

Does Depth Confer Protection? An Assessment of Mesophotic Reefs in Hawai'i as Fishing and Climate Change Refugia



Photo by B. Zygliczynski 2018

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Does Depth Confer Protection? An Assessment of Mesophotic Reefs in Hawai‘i as Fishing and Climate Refugia

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Cover Photo: Divers collect fish and benthic data on West Hawaii mesophotic reefs. (Photo by B. Zgliczynski).

1.0 Executive Summary

Coral reef habitat often extends deeper than the limit to which most scientific studies have been conducted, and relatively little is known about the importance of these deep reef communities to shallow-water fisheries and coral populations. Recent studies in Hawai‘i suggest fishing has caused decreases in the size and abundance of targeted species, raising legitimate concerns that several shallow-water fish species have been overfished. And mass coral bleaching events in 2014 and 2015 have severely reduced coral cover in shallow reef areas at many sites across Hawai‘i and highlighted the importance of identifying reef areas that may be more resilient to climate change impacts.

In Hawai‘i, mesophotic reefs lie sufficiently deep (>30 m) that fishing pressure is likely greatly reduced compared to their shallow-water counterparts. Mesophotic reefs may therefore act as a refuge for species heavily targeted in Hawai‘i, and could be an important source population for replenishing depleted shallow-water fisheries, either directly through migration up the reef slope (*e.g.*, adult spillover) or through heightened recruitment from deep-water populations (*e.g.*, larval spillover). Similarly, mesophotic reefs may provide cooler and more stable water for coral populations, decreasing the likelihood and severity of bleaching events and protecting a source population that could replenish shallow water coral populations through larval spillover. Improving our knowledge of the role deep reefs play in supporting shallow-water assemblages is critical to sustainable reef management.

For this study, The Nature Conservancy partnered with Scripps Institution of Oceanography, NOAA Pacific Islands Fisheries Science Center, and the State of Hawai‘i Division of Aquatic Resources to collect biological information from mesophotic reefs to assess their significance as refugia and their potential vulnerability to climate change stressors. Divers used advanced diving technologies in the form of closed-circuit rebreathers to survey 32 reef sites at four depths (10 m, 20 m, 30 m, and 60 m) on the reefs along the west coast of Hawai‘i Island (West Hawai‘i). Survey sites were located within and outside of existing fishery management areas. At all depths, data were collected on fish abundance and biomass using visual census techniques, benthic cover and topography via large image analysis, and water temperature via automated data logging sensors.

Reef fish assemblages at 60 m had significantly lower biomass and richness, and different trophic structure and species composition compared to shallower sites. The mesophotic fish assemblage was more carnivore-dominated than its shallow-water counterpart, and 20% of the species present at 60 m did not occur at shallower sites, but had been observed on deeper reefs elsewhere in Hawai‘i. These differences in assemblage structure were consistent with increases in unconsolidated sediment and turf-covered hard bottom at depth, which likely contributed to a reduction in topographic relief. No difference was found between the fishery management strategies.

While we did not find compelling evidence that mesophotic reefs were significant refugia from fishing, they may provide some small benefits. Apex predator biomass was higher at deep compared to shallow sites, though was still low compared to shallow-water remote areas with little or no fishing. Likewise, relatively high overlap in species composition between mesophotic

and shallow-water fish assemblages suggest the potential for deep reefs to serve as a general refuge, although the abundance and biomass at depth were significantly lower than on shallow-water reefs, raising concerns about the ability of mesophotic fish assemblages to serve as significant source populations for larval production or post-settlement immigration into shