinus melanopterus,* sandbar *Carcharhinus plumbeus,* tiger *Galeocerdo cuvier,* and whitetip reef sharks *Triaenodon obesus*), 2.) all reef sharks, i.e. the four shark species most closely associated with reefs in the Hawaiian Archipelago (*Carcharhinus galapagensis*, *Carcharhinus amblyrhynchos*, *Carcharhinus melanopterus*, *Triaenodon obesus*), excluding tiger and sandbar sharks that we considered to be less strongly associated with coral reefs or hard-bottom substrates (Nadon et al. 2012); 3.) *Carcharhinus galapagensis* and *Carcharhinus amblyrhynchos*, which are the numerically dominant shark species observed by divers in the NWHI.

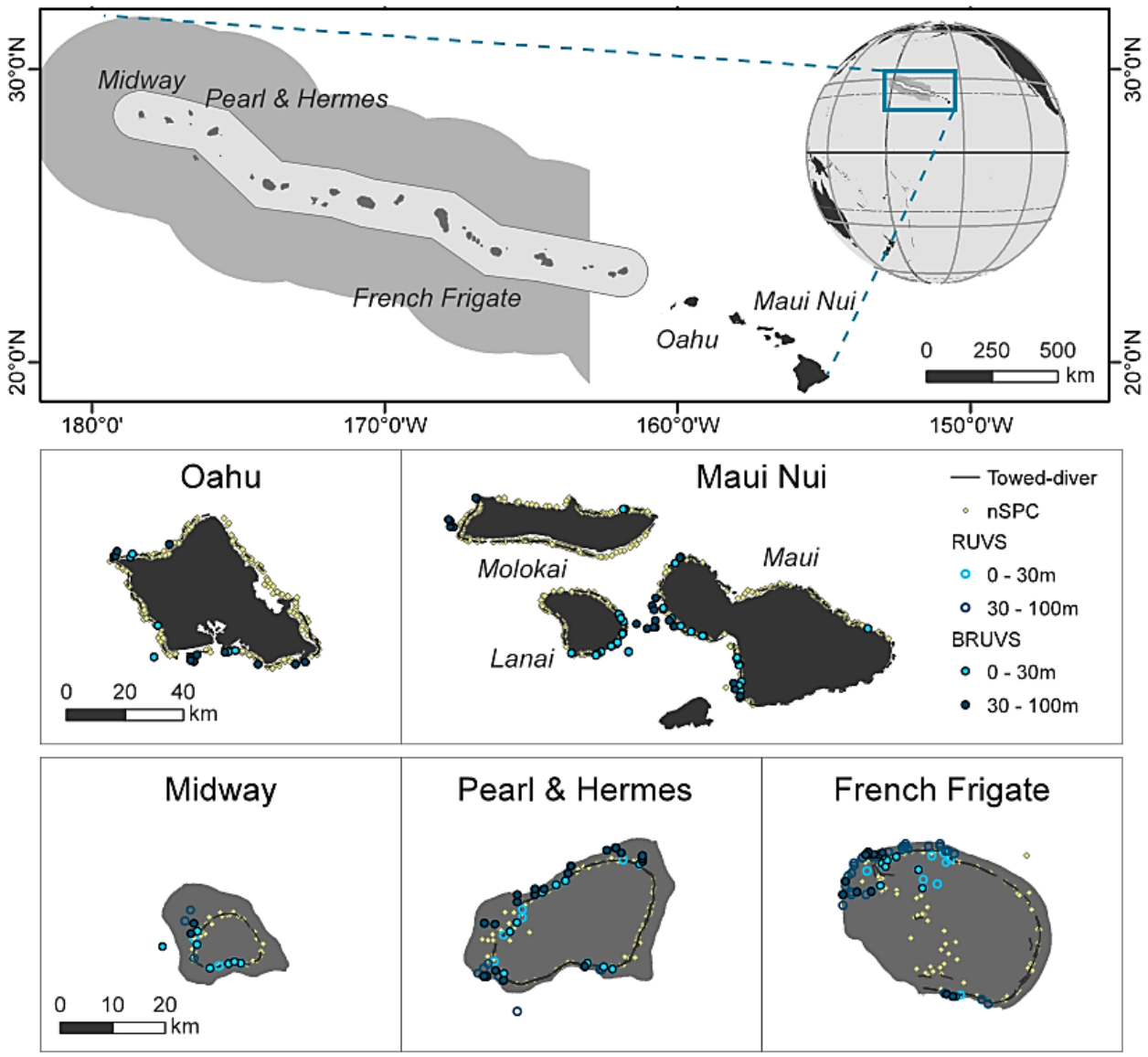


Figure 5.2. Diver stationary point count (SPC), towed-diver, RUVS, and BRUVS surveys across the Hawaiian Archipelago. Top panel: Surveys split between the Main Hawaiian Islands (MHI; unshaded) and Northwestern Hawaiian Islands (NWHI; shaded). Middle panel: MHI surveys around Oahu and Maui-Nui (Maui, Molokai, and Lanai). Shaded areas indicate island outlines. Bottom panel: NWHI surveys around Midway, Pearl and Hermes, and French Frigate Shoals. Shaded areas indicate 100 m depth contours.

We only had sufficient data to compare relative abundances (by method) for 4 individual species: *Aprion virescens*, *Triaenodon obesus, Caranx ignobilis* and *Caranx melampygus.* Finally, the pink snapper *Pristipomoides filamentosus* was sampled by RUVS and BRUVS in mesophotic depths at a small number of sites across the Hawaiian Archipelago; however, these bottom fish are nearly always found below depths surveyed by divers on open-circuit SCUBA, and were excluded from analysis (Ellis and Demartini 1995; Moffitt and Parrish 1996).

Analysis

The primary objective was a comparison of the relative abundance of roving predators between NWHI and MHI generated by a variety of survey methods, with an ancillary focus on size distributions and species encounters.

Relative abundance metrics

In order to compare roving predator densities between NWHI and MHI, we first generated abundance metrics for each survey method. Fish counts from diver SPCs and towed-divers surveys were converted to densities per unit area by dividing counts by the sample areas. For RUVS and BRUVS surveys, we used the *MaxN* value per 60 minute deployment - i.e. maximum number of that species observed within any video frame during the course of the deployment (Ellis and Demartini 1995; Willis and Babcock 2000a; Willis et al. 2000b).

Roving predator fork-length measurements were also taken for each species at the time of that species' MaxN. All species annotations were reviewed prior to data analysis, with quality control completed by one analyst to maintain consistency across samples (Wilson et al. 2007).

Analysis of Relative Abundance between the NWHI and MHI

We used a bootstrapping approach to generate relative abundance ratios (AR) between NWHI and MHI, via the *boot* and *boot.ci* functions from the *boot* package in R, Version 3.3.0 (R Core Team 2016). This was comparable to the technique described in Williams et al. (2011, 2012), Gray et al. (2016), and Williams et al. (2016), which was originally adapted from the analysis of ground fish trawl surveys and particularly well-suited for small sample sizes (Smith 1997). Unlike the direct use of replicates to calculate 95% confidence intervals produced from parametric methods, we generated pseudo samples of the same size (Henderson 2005) by repeatedly resampling and replacing the original predator abundance data respective to each method and strata (SPC/towed-diver: shallow water only; RUVS/BRUVS: shallow, mesophotic, and all depths pooled). Inferences are therefore made on empirical distributions of survey data versus assumptions based on distribution form, e.g. presuming data are distributed normally, simulating results as if field surveys were repeated multiple times (Williams et al. 2012).

Here, in each of 1000 iterations, we first generated a mean abundance value for each island from resampled data, and converted those to MHI and NWHI mean abundance, weighting each island by the amount of shallow-water hard-bottom habitat at that island (Supplementary Materials, Table S.5.1). Using this approach, we generated 1000 bootstrapped NWHI:MHI abundance ratios for each combination of fish group, survey method, and depth zone (shallow water or mesophotic) and calculated the mean and 95% quantile range [95%QR] of those ratios. The 95%QR covers the middle 95% of the distribution (i.e. 2.5% to 97.5% quantiles), and is analogous to 95% confidence interval of the NWHI:MHI ratio. We interpreted a 95%QR of the NWHI:MHI ratio not overlapping 1 as evidence of difference between archipelagic sub-regions, with 95%QR > 1 indicating higher abundance in NWHI, and

95%QR < 1 as evidence of lower abundance in NWHI. We also used the shallow-water habitat area to weight each island's mesophotic densities (which we had for RUV and BRUV) because we wanted to be able to meaningfully compare shallow-water and mesophotic NWHI:MHI ratios – without those being affected by different island weightings for shallow and mesophotic data. Finally, we also generated NWHI:MHI 'all depth zones' ratios from BRUV and RUV survey data, weighting the shallow water and mesophotic density estimates equally.

Length-based measurements

SPC and towed-diver estimates rely on total length (TL) measurements of fishes (nose to longest caudal fin lobe), while RUVS and BRUVS surveys gather fork lengths (nose to caudal fork, FL) at the time of MaxN. As a result, RUV and BRUV FLs were transformed to TLs via conversions specified in FishBase (Froese and Pauly 2014). In addition, towed-diver surveys only count fishes with a minimum TL of 500 mm TL and as a result, all jacks and the snapper *Aprion virescens* recorded during towed-diver surveys were excluded from length-based comparisons with other methods. However, *Carcharhinus galapagensis* and *Triaenodon obesus* exceed 500 mm at birth and are frequently encountered in the NWHI (Compagno 1984), allowing for towed-diver length comparisons with other diver and video-based methods in the NWHI.

Notched box plots provide initial indications of differences between length measurements collected by each method, with median notch widths being proportional to interquartile range and inversely proportional to sample size (McGill et al. 1978). While not a formal or strict test, cases where notches do not overlap are indicative of significant differences in median length, independent of assumptions of data normality of distributions or equivalence of variances (Chambers et al. 1983; Harvey et al. 2012b).

Non-parametric kernel density estimates (KDEs) were further used to approximate pair-wise comparisons in length frequency distributions between methods in shallow-water strata, based on a null model of no difference between groups and a permutation test (n=100000) following the approach used by Langlois et al. (2012). KDE tests between species, regions, and methods were constrained to shallow-water subsets recording a minimum of 9 length measurements for RUVS and BRUVS, with SPC and towed-diver surveys consistently collecting larger sample sizes across broader length ranges (as a result of more broad-based spatial and temporal sampling). KDE bandwidths were selected using Sheather-Jones assignment protocol (Sheather and Jones 1991) via the function *dpik* in the package *KernSmooth* in the R statistical program version 3.3.0 (Wand and Jones 1995; Wand 2011; Langlois et al. 2012; R Core Team 2016). Given the sensitivity of length-distribution tests to differences in shape and location, data were also standardized by median and variance to assess shape-only effects (Bowman and Azzalini 1997; Langlois et al. 2012).

Results

Scales of relative abundance between regions

All predator NWHI:MHI ratios are shown (for each method) in Figure 5.3 and Supplementary Materials,

Table S.5.1, with 95% quantiles presented in brackets and whiskers respectively [95% QR, lower QR, upper QR].

Abundances of Carcharhinidae (primarily consisting of reef sharks) and the snapper *Aprion virescens* were generally higher in the NWHI than the MHI, irrespective of method used. However, the abundance ratios (AR) tended to be much larger for SPC and towed-diver surveys than for RUVS and BRUVS. *Aprion virescens* registered similar NWHI:MHI shallow water abundance ratios for RUVS (AR: 3.2, 1.4 – 5.1) and BRUVS (AR:3.6, 2.5 – 4.8), which were 3 – 8 times lower than those recorded by SPC (AR: 10.3, 9.0 – 11.6; 58% less than towed diver values) or towed-diver surveys (AR: 24.3, 20.3 – 28.9), with ratios for mesophotic RUV and BRUV deployments being consistent with those recorded in shallow water. No sharks were recorded during MHI shallow water RUV surveys; however, shallow water BRUV ratios (AR: 6.2, 3.0 – 9.4) were between 12 – 23 times lower than for SPC (AR: 142, 105.1 – 179.6) and towed-diver estimates (AR: 76.3, 51.1 – 106.1; 46% lower than SPC), with mesophotic RUVS (AR: 10.8, 5.7 –16.5) and BRUVS (A: 18.1, 10.0-26.6) also registering lower than diver-based estimates.

In several cases, it was not possible to generate AR values for shark groupings. This frequently occurred where there were considerable count data from NWHI, but zero in the MHI (e.g. SPC, towed-diver, or RUVS sightings of grey reef/Galapagos sharks). However, shallow water BRUVS ratios (AR: 3.0, 0.2 – 5.9) were over three times lower than for mesophotic RUVS (AR: 10.9, 5.4 – 16.8) and nearly 14 times lower than mesophotic BRUVS (AR: 41.1, 21.0 – 59.8). No *Triaenodon obesus* ARs could be generated for either RUVS or BRUVS as a result of zero sightings in the MHI; however, NWHI:MHI ratios for SPC (AR: 39.7, 25.9 – 55.1) and towed-diver surveys (AR: 32.6, 23.4 – 42.3) remained comparable.

The NWHI:MHI predator ratios for Carangidae were largely driven by trevally jacks, and particularly *Caranx ignobilis,* which was the most abundant species encountered in the NWHI across all methods. Ratios from diver SPC surveys (AR: 1885.1, 1009.7 – 3052.2) were the largest AR for any method or response group. Towed-diver AR was more than two orders of magnitude lower (AR 12.1, 6.9 – 19.2), followed by RUVS (AR: 2.8, 0.4 – 5.6). BRUVS did not record any *Caranx ignobilis* within 0 – 30 m in the MHI, which precluded shallow-water ratio comparisons with other methods; however, both mesophotic RUVS (AR: 1.5, 0.0 – 3.6) and mesophotic BRUVS (AR: 3.2, 0.1 – 6.2) were comparable with shallow-water RUV estimates. Interestingly, when BRUV estimates were pooled between shallow and mesophotic depths (AR: 12.2, 5.9 – 19.5), NWHI:MHI ratios were highly similar to those recorded by towed-diver surveys.

Conversely, ratios for *Caranx melampygus* were relatively closely aligned between shallow water SPC (AR: 1.2, 0.4 – 2.0), RUVS (AR 2.1, 1.1 – 3.2), and BRUVS (AR: 0.9, 0.4 – 1.5) along with mesophotic RUVS (AR: 1.9, 0.3 – 3.5) and BRUVS (AR: 1.0, 0.0 – 2.1), with assessments being 23 – 55 times lower than towed-diver estimates (AR: 49.8, 33.9 – 69.6). Abundance ratios for *Seriola* spp. also showed greater similarity between SPC (AR: 5.9, 2.5 – 9.7), towed-diver (AR: 3.0, 1.2 – 5.2), and pooled BRUVS (AR: 2.8, 0.0 – 5.8). Finally, abundance ratios for *Carangoides orthogrammus* were comparable between SPCs (AR: 4.6, 1.9 – 8.3) and towed-diver surveys (AR: 6.1, 2.8 – 9.5), both of which were 4 – 15 times higher than for shallow water RUVS (AR: 1.1, 0.0 – 2.7), shallow water BRUVS (AR: 0.9, 0.0 – 2.8), mesophotic RUVS (AR: 0.5, 0.0 – 1.3), and mesophotic BRUVS (AR: 0.4, 0.0 – 1.1).

Abundance ratios for less-common shark and jack species are given in Supplementary Materials, Table S.5.1.

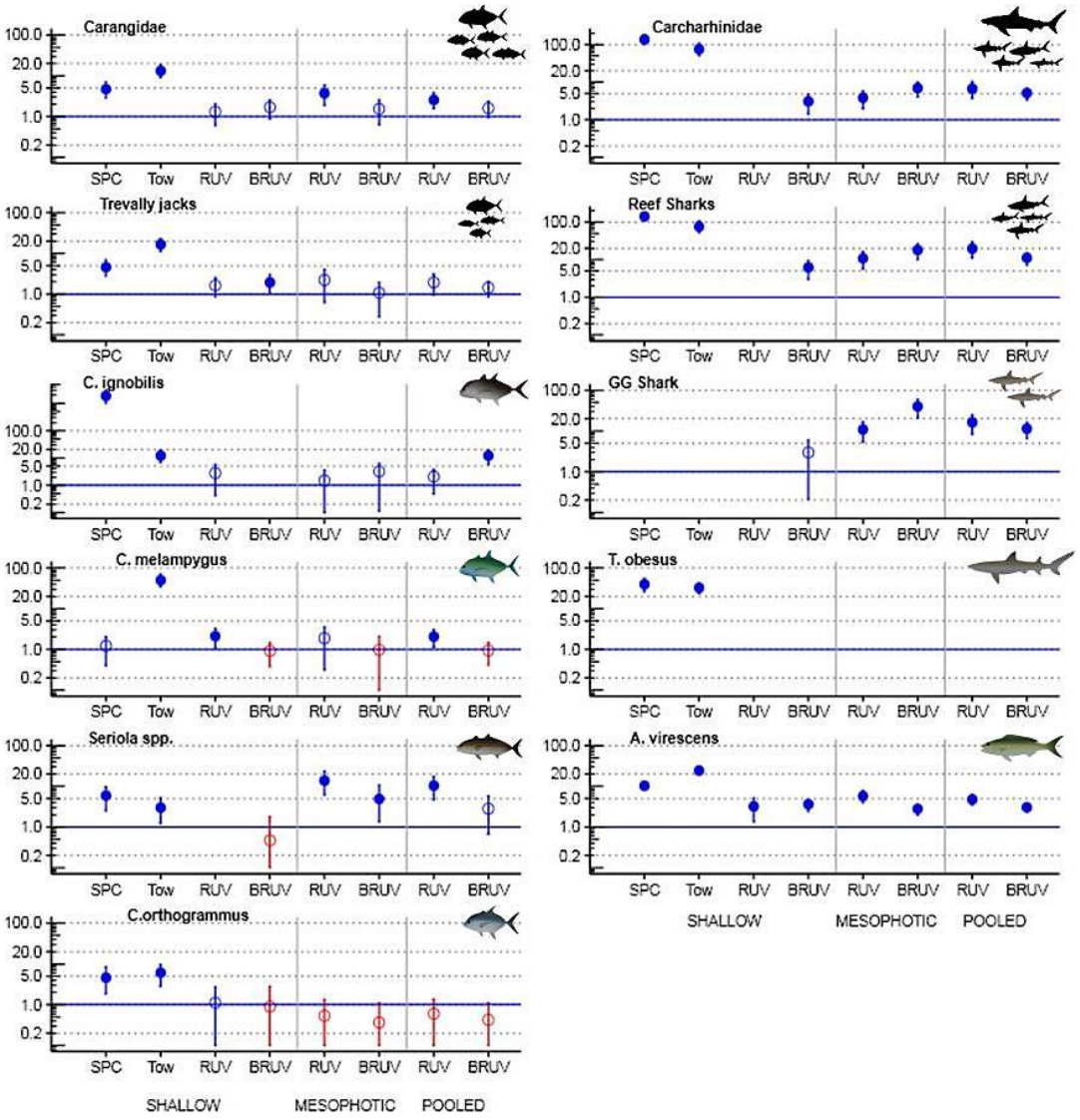


Figure 5.3. Differences in roving predator abundances in the Hawaiian Archipelago, presented as the ratio of relative abundances between the NWHI and MHI for each predator group and target species. The blue line represents a ratio of one (no differences in abundance between sub-regions). Vertical bars indicate the 95% quantile range (QR). Red circles: abundance ratio (AR) < 1. Blue circles: AR > 1. Open circles: 95% QR overlaps one. Closed circles: 95% QR does not overlap with one. Shallow water (0 – 30 m): MHI = 588 SPC, 243 towed-diver, 65 RUVS, and 39 BRUVS surveys. NWHI = 325 SPC, 166 towed-diver, 39 RUVS, and 27 BRUVS surveys. Mesophotic (30 – 100 m): MHI = 100 RUVS and 33 BRUVS surveys. NWHI = 39 RUVS and 42 BRUVS surveys. RUVS and BRUVS results are subdivided into three panels. Left: shallow, middle: mesophotic, right: pooled.

Length-frequencies

Summarized results are given in Table 5.1 and Figure 5.4. Note that length-based inferences where notches appear outside interquantile ranges (IQRs) should be interpreted with caution, as these may not adequately represent size distributions due to small sample sizes.

Table 5.1. Roving predator mean lengths in the MHI and NWHI by method. Dashed lines separate measurements made in shallow versus mesophotic depths (RUVS/BRUVS only). Note: due to small sample sizes, *Caranx ignobilis* measurement comparisons were only calculated for the NWHI. Values are displayed as mean ± SE.

		Main Hawaiian Islands		*Northwestern Hawaiian Islands*	
Species	Method	Mean length (± SE)	Measurements (N)	Mean length (± SE)	Measurements (N)
Apion virescens	SPC	415.1±11.2	132	554.4±8.0	406
	RUVS	449.5±112.5	3	621.3±50.0	9
	BRUVS	490.5±123.8	6	637.8±29.8	21
	RUVS (mesopotic)	308.0±0.0	1	607.1±31.3	34
	BRUVS (mesophotic)	529.5±72.9	6	651.6±14.0	25
Caranx melampygus	SPC	254.7±5.4	185	461.9±7.2	215
	RUVS	318.2±19.2	20	528.6±28.2	21
	BRUVS	335.2±22.4	26	526.5±45.3	12
	RUVS (mesopotic)	484.8±59.6	3	466.8±21.5	21
	BRUVS (mesophotic)	454.4±34	7	465.8±35.7	8
Caranx ignobilis	SPC	110±0.0	1	815.1±10.3	319
	RUVS	337.6±0.9	2	860.7±22.9	7
	BRUVS	-	0	828.3±41.8	27
	RUVS (mesopotic)	572.4±0.0	1	983.0±92.7	2
	BRUVS (mesophotic)	740.0±17.0	4	1017.8±26.9	6
Carcharhinus galapagensis	SPC	-	-	1151.1±34.8	68
	Towed-diver	-	-	1087.8±35.9	41
	RUVS	-	-	980.2±4.1	2
	BRUVS	-	-	934.1±15.2	9
	RUVS (mesopotic)	-	-	1220.1±81.2	9
	BRUVS (mesophotic)	-	-	1280.7±44.5	11
Triaenodon obesus	SPC	-	-	1111.3±27.8	43
	Towed-diver	-	-	1387.2±37.5	43
	RUVS	-	-	1081.5±56.7	4
	BRUVS	-	-	1065.5±61.9	5
	RUVS (mesopotic)	-	-	1064.5±38.6	3
	BRUVS (mesophotic)	-	-	1196.4±24.9	10

Only *Caranx melampygus* was able to be assessed across the archipelago, with significant differences noted between SPC and RUVS (MHI: $p < 0.01$, NWHI: $p < 0.05$), and between SPC and BRUVS (MHI: $p < 0.001$, NWHI: $p < 0.05$) in both shape and location (Table 5.2, Supplementary Materials, Figure S.5.1). Mean SPC lengths were consistently smaller than either RUVS or BRUVS (Figure 5.4, Supplementary Materials Figure S.5.1); however, shape tests found no differences between methods, indicating significance was driven between locations of length distributions only (i.e. differences in median length). An exception was noted between SPC and BRUVS being significant for shape tests in the MHI ($p < 0.05$; Table 5.2, Supplementary Materials, Figure S.5.2).

Caranx ignobilis size data showed significant shape and location differences between SPC and BRUVS in the NWHI ($p < 0.01$) along with significant shape only tests ($p < 0.05$). This was a likely byproduct of length distributions being unimodal for SPC and bimodal for BRUVS, and lower overall number of BRUVS measurements being driven by the first mode of smaller fishes. Size estimates from *Carcharhinus galapagensis* by BRUVS were significantly smaller than those from SPC and towed-diver surveys (Figure 5.4, Supplementary Materials Figure S.5.1). Even though shape-only tests found no differences between BRUVS and other methods (Table 5.2), results should be treated with caution due to the small number

of BRUV samples.

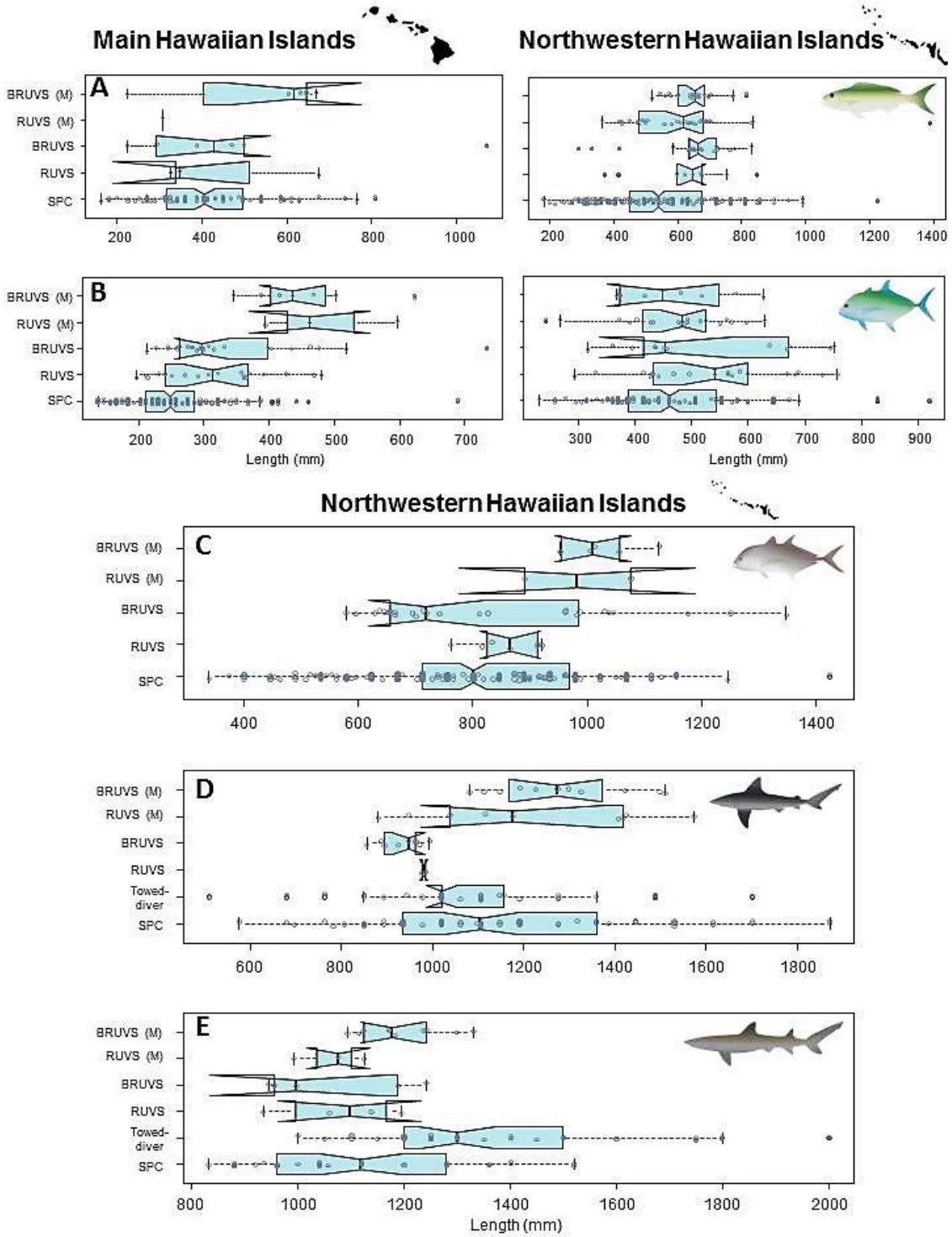


Figure 5.4. Notched Tukey boxplots of median lengths (length of caudal fork, mm). Bold vertical line indicates the median, boxes indicate the 25th and 75th percentiles, and whiskers indicate 1.5 x interquartile ranges (IQR). Boxplot notches represent 95% confidence intervals of median (median ±1.57*IQR/n$^{0.5}$). A.) *Aprion virescens*, and B.) *Caranx melampygus* sampled by SPC, RUVS, and BRUVS (shallow and mesophotic for both video-sampling methods) in the MHI and NWHI. Additional NWHI-inclusive comparisons were conducted for C.) *Caranx ignobilis*, D.) *Carcharhinus galapagensis*, and E.) *Triaenodon obesus*. Towed-diver estimates are included for the latter two species.

Table 5.2. Outputs of kernel density tests of differences between pairs of fish length-frequency distributions sampled by SPC, towed-diver RUVS, and BRUVS (shallow-water only). Significance tests on raw data test for differences in location and shape of length-frequency distributions. Tests on standardized data provide a test of shape only.

Location	Main Hawaiian Islands			Northwestern Hawaiian Islands	
Species	Method comparison	Shape and Location	Shape only	Shape and Location	Shape only
Aprion virescens	SPC vs. RUVS	-	-	0.276	0.202
	SPC vs. BRUVS	-	-	**< 0.001**	0.292
	RUVS vs. BRUVS	-	-	0.756	0.872
Caranx melampygus	SPC vs. RUVS	**0.008**	0.834	**0.036**	0.446
	SPC vs. BRUVS	**<0.001**	**<0.04**	**0.028**	0.132
	RUVS vs. BRUVS	0.170	0.140	0.518	0.440
Caranx ignobilis	SPC vs. BRUVS	-	-	**0.004**	**0.02**
Carcharhinus galapagensis	SPC vs. Tow	-	-	0.240	**0.018**
	SPC vs. BRUVS	-	-	**< 0.001**	0.462
	Tow vs. BRUVS	-	-	**< 0.001**	0.516
Triaenodon obesus	SPC vs. Tow	-	-	**< 0.001**	0.292

In contrast, significant shape tests ($p < 0.02$; no difference in tests for shape and location) results of comparisons between SPC and towed-diver indicate that each method was either sampling different portions of the population (with the average towed-diver length estimates being 5.6% smaller than diver SPCs), or with one method (SPC) possibly over- or (tow) under-sizing *Carcharhinus galapagensis* lengths. Finally, mean length estimates for Triaenodon obesus were around 20% smaller for SPC than for towed-divers ($p < 0.001$ for shape and location; no differences for shape-only tests).

Species specific to visual assessment type

Several species were sighted exclusively on either diver or video sampling. Among Carangidae, these included *Caranx sexfasciatus* (SPC and tow only, NWHI), *Elagatis bipinnulata* (SPC and tow only, MHI and NWHI), *Seriola lalandi* (RUVS and BRUVS only, NWHI mesophotic depths only), and *Gnathanodon speciosus* (BRUVS only, MHI and NWHI).

A number of shark species were also recorded solely during video sampling. These included *Galeocerdo cuvier* (RUVS and BRUVS) and *Carcharhinus plumbeus* (RUVS and BRUVS, mesophotic only). In addition, a single sighting of *Carcharhinus melanopterus* was recorded by a shallow-water BRUVS in the MHI. Finally, *Carcharhinus limbatus* was noted during RUVS and BRUVS recordings in the MHI, along with a single scalloped hammerhead (*Sphyrna lewini*, shallow-water RUVS only), which all occurred outside of one-hour sampling periods (i.e. during camera station descents or following the conclusion of sampling).

Discussion

This research expands on other underwater census studies in Hawaii, including comparisons between coral reef fish SPC surveys on open-circuit SCUBA versus closed circuit rebreathers (Gray et al. 2016). Here, we conducted the first large-scale predator comparison study between diver SPC, towed-diver,

RUVS, and BRUVS, with the primary goal of appraising relative abundances between the NWHI and MHI. While results remained broadly consistent, in that many predator groups and individually assessed species were much more common in the NWHI than in the MHI, there were also substantial discrepancies depending on the assessment approach used. This highlights the common challenges encountered by research programs examining large-bodied roving predator populations, i.e. their inherent patchiness (especially in areas prone to fishing pressure), high general degrees of mobility, variable, species-dependent behavioral responses to divers between regions, and wide-ranging horizontal and vertical distributions (Wetherbee et al. 1997; Meyer et al. 2007b; Meyer et al. 2009b; Vaudo et al. 2014; Papastamatiou et al. 2015). Seasonal, diurnal, and lunar drivers may also influence predator movements, providing additional challenges to obtaining accurate predator abundance estimates (Merson and Pratt 2001; Speed et al. 2011; Whitney et al. 2012; Vianna et al. 2013).

It was noteworthy that NWHI:MHI abundance ratios derived from RUVS and BRUVS surveys were similar for several groups (e.g. Carcharhinidae for pooled depths) and species (e.g. *Aprion virescens* in all RUVS and BRUVS depths, pooled reef and Galapagos-grey reef sharks, *Carangoides orthogrammus*). Although BRUVS recorded consistently higher encounter rates than RUVS for this species in both regions (see Chapter 2), it appears that increased encounter rates (due to baiting effects) were generally of similar scale in each region. These results may therefore reduce some of the concerns surrounding the potential for baiting biases, and consequent inflation of predator density estimates due to fish being drawn from outside of visible sampling areas. However, as neither BRUVS nor RUVS effectively sampled some of the species encountered (albeit rarely) in the MHI (e.g. *Triaenodon obesus*), and because there were still some differences between BRUV and RUV abundance ratios (e.g. Galapagos sharks in mesophotic areas), there is still a need for specifically-designed, rigorous methods comparison studies.

Although towed diver abundance ratios had a tendency to be higher than RUVS or BRUVS in shallow water, they were surprisingly consistent for *Caranx ignobilis* and *Seriola* spp. when compared with pooled (combined shallow and mesphotic) data from RUVS and/or BRUVS. One possible explanation is predators were being drawn into towed-diver sampling swaths from deeper depths, where some species (e.g. *Seriola* spp.) are known to occur in greater numbers (Misa et al. 2016; Tamaru et al. 2016). Towed-divers also observed occasional changes in predator behavior, particularly in high density areas where, at times, aggregations of predators may trail divers during surveys (J. Asher, *pers. obs.*, Figure 5.5), paralleling foraging activities noted between top-level roving predators and Hawaiian monk seals (*Monachus schauinslandi)* (Parrish et al. 2008). While groups of predators trailing towed divers are not recorded during surveys, those aggregations do indicate that roving predators are being attracted to divers and therefore drawn from other habitats (e.g. potentially deeper water), and may account for the high NWHI:MHI ratios for sharks and other jack species (e.g. pooled trevallies, *Caranx melampygus*, *Carangoides orthogrammus*).

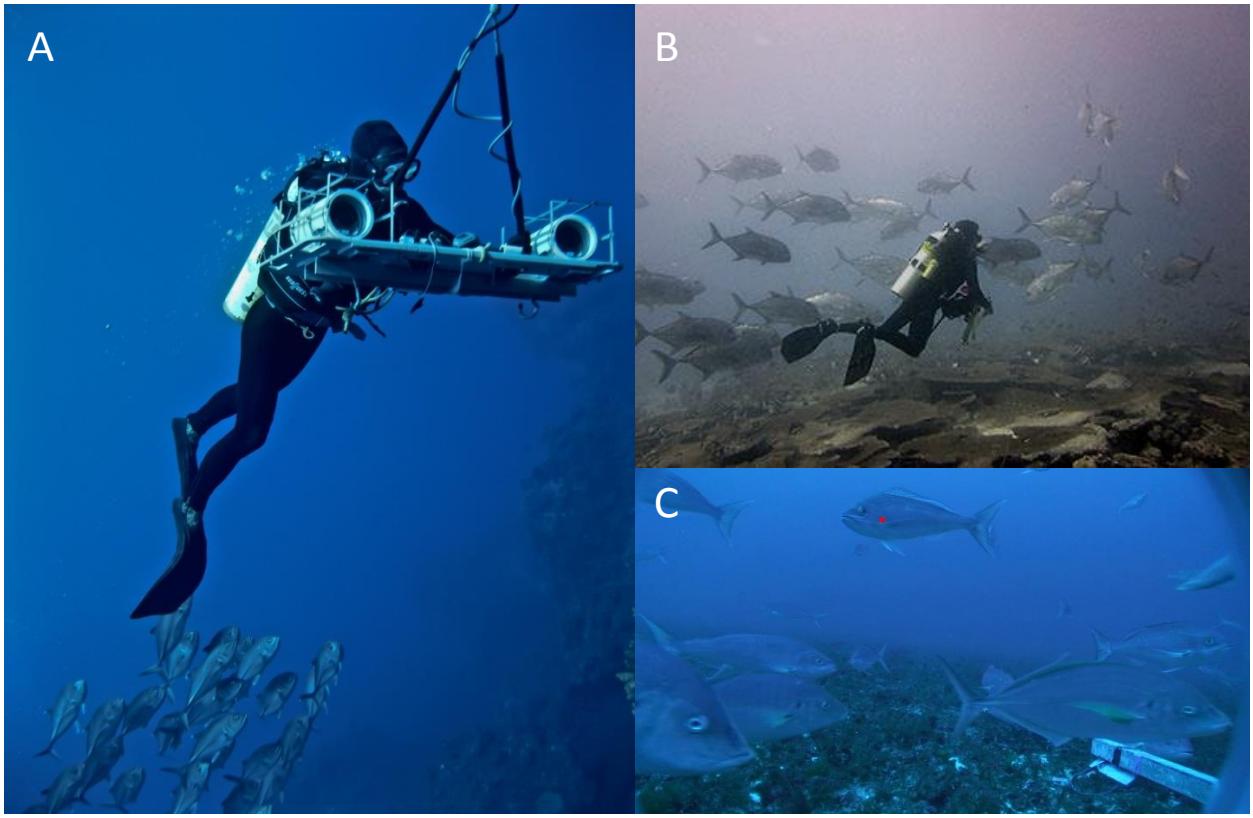


Figure 5.5. Examples of predator attraction behaviors. A.) School of *Caranx sexfasciatus* trailing towed-diver. Photograph by J.Asher. B.) School of *Caranx ignobilis* surrounding SPC diver. Photograph by NOAA. C.) Mixed school of *Seriola* spp., *Pseudocaranx cheilio*, and *Pristipomoides filamentosus* surrounding RUVS. Photograph by J. Asher.

It appears that, in some circumstances, towed-diver surveys can also be subject to negatively biased counts (i.e. underestimates). For example shallow water towed diver densities were between 200 – 900% lower than those from timed-swim surveys, BRUVS, and audible stationary counts in Australia (Rizzari et al. 2014). It is possible that noise or other disturbance caused by a moving small boat may drive sharks and potentially other roving predators out of the immediate path of towed divers, particularly in shallow water. Certainly, vessel noise can either attract, repulse, or alter roving predator behaviors in other ways, or have no measurable effects (Røstad et al. 2006; Meyer et al. 2009b; Fitzpatrick et al. 2011; Smith et al. 2016); however, the only study we are aware of in the NWHI found no impact acoustic of playback of motorized vessels on Galapagos shark-monk seal predation rates (Gobush and Farry 2012).

Diver SPC surveys are, in several ways, well-suited to sampling of demersal, site attached species or those mobile species that are relatively unaffected by the presence of divers. However, predator abundance inflation is a concern, particularly in remote locations where predators are abundant and where they are likely to be attracted to the relative novelty of divers' presence. Conversely, small scale diver surveys may underrepresent their abundance in populated areas, where species can become averse to divers (Januchowski-Hartley et al. 2012; Lindfield et al. 2014; Gray et al. 2016). Of the predatory species examined, *Caranx ignobilis* had the widest abundance discrepancies in abundance ratios between methods, with over two orders of magnitude separating diver SPC censuses to towed-

diver, RUVS, and BRUVS surveys. For this species, it seems very likely that divers overestimate densities in small area surveys, particularly for non-instantaneous methods (Friedlander and DeMartini 2002; Sandin et al. 2008b; Ward-Paige et al. 2010a; Richards et al. 2011; Nadon et al. 2012). As the most commonly encountered jack species with the highest overall predator biomass in the NWHI, this species isn't observed in comparable numbers anywhere else in Hawaii or the US Pacific Territories. Overall, the very high NWHI:MHI SPC ratios are probably indicative of both strong SPC attraction effects inflating density estimates in the NWHI (Figure 5.4), coupled with real low abundance in the MHI - evident across all survey methods, and potentially indicative of depleted populations there (Friedlander and DeMartini 2002; Dale et al. 2010; Santos et al. 2011; Nadon 2017). While towed-diver surveys aren't immune to overinflating predator counts, they cover considerably larger areas, with divers moving at ~ 45 m/minute, in contrast to divers conducting SPC and belt transects, who are stationary or moving slowly - which likely reduces the impacts of predator aggregation and attraction on towed diver surveys (Richards et al. 2011; Nadon et al. 2012). However, towed-diver abundance ratios were still considerably higher than for shallow water RUVS and BRUVS, e.g. for pooled trevally jacks and *Caranx melampygus*, and the possibility of inflated predator abundance ratios in the NWHI remains a concern.

RUVS and BRUVS have several advantages over diver-based censuses. They are able to survey the (frequently substantial) portions of predator populations below the safe diving limits of open-circuit SCUBA depths (i.e. > 30 m), which also means that they can provide data on deeper predatory species that are rarely seen be divers. They also generate permanent data records, and are not affected by behavioral influences associated with diver attraction or avoidance. BRUVS, in particular, are able to provide robust estimates of carnivorous fish abundance in comparison with other visual assessment methods, but without generally decreasing the abundance and richness of herbivorous or omnivorous species (Harvey et al. 2007; Langlois et al. 2010; Watson et al. 2010; Rizzari et al. 2014). However, BRUVS are prone to potential biases and sampling artifacts that do not affect diver censuses, which include unknown areas of attraction in part due to variable bait plumes driven by current, wave, and tidal forces (Watson et al. 2005; Harvey et al. 2007; Dorman et al. 2012). As described in Chapter 2, RUVS surveys collect data in the absence of bait, which removes biases associated with baiting; however, predator abundance variances are notably higher for RUVS than BRUVS, with more samples necessary to achieve comparative power. Lower RUVS encounter rates are an especially important consideration in areas where predator populations are patchy and/or rarely encountered, e.g. in areas where they are depleted by fishing (Harvey et al. 2007). RUVS are also not completely shielded from biases, particularly in light of "structural attraction" effects whereby predators may be drawn to camera stations deployed in low complexity, featureless plains (e.g. sand flats or low-lying, consolidated pavement flats, Figure 5.4). Finally, both RUVS and BRUVS may be vulnerable to count saturation (hyperstability) in areas where predator densities are extremely high (Schobernd et al. 2014; Bacheler and Shertzer 2015).

There were several inconsistencies between predator length distributions generated from different methods. For example, mean predator size and length distributions for *Caranx melampygus* (and most other species) were consistently smaller from diver SPC. If this represents a real weakness of SPC – e.g. that diver surveys tend to underrepresent large individuals – then population assessments generated from small-scale diver SPC data may overestimate scales of depletion. In addition, with mean lengths

falling below the 500 mm measurement threshold, the majority of *Caranx melampygus* in the MHI and to a lesser extent *Aprion virescens* in the NWHI also fall outside of the current detection range for towed-diver surveys, which may constrain population estimates, particularly when examining predators in depleted areas or in areas of high fishing pressure (Nadon et al. 2015; Nadon 2017). Of additional interest were sightings of much larger *Triaenodon obesus* by towed-divers in comparison with diver SPCs. This may indicate another source of systemic sizing bias among methods, which in this case, relate to sighting distances and detectability, as SPC divers can observe partially hidden, resting white tip reef sharks more clearly than towed-divers can as they move through the water column (Whitney et al. 2007; Barnett et al. 2012). Finally, the detection of larger and fewer jacks by RUVS and/or BRUVS (e.g. *Caranx melampygus, Caranx ignobilis*) versus those collected by SPC and towed-divers indicates the potential for intraspecific competition biases. Attracted by the structural components of the RUV/BRUV camera stations themselves (e.g. in low-complexity environments), or by baited attractants (in the case of BRUVS), larger fish may competitively exclude smaller, subordinate fish from the limited fields of view.

An additional data source for roving predator populations comes from longline catch data which, like BRUVS and RUVS, are able to survey reef-associated predatory species that tend to be poorly represented in diver censuses. For example, examination of MHI longline CPUE data collected by Hawaiian shark control programs between 1959 - 1976 showed that, although gray and Galapagos sharks were rarely caught around the more populated parts of the MHI, tiger (*Galeocerdo cuvier*) and sandbar (*Carcharhinus plumbeus*) sharks were regularly hooked (Papastamatiou et al. 2006; Dale et al. 2011). Similarly, RUV and BRUV surveys recorded several *Galeocerdo cuvier* and *Carcharhinus plumbeus* (both species in the MHI and NWHI), as well as jack species (e.g. *Seriola lalandi*) not recorded by divers – either in tow or SPC (Figure 5.5), with the latter two species encountered exclusively in mesophotic surveys. The absence of *Galeocerdo cuvier* from diver surveys, despite the fact that they were recorded in shallow water by both RUVS and BRUVS, together with the considerably greater number of those diver surveys, is suggestive of diver avoidance by that species (Dale et al. 2011). *Seriola rivoliana* were also observed during both RUVS and BRUVS (primarily in mesophotic depths), but not during any diver surveys. However, as it is very similar in appearance to *Seriola dumerili* and often forms mixed schools, it is likely that SPC and towed-diver observers recorded all *Seriola* spp. as *Seriola dumerili*. Finally, as mark-and-recapture and long-term tracking studies indicate that large portions of populations of several roving predator species (e.g. *Aprion virescens*, *Caranx ignobilis*, *Carcharhinus galapagensis*) are more abundant in mesophotic depths, it is clear that complimentary methods, capable of sampling deeper habitats, are needed to fully assess the status of roving predator populations (Holland et al. 1999; Meyer et al. 2007a; Nakamura et al. 2011; Pickard 2013; Papastamatiou et al. 2015). It is important to note that while tracking and mark-and-recapture techniques represent viable and valuable methods to assess roving predator populations, they are not a panacea, as they remain susceptible to their own information gaps, e.g. potential omission of predator interisland movements (Tagawa and Tam 2006; Meyer et al. 2007a; Nadon 2017).

In contrast, two schooling *Carangidae* (*Elagatis bipinnulata*, *Caranx sexfasciatus*) were absent from surveys by both video methods in shallow water, but recorded by SPC and/or towed-diver surveys.

These represented rare sightings of primarily pelagic species moving closer to shore (in the case of *Elagatis bipinnulata*), or intermittent, inherently patchy distributions (*Caranx sexfasciatus*) of species being missed by the more spatially and temporally limited video surveys used in this study (Schwarz 2004; Schroeder and Parrish 2006; Froese and Pauly 2014).

Figure 5.6. Species encountered solely during stereo-video sampling, recorded by both RUVS (right panels) and BRUVS (left panels). A.) *Carcharhinus plumbeus* B.) *Galeocerdo cuvier* C.) *Seriola lalandi*. Note that *Carcharhinus plumbeus and Seriola lalandi* were recorded in mesophotic depths only.

The evidence used to support so called 'inverted biomass' or trophic pyramids, in which greatest biomass occurs at the top of the food chain than, comes primarily from diver-based (belt-transect) underwater visual surveys at remote atolls and islands (Newman et al. 2006; DeMartini et al. 2008; Sandin et al. 2008b; de León et al. 2016; Bradley et al. 2017). Top-level predator systems can be sustained through subsidiary inputs, i.e. seasonal or episodic immigration of schooling mobile invertivores, planktivores, and lower-level functional groups, or during spawning events (Polis et al. 1997; Mourier et al. 2016; Trebilco et al. 2016). Lastly, inverted pyramids may be sustained in areas hosting habitats with complex or extensive hiding (refuge) spaces for prey species (Wang et al. 2009). Although our study does not attempt to determine the trophic structure of reef fishes in the Hawaiian archipelago, our results corroborate other studies which have suggested that other than in

circumstances described above, they are likely to be an artifact of behavioral bias, e.g. attraction of roving predators to divers in remote areas, combined with a methodological bias for overcounting mobile species in small sampling areas (Friedlander and DeMartini 2002; Sandin et al. 2008b; Ward-Paige et al. 2010a; Williams et al. 2011a; Nadon et al. 2012). However, consistently higher towed-diver abundance ratios suggest that in areas hosting high-density predator populations, diver attraction may still be occurring; and 2.) Inflated diver-based predator estimates occurring as a result of counting biases. These could be linked to asymmetric predator "over counts" due to increased predator mobility (versus slower, less active trophic groups) seen with non-instantaneous underwater visual censuses, or diver attraction as previously described with SPC and belt-transects (Sandin et al. 2008a; Ward-Paige et al. 2010a; Dickens et al. 2011; Nadon et al. 2012). Lastly, separate mark-and-recapture surveys of gray reef sharks similarly suggests predator biomass at Palmyra atoll may be inflated by up to 56%, which would shift pyramid structure to being top-heavy, but not inverted (Bradley et al. 2017). Given the uncertainties in predator population estimates depending on the type of method used, continued assessments of predator populations through the use and evaluation of multiple methods, remain paramount.

Conclusions

In conclusion, assessments comparing large-bodied roving predators between remote versus human population centers remains challenging. Specific approaches may be needed to effectively measure the abundance of particular species, or research programs may need to incorporate a combination of methods. Overall, diver SPC surveys appear prone to substantial overestimation of relative NWHI:MHI abundance for nearly all of the predatory species examined. Similarly, towed-diver surveys likely overestimate MWHI:MHI ratios for several sharks and jack species (e.g. *Caranx melampygus*), but may provide more accurate estimates for other species such as *Caranx ignobilis*, and *Seriola* spp., for which the towed-diver ARs were similar to those from RUVS and BRUVS surveys (pooled across all depths). RUVS and/or BRUVS might provide a less biased, holistic representation of NWHI:MHI predator ratios and possibly predator length-frequencies, given they can sample a greater depth range without the confounding behavioral effects or size-estimation discrepancies noted with divers; however, there may be reservations with the use of length-frequency data collected through any underwater visual census (diver or video), without first considering size-related behavioral responses (Harvey et al. 2013a). Finally, the absence of several predators (e.g. *Triaenodon obesus*) from RUV and BRUV surveys in the MHI suggests that these methods may not be appropriate for sampling some predator species.

Diver-based visual surveys will undoubtedly continue to be used to assess coral reef fish assemblages, including predatory species, across the Hawaiian Archipelago and US Pacific Territories. However, this study and other recent works (Dale et al. 2011; Lindfield et al. 2014; Gray et al. 2016; Bradley et al. 2017) underline the need for careful methods choice and awareness of the potential for methodological bias, particularly for those roving predatory species that can visibly adjust their behavior in response to presence of divers, camera systems, and/or other stimuli. In our experience, the aggregation of sharks and jacks near divers is particularly noticeable in the NWHI; therefore, there would be considerable value in extending these investigations to other methods in remote, predator-heavy ecosystems.

Supplementary Materials

Table S.5.1. Table of NWHI:MHI roving predator abundance ratios between survey methods. Diver methods include: stationary point count (nPSC) and towed-diver (tow). Videographic methods include: shallow-water RUVS/BRUVS, and mesophotic RUVS/BRUVS. Values are depicted as abundance ratios (AR), quantile range is listed in parentheses (95% QR, lower QR, upper QR).

Method	Target Group/ Species	MHI	NWHI	Ratio
nSPC	Carangidae	35.05 [18.37, 56.02]	164.48 [104.87, 243.38]	4.7 [2.9, 7]
nSPC	TREVALLY	33 [17.05, 53.2]	151.05 [95.09, 225.12]	4.6 [2.8, 6.8]
nSPC	*Carangoides ferdau*	1.41 [0.28, 3.26]	0.48 [0.1, 0.98]	0.3 [0, 1.3]
nSPC	*Caranx ignobilis*	0.04 [0, 0.13]	83.45 [44.7, 135.09]	1885 [1009.7, 3052.2]
nSPC	*Caranx melampygus*	30.79 [15.12, 52.02]	37.96 [24.35, 55.96]	1.2 [0.4, 2]
nSPC	*Carangoides orthogrammus*	1.04 [0.42, 1.87]	4.78 [2, 8.53]	4.6 [1.9, 8.3]
nSPC	*Caranx sexfasciatus*	-	22.99 [0.2, 65.09]	NWHI only
nSPC	*Elagatis bipinnulata*	0.09 [0, 0.26]	9.6 [0.19, 27.92]	112 [2.1, 326.8]
nSPC	*Gnathanodon speciosus*	-	-	-
nSPC	Unident. Jack	-	-	-
nSPC	*Pseudocaranx cheilio*	-	0.49 [0, 1.37]	NWHI only
nSPC	*Scombroides lysan*	1.75 [0.84, 2.84]	0.42 [0, 1.09]	0.2 [0, 0.9]
nSPC	*Seriola dumerili*	0.38 [0.09, 0.78]	2.3 [1.17, 3.65]	6 [2.8, 9.7]
nSPC	*Seriola lalandi*	-	-	-
nSPC	*Seriola rivoliana*	-	-	-
nSPC	*Seriola* spp.	0.38 [0.07, 0.77]	2.25 [1.07, 3.6]	5.9 [2.5, 9.7]
nSPC	Carcharhinidae	0.13 [0, 0.3]	18.32 [13.22, 24.06]	138.1 [99.7, 181.3]
nSPC	All Reef Sharks	0.13 [0, 0.3]	18.37 [13.58, 23.3]	142 [105.1, 179.6]
nSPC	Galapagos-grey reef	-	13.13 [8.72, 18.22]	NWHI only
nSPC	*Carcharhinus amblyrhynchos*	-	5.5 [2.29, 9.97]	-
nSPC	*Carcharhinus galapagensis*	0 [0, 0]	7.71 [5.21, 10.72]	NWHI only
nSPC	*Charcharhinus melanopterus*	-	-	-
nSPC	*Triaenodon obesus*	0.13 [0, 0.3]	5.2 [3.45, 7.19]	39.7 [25.9, 55.1]
nSPC	*Galeocerdo cuvier*	-	-	-
nSPC	*Charcharhinus plumbeus*	-	-	-
nSPC	*Aprion virescens*	6.07 [4.76, 7.53]	62.23 [54.42, 70.21]	10.3 [9, 11.6]
Tow	Carangidae	0.25 [0.05, 0.62]	3.31 [2.31, 4.57]	13.3 [9.1, 18.6]
Tow	TREVALLY	0.19 [0.01, 0.56]	3.19 [2.24, 4.36]	16.6 [11.2, 22.8]
Tow	*Carangoides ferdau*	0 [0, 0.01]	0.01 [0, 0.02]	5.4 [0, 11.7]
Tow	*Caranx ignobilis*	0.18 [0, 0.53]	2.2 [1.32, 3.44]	12.2 [6.9, 19.2]
Tow	*Caranx melampygus*	0.01 [0, 0.02]	0.49 [0.34, 0.69]	49.8 [33.9, 69.6]
Tow	*Carangoides orthogrammus*	0.01 [0, 0.04]	0.08 [0.04, 0.12]	6.1 [2.8, 9.5]
Tow	*Caranx sexfasciatus*	-	0.11 [0, 0.28]	NWHI only
Tow	*Elagatis bipinnulata*	0.02 [0, 0.05]	0.03 [0, 0.07]	1.8 [0, 4.6]
Tow	*Gnathanodon speciosus*	-	-	-
Tow	Unident. Jack	-	-	-
Tow	*Pseudocaranx cheilio*	-	0.31 [0.07, 0.62]	NWHI only
Tow	*Scombroides lysan*	0 [0, 0.01]	0 [0, 0]	MHI only
Tow	*Seriola dumerili*	0.03 [0.01, 0.05]	0.08 [0.04, 0.14]	2.9 [1.1, 5.1]
Tow	*Seriola lalandi*	-	-	-
Tow	*Seriola rivoliana*	-	-	-
Tow	*Seriola* spp.	0.03 [0.01, 0.05]	0.08 [0.04, 0.14]	3 [1.2, 5.2]
Tow	Carcharhinidae	0.01 [0, 0.03]	0.91 [0.61, 1.3]	75.1 [49.8, 107.2]
Tow	All Reef Sharks	-	0.53 [0.25, 0.83]	NWHI only
Tow	Galapagos-grey reef	0.01 [0, 0.03]	0.92 [0.62, 1.28]	76.3 [51.1, 106.1]
Tow	*Carcharhinus amblyrhynchos*	-	0.32 [0.11, 0.62]	NWHI only
Tow	*Carcharhinus galapagensis*	-	0.21 [0.09, 0.37]	NWHI only
Tow	*Charcharhinus melanopterus*	-	-	-
Tow	*Triaenodon obesus*	-	-	-
Tow	*Galeocerdo cuvier*	-	-	-
Tow	*Charcharhinus plumbeus*	0.01 [0, 0.03]	0.39 [0.28, 0.51]	32.6 [23.4, 42.3]
Tow	*Aprion virescens*	0.09 [0.05, 0.13]	2.12 [1.78, 2.52]	24.3 [20.3, 28.9]

Method	MHI	NWHI	Ratio
RUVS	0.7 [0.43, 1]	0.91 [0.56, 1.33]	1.3 [0.6, 2.1]
RUVS	0.56 [0.33, 0.81]	0.92 [0.56, 1.34]	1.6 [0.9, 2.5]
RUVS	0.05 [0, 0.15]	0.03 [0, 0.11]	0.7 [0, 2.5]
RUVS	0.04 [0, 0.11]	0.12 [0.04, 0.23]	2.8 [0.4, 5.6]
RUVS	0.3 [0.13, 0.5]	0.64 [0.39, 0.94]	2.1 [1.1, 3.2]
RUVS	0.07 [0, 0.15]	0.08 [0, 0.17]	1.1 [0, 2.7]
RUVS	-	-	-
RUVS	-	-	-
RUVS	-	-	-
RUVS	0.04 [0, 0.1]	-	MHI only
RUVS	-	-	-
RUVS	0.11 [0.03, 0.2]	-	MHI only
RUVS	0.03 [0, 0.09]	-	MHI only
RUVS	-	-	-
RUVS	-	-	-
RUVS	0.03 [0, 0.09]	-	MHI only
RUVS	-	0.19 [0.05, 0.36]	NWHI only
RUVS	-	0.19 [0.06, 0.36]	NWHI only
RUVS	-	0.1 [0.01, 0.24]	NWHI only
RUVS	-	-	-
RUVS	-	0.1 [0.01, 0.24]	NWHI only
RUVS	-	-	-
RUVS	-	0.1 [0.02, 0.19]	NWHI only
RUVS	-	-	-
RUVS	-	-	-
RUVS	0.08 [0.02, 0.14]	0.25 [0.13, 0.39]	3.2 [1.4, 5.1]
BRUVS	1.05 [0.58, 1.57]	1.78 [1.14, 2.57]	1.7 [0.9, 2.5]
BRUVS	0.88 [0.44, 1.31]	1.7 [1.02, 2.52]	1.9 [1, 3]
BRUVS	0.04 [0, 0.12]	-	MHI only
BRUVS	-	1.02 [0.43, 1.79]	NWHI only
BRUVS	0.66 [0.36, 0.93]	0.6 [0.35, 0.85]	0.9 [0.4, 1.5]
BRUVS	0.09 [0, 0.25]	0.08 [0, 0.22]	0.9 [0, 2.8]
BRUVS	-	-	-
BRUVS	-	-	-
BRUVS	0.01 [0, 0.04]	-	MHI only
BRUVS	-	-	-
BRUVS	-	-	-
BRUVS	0.02 [0, 0.05]	-	MHI only
BRUVS	-	0.05 [0, 0.16]	NWHI only
BRUVS	-	-	-
BRUVS	0.16 [0, 0.49]	0.03 [0, 0.08]	0.2 [0, 1.3]
BRUVS	0.17 [0, 0.49]	0.08 [0, 0.19]	0.5 [0, 1.8]
BRUVS	0.16 [0, 0.33]	0.5 [0.31, 0.73]	3.1 [1.4, 4.8]
BRUVS	0.08 [0, 0.24]	0.24 [0.1, 0.43]	3 [0.2, 5.9]
BRUVS	0.08 [0, 0.25]	0.51 [0.32, 0.71]	6.2 [3, 9.4]
BRUVS	0.08 [0, 0.24]	-	MHI only
BRUVS	-	0.23 [0.1, 0.42]	NWHI only
BRUVS	0 [0, 0.01]	-	MHI only
BRUVS	-	-	-
BRUVS	0.08 [0, 0.24]	-	MHI only
BRUVS	-	0.27 [0.15, 0.37]	NWHI only
BRUVS	0.22 [0.04, 0.44]	0.8 [0.61, 0.95]	3.6 [2.5, 4.8]

Method	MHI	NWHI	Ratio
RUVS (Meso)	0.7 [0.31, 1.21]	2.62 [1.37, 4.15]	3.7 [1.9, 5.9]
RUVS (Meso)	0.61 [0.25, 1.1]	1.36 [0.55, 2.48]	2.2 [0.6, 4]
RUVS (Meso)	0.03 [0, 0.09]	0.11 [0.01, 0.28]	3.9 [0, 9.9]
RUVS (Meso)	0.05 [0, 0.12]	0.07 [0, 0.17]	1.5 [0, 3.6]
RUVS (Meso)	0.11 [0.02, 0.22]	0.21 [0.08, 0.37]	1.9 [0.3, 3.5]
RUVS (Meso)	0.39 [0.14, 0.74]	0.21 [0.07, 0.39]	0.5 [0, 1.3]
RUVS (Meso)	-	-	-
RUVS (Meso)	-	-	-
RUVS (Meso)	-	-	-
RUVS (Meso)	-	-	-
RUVS (Meso)	-	0.77 [0.01, 1.99]	NWHI only
RUVS (Meso)	-	-	-
RUVS (Meso)	-	0.78 [0.27, 1.6]	NWHI only
RUVS (Meso)	-	0.02 [0, 0.06]	NWHI only
RUVS (Meso)	0.06 [0, 0.18]	0.44 [0.13, 0.81]	7.3 [2.1, 14]
RUVS (Meso)	0.09 [0, 0.27]	1.28 [0.58, 2.13]	13.7 [6.1, 23.2]
RUVS (Meso)	0.07 [0, 0.16]	0.27 [0.16, 0.38]	3.8 [2, 5.7]
RUVS (Meso)	0.02 [0, 0.06]	0.22 [0.12, 0.33]	10.8 [5.7, 16.5]
RUVS (Meso)	0.02 [0, 0.06]	0.22 [0.12, 0.33]	10.9 [5.4, 16.8]
RUVS (Meso)	0.02 [0, 0.06]	0.03 [0, 0.07]	1.5 [0, 4.5]
RUVS (Meso)	-	0.18 [0.08, 0.28]	NWHI only
RUVS (Meso)	-	-	-
RUVS (Meso)	-	0.01 [0, 0.03]	NWHI only
RUVS (Meso)	-	0.01 [0, 0.04]	NWHI only
RUVS (Meso)	0.05 [0, 0.13]	0.02 [0, 0.06]	0.4 [0, 1.7]
RUVS (Meso)	0.12 [0.03, 0.23]	0.68 [0.49, 0.91]	5.7 [4, 7.8]
BRUVS (Meso)	1.44 [0.93, 1.95]	2.21 [0.99, 3.54]	1.5 [0.6, 2.6]
BRUVS (Meso)	1.23 [0.77, 1.73]	1.34 [0.5, 2.24]	1.1 [0.3, 1.9]
BRUVS (Meso)	0.04 [0, 0.12]	0.05 [0, 0.15]	1.3 [0, 3.8]
BRUVS (Meso)	0.11 [0.02, 0.23]	0.36 [0.04, 0.67]	3.2 [0.1, 6.2]
BRUVS (Meso)	0.38 [0.13, 0.67]	0.37 [0.11, 0.71]	1 [0, 2.1]
BRUVS (Meso)	0.62 [0.25, 1.05]	0.23 [0, 0.52]	0.4 [0, 1.1]
BRUVS (Meso)	-	-	-
BRUVS (Meso)	-	-	-
BRUVS (Meso)	0.04 [0, 0.12]	-	MHI only
BRUVS (Meso)	-	-	-
BRUVS (Meso)	-	0.32 [0.09, 0.57]	NWHI only
BRUVS (Meso)	0.04 [0, 0.12]	-	MHI only
BRUVS (Meso)	0.17 [0.02, 0.36]	0.59 [0.09, 1.47]	3.4 [0, 8.9]
BRUVS (Meso)	-	0.01 [0, 0.04]	NWHI only
BRUVS (Meso)	-	0.18 [0.07, 0.29]	NWHI only
BRUVS (Meso)	0.17 [0.02, 0.38]	0.83 [0.3, 1.76]	4.9 [1.4, 10.6]
BRUVS (Meso)	0.2 [0.05, 0.4]	1.34 [0.82, 1.89]	6.9 [4, 10]
BRUVS (Meso)	0.02 [0, 0.07]	0.97 [0.52, 1.44]	40.1 [21, 59.8]
BRUVS (Meso)	0.06 [0, 0.17]	1.17 [0.66, 1.7]	18.1 [10, 26.6]
BRUVS (Meso)	0.02 [0, 0.07]	0.05 [0, 0.15]	2.1 [0, 7]
BRUVS (Meso)	-	0.87 [0.45, 1.32]	NWHI only
BRUVS (Meso)	-	-	-
BRUVS (Meso)	0.04 [0, 0.12]	0.09 [0.01, 0.21]	2.4 [0, 5.8]
BRUVS (Meso)	0.09 [0, 0.2]	0.01 [0, 0.04]	0.2 [0, 1.2]
BRUVS (Meso)	-	0.25 [0.06, 0.59]	NWHI only
BRUVS (Meso)	0.4 [0.19, 0.64]	1.11 [0.88, 1.33]	2.8 [1.9, 3.6]

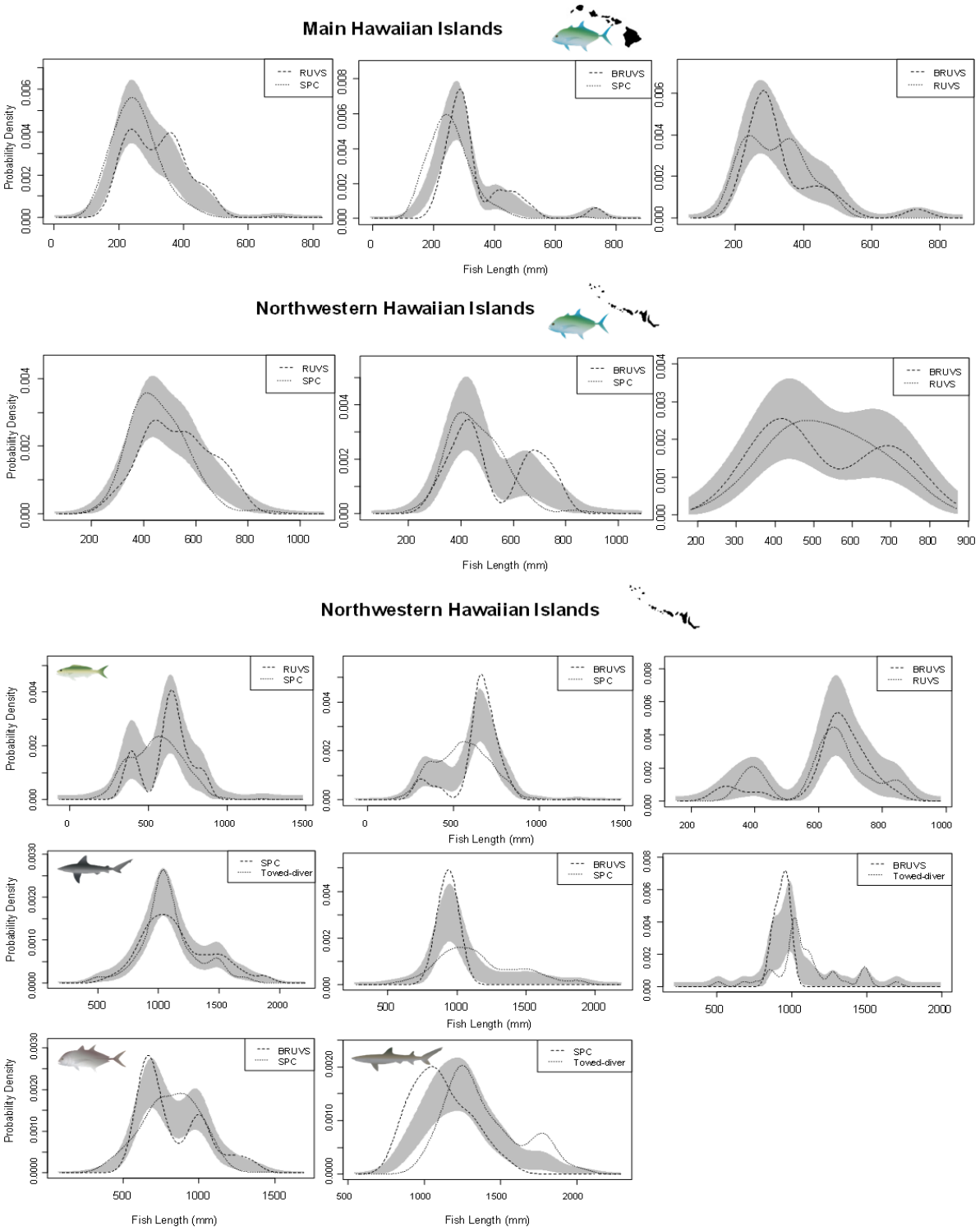


Figure S.5.1. Comparison of kernel density estimate (KDE) probabilities using mean bandwidths for *Caranx melampygus*, *Aprion virescens*, *Carcharhinus galapagensis*, *Caranx ignobilis*, and *Triaenodon obesus* between the length frequency data of paired-methods. Tests for differences in location and shape of length frequency raw data. Grey bands indicate one standard error to either side of the null model.

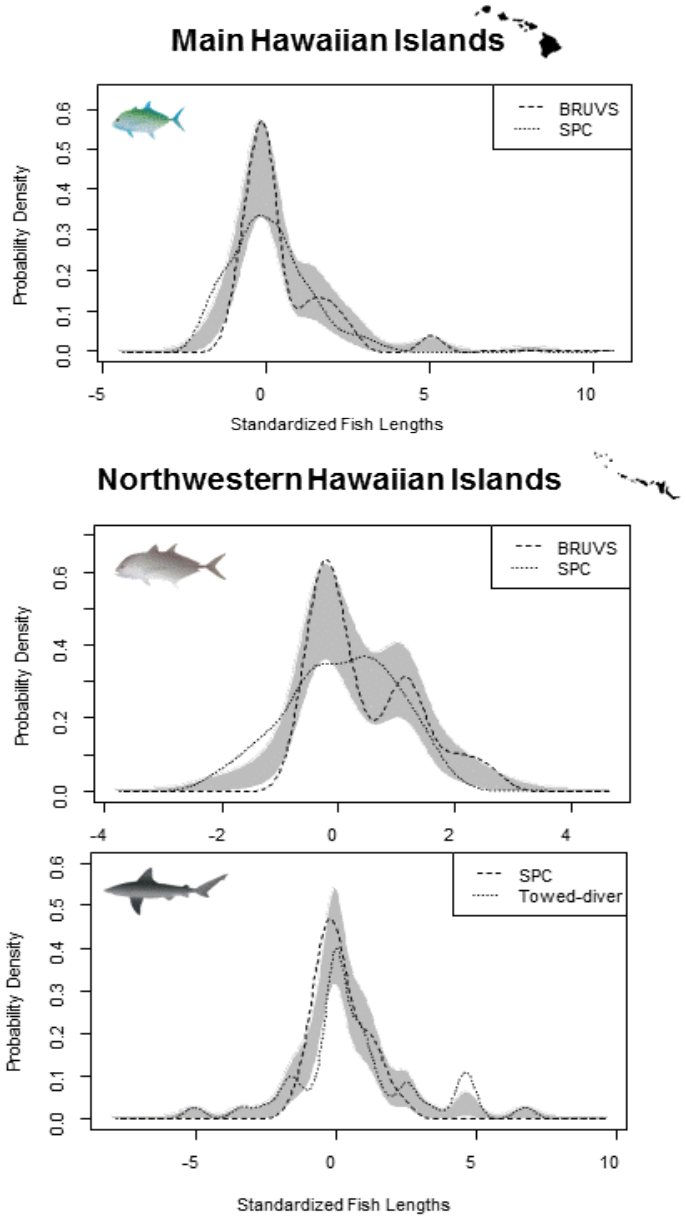


Figure S.5.2. Comparison of kernel density estimate (KDE) probabilities using mean bandwidths for *Caranx melampygus*, *Caranx ignobilis*, and *Carcharhinus galapagensis* between the length frequency data of paired-methods. Tests for differences in shape only (standardized data). Grey bands indicate one standard error to either side of the null model.

Chapter 6 – General discussion

General thesis summary

This thesis represents the outcome of the first large-scale use of BRUVS in the Hawaiian Archipelago, with research focused on methodological and ecological questions relating to coral reef fishes and underwater visual surveys. In Chapter 2, I compared unbaited and baited remote underwater video, and demonstrated that BRUVS were preferable to RUVS for reef fish assemblage and functional group sampling over 60-minute soak-time intervals, being particularly favorable for large-bodied predatory groups and select target species. When BRUVS were used to compare shallow water and mesophotic fishes in the MHI (Chapter 3), I found that herbivores and some other trophic groups declined rapidly below 30 m. Conversely, mobile invertivores and large-bodied predators increased with depth, with evidence of mesophotic depth refuges for some species. Densities of endemic species also declined beyond 30 m, contrasting with results reported for the NWHI (Fukunaga et al. 2016). This is likely due to fact that the NWHI surveys targeted specific habitats – i.e. complex slopes and deep ledges – whereas MHI surveys sampled a broader range of (mostly) less complex habitats (Kane et al. 2014; Kosaki et al. 2016). Finally, the discovery of schooling, juvenile *Pristipomoides filamentosus* in mesophotic *Halimeda* beds is important novel information for bottomfish stock researchers and managers.

In Chapter 4, BRUVS surveys across the Hawaiian Archipelago found substantial predator assemblage dissimilarities between the MHI and NWHI, with large shifts in abundance and richness metrics along depth gradients. Regional patterns (i.e. NWHI – MHI differences) derived from BRUVS were generally consistent with those previously recorded by divers. However, comparative analyses of NWHI:MHI predator abundance ratios (Chapter 5) found RUVS and BRUVS ratios to be much lower than those derived from diver-based visual censuses, suggesting that data gathered by divers may be subject to behavioral or methodological inflation biases. In addition, this further undermines the concept of inverted biomass or trophic pyramids on remote coral reefs (Friedlander and DeMartini 2002; Sandin et al. 2008b).

Rather than recycling information described in previous chapters, the general discussion elaborates on a subset of key findings, expands on 'next steps' for future methodological and ecological research in Hawaii and the US Pacific Territories, and considers limitations of the survey approaches used in this thesis.

Methodological evaluation of remote underwater video sampling

As detailed in Chapter 2, the collection of video data has several advantages in comparison with other underwater visual assessment methods. Both RUVS and BRUVS are fishery-independent (i.e. non-extractive), non-invasive, replicable, generate permanent video records available for future researchers, and are logistically simple to use when incorporating 'off the shelf' components. While 20-minute sampling intervals, using either RUVS or BRUVS, were effective at providing snapshots of overall functional group structure, BRUVS with longer soak times were better suited for assessing sessile macropiscivores (eels, which were rarely observed during RUVS surveys, but were frequently observed during BRUV surveys) and large-bodied coral reef roving predators (generalist macropiscivores),

particularly in the MHI where predators are generally depleted. However, while hour-long BRUVS surveys appear to be a superior approach in most regards - particularly as that also maximizes comparability with other BRUVS studies - there clearly can be cases where operational constraints or specific survey targets would justify alternative approaches.

An important benefit of using 60-minute BRUVS deployments is consistency with the majority of other stereo-video coral reef sampling programs around the Pacific. For example, previous research using 60-minute BRUVS focused on mesophotic depth refuges around Guam, the Commonwealth of the Northern Mariana Islands, and Micronesia, assessed the effectiveness of marine reserves and depth refuges for sharks and artisanal fisheries around Fiji and Indonesia, and compared shark population estimates against other assessment methods along the Great Barrier Reef (Goetze et al. 2011; Goetze and Fullwood 2013; Lindfield et al. 2014; Rizzari et al. 2014; Beer 2015; Lindfield et al. 2016). Lastly, with the increase of multiregional, cross-border ecosystem and population assessments using 60-minute BRUVS deployments focusing on vulnerable groups (e.g. Global FinPrint elasmobranch project (https://globalfinprint.org/) the NOAA PIFSC might continue collecting hour-long BRUVS data, but limit annotation to species sets aligned with those collected by cooperative projects and/or management directives, or in cases where funding is limited. Aside from the benefits of reduced processing times for target species subsets, videos would also be available for functional group and assemblage analysis at a later date (Goetze et al. 2015; Misa et al. 2016).

To the extent that sufficient resources are available, future remote video research in the Hawaiian Archipelago should default to using 60-minute BRUVS surveys, which would build on the MHI and NWHI research presented in this thesis. One particular gap would be to extend BRUVS sampling to islands in the Hawaiian Archipelago not covered in this work, with additional BRUVS assessments around previously sampled areas providing the basis for long-term monitoring of Hawaiian reef fish assemblages and target species.

Comparisons between diver and video-based predator sampling

There have been several studies between BRUVS and diver-based surveys, including suitability comparisons for assessing reef fish abundance, richness, and taxonomic diversity; however, there are inconsistencies among the reported results. While some diversity measures were apparently better quantified using BRUVS than diver-based visual surveys (Willis and Babcock 2000a; Willis et al. 2000b; Watson et al. 2005), other studies have shown the opposite, with diver-surveys recording higher reef fish diversity over BRUVS (Stobart et al. 2007; Colton and Swearer 2010). Critical assessment of, and methodological/ecological comparisons among survey methods (as is reported on in Chapters 2 and 5), is clearly important for large-scale monitoring and assessment programs such as those conducted by the NOAA PIFSC. In addition to the work described here, NOAA PIFSC staff will continue to compare visual-based assessments in the future, e.g. diver visual survey data gathered on open-circuit SCUBA with data gathered by divers using closed-circuit rebreathers (Gray et al. 2016).

One similarity between RUVS and BRUVS versus diver-based censuses of predators, as described in Chapter 5, was that several species were observed in both video sampling methods, but not in any diver-

based methods. These included predators observed only in mesophotic depths (e.g. *Seriola lalandi*, *Carcharhinus plumbeus*), and *Galeocerdo cuvier*. The blacktip shark (*Carcharhinus limbatus*) was also recorded outside of 1-hour sampling periods by both RUVS and BRUVS, and the only blacktip reef shark (*Carcharhinus melanopterus*) sighted by any methods was by BRUVS, even though diver SPC and towed-diver surveys had many more samples spread over a wider time period. Overall, video sampling obtains more complete estimates of roving predator species, being able to access depths beyond those diver-based surveys are constrained to.

Unsurprisingly, NWHI:MHI roving predator ratios derived from diver SPC surveys appeared to be inflated, likely as a byproduct of some combination of predator attraction to divers in the NWHI (and over-counting of highly mobile species in fixed area surveys, e.g. with large groups of *Caranx ignobilis*), and diver avoidance in the MHI. Ecological outcomes from Chapter 5, including a discussion of predator estimate inflation and inverted biomass pyramids, are considered in greater detail in "Re-examination of inverted biomass pyramids and predator estimates".

One important extension of the methods comparison work presented here will be to extend it to other parts of the US Pacific. Comparative datasets already exist for a number of locations, including the populated islands of Guam and Tutuila (American Samoa), and the remote Jarvis Island in the US Line Islands. There are also sufficient data for more comprehensive shallow water methods comparisons – between diver SPC, RUVS, and BRUVS - focusing on assemblage, functional group, and target species abundance/richness measures in order to better understand methodological similarities, strengths, and weaknesses analogous to those examined in other works.

Outcomes of ecological research

Chapter 3 considers how assemblage and functional group compositions in the MHI change from shallow to mesophotic depths, and provides evidence of depth-based shifts to endemic communities, and the potential for mesophotic habitats to be depth refuges for several fishery-targeted species. Chapter 4 examines differences in roving, generalist macropiscivores assemblages between the populated MHI and remote NWHI, and provides evidence of clear differences between those two sub-regions and among depth zones. Habitat complexity, depth, and percent cover of unconsolidated sediment and macroalgae were found to be the principal environmental variables structuring reef fish assemblages in the MHI (Chapter 3), but clearly there are a variety of other potential environmental co-contributors, including temperature, reef slope, hydrodynamics, and sedimentation that can also affect the distribution of reef fishes in both shallow and mesophotic depths (Locker et al. 2010; Kahng et al. 2014), and which remain a focus for future investigation.

Several issues bearing additional scrutiny are highlighted below.

Holistic benthic habitat sampling and depth expansion of stock assessments

The surveys conducted for this thesis originally targeted hard-bottom habitats in shallow and mesophotic depths; however, Main Hawaiian Islands Multibeam Bathymetry and Backscatter data (http://www.soest.hawaii.edu/HMRG/multibeam/) were either incomplete or absent, particularly for large portions of the Maui-Nui area in the MHI. As a result, mesophotic MHI BRUVS deployments often landed on sand flats (i.e. seemingly bare, unconsolidated sediment cover or macroalgae beds). Results from Chapter 3 revealed these areas to be occupied primarily by mobile invertivores and generalist macropiscivores, including several targeted predatory species (e.g. *Caranx melampygus*, *Caranx ignobilis*, *Aprion virescens*) that were assessed in recent reef fish stock assessment publications (Nadon et al. 2015; Nadon 2017). In addition, juvenile opakapaka (*Pristipomoides filamentosis*), a commercially important Hawaiian bottom fish species, were also recorded by BRUVS in *Halimeda* beds in the Maui-Nui region. These represent the first recognized detection of juveniles in these habitats, with the only other sightings documented in sand flats in 65 – 100 m off eastern Oahu, 37 – 42 m off of Waikiki in southern Oahu (Moffitt and Parrish 1996; Moffitt 2006; Misa et al. 2013; Richards et al. 2016), and more recently over basaltic lava flows between 80 – 120 m near the eastern city of Hilo, Hawaii (Drazen, unpublished data). As such, juvenile bottom fish life cycles and habitat associations are largely unknown in Hawaii, and the discovery of a potentially important Maui-Nui juvenile habitat may lead to increased research and management focus on those areas.

As a parallel example outside of Hawaii, Lindfield *et al.* (2014 and 2016) targeted coral reefs and affiliated hard-bottom substrates, deploying BRUVS along the northwest, north, and northeast coastlines of Guam while investigating refuge areas for fishery-targeted species. Conversely, Guam sampling was limited to 32 m and shallower, as a result of deeper benthic substrates being predominantly composed of sand (which were excluded from analysis), and because small-boat resources didn't allow for a wider area of operation that could have encompassed deeper hard-bottom habitats (Lindfield et al. 2014; Lindfield et al. 2016). However, BRUV surveys conducted during the NOAA 2014 Guam Insular Reef Fish Project encountered 1.) Mesophotic coral reef ecosystems down to 100 m, in areas that had never previously been surveyed (e.g. Pati Point, Cocos Island), and where several shark species (*Carcharhinus amblyrhynchos*, *Triaenodon obesus*, *Carcharhinus albimarginatus*, *Galeocerdo cuvier*) were regularly encountered. 2.) The presence of fishery-targeted species at mesophotic sand flat sites, particularly large-bodied Carangidae (*Caranx melampygus*, *Carangoides orthogrammus*) and Lethrinidae (e.g. *Lethrinus amboinensis*, *Lethrinus obsoletus*).

The Magnuson Stevens Act requires NOAA and partners to generate coral reef fish stock assessments in the Hawaiian Archipelago and US Pacific Territories. As a result, the first Hawaiian inshore reef fish target species assessments were conducted based on fish length distributions from diver surveys and fishery data, and was subsequently published in Nadon *et al*. (2015 and 2017). While data gathered by divers was used for most species, the analysis of a subset of species in the MHI (e.g. *Naso hexacanthus*, *Carangoides orthogrammus*, *Caranx ignobilis*, *Mulloidichthys pfluegeri*, *Seriola dumerili*) relied exclusively on length estimates obtained from commercial catch data, as there were insufficient diver observations in the visual survey datasets (Nadon et al. 2015; Nadon 2017). Consequently, limitations

include depth-constraints assigned to data gathered by divers from the upper 30m of species' ranges only, and that catch data does provide any information on the depths fishes are harvested from. As presented in Chapters 3 and 4, remote video surveys showed that many of the species assessed were encountered in higher abundances and/or at larger sizes in mesophotic depths, signaling possible refugia effects.

Outside of Hawaii, stock assessments of coral reef fishes in the US Pacific Territories (Guam, the Commonwealth of the Mariana Islands, American Samoa, and the Pacific Remote Island Areas) have so far been almost entirely unaddressed, in comparison with their pelagic counterparts, even as coral reef fisheries provide important economic and sociographic inputs to these regions (Sadovy and Domeier 2005; Houk et al. 2012; Weijerman et al. 2016). While future stock assessments may remain heavily-reliant on diver-based visual censuses $\leq$ 30 m in these regions, the addition and/or expansion of BRUVS surveys would provide a length-frequency data source to compliment those already collected during diver-based surveys (Lindfield et al. 2014; Williams et al. 2015), along with expanding sampling domains to include a wide variety of mesophotic habitats where target species are not only present, but where in many cases the bulk of their populations may be found. This would represent a shift analogous to BotCam and MOUSS sampling efforts (which targets both hard and soft-bottom habitats) conducted by bottom fish researchers (Misa et al. 2013; Moore et al. 2013; Richards et al. 2016), rather than exclusively targeting shallow water and mesophotic hard-bottom substrates. As such, there appears to be substantial amounts of mesophotic hard and/or soft-bottom habitats around Guam, the CNMI, and American Samoa that remain poorly understood, and are almost certainly host to important populations of target species, justifying the expansion of BRUVS research to support more effective reef fish stock management. In conclusion, a combined research assessment and monitoring approach using diver-based and BRUVS surveys, creel and commercial fisheries data, and market-based catch inventories may be required in order to support more effective, holistic management of coral reef fish stocks in the face of increasing fishing pressures (Lindfield et al. 2014; Zeller et al. 2015; Lindfield et al. 2016; Weijerman et al. 2016).

Re-examination of inverted biomass pyramids

So called 'inverted biomass pyramids', whereby predator biomass exceeds that of lower trophic levels, have been reported at a number of predator-dominated, remote coral reef areas, e.g. the NWHI, Palmyra Atoll, and Kingman Reef (Friedlander and DeMartini 2002; DeMartini et al. 2008; Sandin et al. 2008b). The basis for inverted biomass pyramids in remote coral reef ecosystems, and much of the research to date comparing remote, predator-heavy locations, has relied on data gathered primarily by open circuit SCUBA divers in $\leq$ 30 m using belt or point count underwater visual surveys. Results presented in Chapter 5 indicate that those survey approaches tend to exaggerate differences between remote and populated areas, presumably due to a combination of predator attraction to divers in remote areas and avoidance in populated areas.

Other studies, based on towed-diver and mark-and-recapture data, have similarly questioned the validity of inverted biomass pyramids in remote coral reef ecosystems (Nadon et al. 2012; Bradley et al. 2017). Short lived inverted pyramids remain feasible under certain conditions, e.g. through energetic

subsidies generated via the interception and consumption of allochthonous resources, production pulses in lower trophic levels, or during spawning events (Polis et al. 1997; Rowden et al. 2010; Mourier et al. 2016; Simpfendorfer and Heupel 2016; Trebilco et al. 2016). However spurious, and inflated biomass estimates in remote areas, particularly those generated by small-scale diver surveys at the core of inverted pyramids, are more symptomatic of: a.) Fish behavioral biases, predator mobbing or attraction in remote areas. In the NWHI, a comparable example occurs with large predator groups trailing Hawaiian monk seals as "foraging escorts" (Parrish et al. 2008). Divers in other predator-heavy, remote areas (e.g. US Pacific Remote Islands) may conceivably also attract sharks, jacks and snapper out of simple curiosity, as divers are rarely encountered in these environments; and b) Methodological predator "over counts", as a byproduct of non-instantaneous tallies of highly mobile species within small, fixed sampling areas (Ward-Paige et al. 2010a; Pais and Cabral 2017).

Inverted biomass pyramids weren't a primary focus in this thesis, and all methods consistently placed NWHI predator populations higher than those in the MHI. However, the biases listed above have very likely contributed to the disproportionately large predator NWHI:MHI ratios generated by divers in small area surveys in Chapter 5. In particular *Caranx ignobilis* was: a.) The most numerically dominant, large-bodied roving predator in the NWHI (Friedlander and DeMartini 2002; Friedlander and Dalzell 2004); and b.) recorded NWHI:MHI abundance ratios that were more than two orders of magnitude higher in small-scale diver surveys (SPC) than the next highest difference (towed-diver). For the combined reef sharks group, SPC NWH:MHI ratios were again the highest of any method compared, although the SPC NWHI:MHI ratio was only twice that derived from towed-diver surveys. It is worth noting that this trend was not entirely consistent among species, e.g. *Caranx melampygus* and *Aprion virescens* ratios were relatively close for SPC, BRUVS, and RUVS, with the outlier method being towed-diver surveys. This was likely in part due to towed divers only recording fishes > 50cm, and therefore missing portions of their populations.

Finally, the scales of NWHI:MHI ratios between RUVS and BRUVS were consistently quite close to each other, and much closer than to either diver method. Thus it appears that the use of bait didn't change overall patterns between areas with relatively high and relative low predator densities. While this topic certainly highlights the apparently strong likelihood of over inflation by diver-based surveys of roving predator differences between remote and populated areas, additional research is merited across other predator dominant versus depauperate environments, as studies in other regions have concluded that diver surveys can be suitable for shark assessments (McCauley et al. 2012; Rizzari et al. 2014). Predator behavioral biases associated with each method might be also further evaluated through complex modeling (e.g. movement algorithms incorporating predator behavioral traits and the presence of SPC divers or underwater video equipment). By modeling predator behavior, it may be possible - albeit difficult - to tease out biases associated with detectability and non-instantaneous sampling which could be used to calculate conversion factors for past, present, and/or future camera or diver-based surveys (Pais and Cabral 2017).

Continued methodological research and development

MaxN vs. MeanCount

The MaxN metric is variously labeled as N_{Max}, mincount, *Maxsna*, or MaxNO in other works and remains the standard for measuring the relative abundance of insular reef fish and roving predators with BRUVS (Ellis and Demartini 1995; Willis and Babcock 2000a; Willis et al. 2000b; Cappo et al. 2003; Cappo et al. 2006b; Gledhill et al. 2006; Stoner et al. 2008; Langlois et al. 2010). However, some concerns include that MaxN can be nonlinearly related to true abundance, providing increasingly dampened estimates of abundance with increasing true abundance, which can result in positively biased indices of abundance for declining fish stocks, or negatively based abundance indices when stocks are increasing (Schobernd et al. 2014). Also, because MaxN has been shown to be a conservative index, it may not be an optimal method for tracking changes in fish abundance within marine protected areas (Cappo et al. 2003; Stobart et al. 2015). Finally, MaxN may be not properly representative of a fish assemblage, as "the bias of MaxN depends on abundance, schooling behavior, and movement patterns of focal species" (Schobernd et al. 2014).

One alternative to MaxN is *MeanCount*, which is defined as "the mean number of fish observed in a series of randomized (or possibly systemic, e.g. every 30 seconds) snapshots over a viewing interval" (Schobernd et al. 2014). Similar to instantaneous counts used by SPC divers, a possible advantage of this method is that simulation tests showed that MeanCount tracked linearly to true abundance, versus MaxN which progressively underrepresented changes to true abundance at higher abundance levels (Schobernd et al. 2014). Further, variability of MeanCount and MaxN estimates are similar, and tend to be highly correlated (Schobernd et al. 2014; Ayotte et al. 2015b; Campbell et al. 2015). Conversely, MeanCount has its own inherent drawbacks. A performance comparison of MaxN and MeanCount using a delta lognormal model of relative indices of abundance demonstrated a high correspondence, with little change in the information content between indices (Campbell et al. 2015). However: a.) MeanCount inflated the number of zero observations; and b.) appeared to underestimate abundance in comparison with MaxN, with higher MeanCount intervals resulting in greater underestimation, particularly for highly mobile species. Use of MeanCount also increased the risk of missing rarer species, as not every frame is analyzed (Schobernd et al. 2014; Campbell et al. 2015).

A planned extension of this thesis work, particularly in comparison with the RUV and BRUV analyses presented in Chapter 5, will assess the relative utility and degree of comparability between MaxN and MeanCount for quantifying sharks, jacks, and snappers in areas of known low (i.e. MHI) and high densities (NWHI).

Progression in video technologies

A BRUVS analogue that has been recently developed by the NOAA PIFSC is the 'Modular Optical Underwater Survey System' (MOUSS). The MOUSS systems is a technical upgrade on the BotCam system that was previously used to assess commercially valuable bottom fish populations between 100 - 300 m in the MHI (Merritt 2005; Merritt et al. 2011; Misa 2012; Misa et al. 2016; Richards et al. 2016). While

the MOUSS can be an effective tool for collecting bottom fish data, it is less suited to shallower surveys (e.g. < 30 m) because of: 1.) High per-unit costs and a large footprints which means they cannot be easily be deployed from small boats; 2.) in its current configuration, cameras hover ~ 3 – 4 m above the seabed. While this height is ideal for targeting benthopelagic eteline snappers, this makes them more prone to waves/swells than BRUV units deployed on the bottom, and also moves the camera field of view above the area close to the reef, where the majority of demersal coral reef fishes will tend to remain; and 3.), as they are tailored for very low light environments in deep water, MOUSS video imagery is only collected in black and white.

Underwater video sampling technologies have become increasingly miniaturized, with off-the-shelf components allowing for higher image quality in ambient low-light environments. While existing MOUSS units could be reconfigured to collect color-based video data and modified to directly sample benthic environments (i.e. direct contact with the seabed), the availability of inexpensive, replaceable, and easy-to-fabricate BRUVS systems provides a viable alternative for shallow water and mesophotic research, and one that is increasingly used globally for reef fish research, monitoring, and stock assessments (Letessier et al. 2013; Letessier et al. 2015; Jaiteh et al. 2016). The inclusion of smaller, cheaper BRUVS systems would therefore compliment future coral reef ecosystem research in Hawaii and the US Pacific Territories.

Finally, two BRUVS drawbacks include unidirectional fields of view, and annotation time as previously described. Alternative methods, including rotating underwater survey systems (e.g. STAVIRO or other rotating video arrays), 360^{o} video sampling, and automated image analysis (as is being explored for large-bodied species) have potential to improve the suitability and feasibility of remote video surveys (Costa et al. 2006; Pelletier et al. 2011; Shortis et al. 2013; Mallet et al. 2014; Koenig and Stallings 2015; Ravanbakhsh et al. 2015; Shortis et al. 2016; Starr et al. 2016).

Thesis limitations

The overall geographic focus of this thesis in the Hawaiian Archipelago was partially driven by resource availability (NOAA research vessels and small boats) and affiliated subsidy sources for participating staff, consumables, and field equipment. Given the challenges assigned to accessing hard-to-reach areas in the MHI (e.g. Maui-Nui area) and the NWHI, RUVS and BRUVS sampling designs and field execution were constrained by a.) NOAA research vessels hosting multiple teams and simultaneous mission profiles conducted over long distances (i.e. limited day-to-day area retention); and b.) Larger mission goals that did not provide scope for high-density sampling in smaller areas.

The comparisons of functional group (Chapter 3) and roving predator (Chapter 4) structure from shallow to mesophotic depth gradients were limited to seasonal windows based on NOAA research vessel availability, with all operations occurring during daylight hours. Future BRUVS sampling conducted from NOAA platforms will likely remain dependent on mission prioritization and resource availability, with shallow water night-time surveys in remaining out of bounds due to safety considerations. Currently, assessments of nocturnal coral reef fish populations is not a priority within the NOAA PIFSC; however, one principal benefit from the addition of night time surveys would be a more holistic examination of

habitat use by coral reef fishes, including those that may be of management concern. Comparative examples include the migration of snappers from coral reef refuges to seagrass foraging areas, shifts in nocturnal reef fish assemblages and functional groups versus their daytime counterparts, and increased nighttime movements of some predator species in Hawaiian Marine Life Conservation Districts (Harvey et al. 2012a; Filous et al. 2017; Hammerschlag et al. 2017).

Additional thesis considerations included limited funding streams for video annotation, which were partially mitigated through the use of internships (e.g. NOAA Pacific Young Scientist Opportunity) and volunteers (e.g. NOAA PIFSC CREP fish team scientists, NOAA PIFSC Scientific Operations Team and Stock Assessment technicians). Given considerable time-lags between video annotation and analysis versus possible funding constraints, the selection of reef fish species subsets, e.g. fishery targeted species, would significantly reduce the time needed to process videos, with archives available for later analysis.

Concluding thoughts

The use of BRUVS provides a robust and replicable ecosystem sampling approach across a wide depth range, and has the potential to provide data applicable to ecosystem and stock assessment management priorities in Hawaii and the US Pacific Territories. While thesis results provide insights useful to scientists and environmental managers in Hawaii, it is important to emphasize that this is the first such work in the region, with value in extending and continuing this work. Additional, rigorous methods comparisons between diver and baited stereo-video surveys, contrasts between MaxN and MeanCount abundance metrics, expansion of mesophotic research into other parts of the US Pacific using BRUVS and other approaches (e.g. diver CCR censuses), and a renewed focus on predator-dominated ecosystems remain of high research interest in order to foster better a understanding and preservation of global coral reef biodiversity.

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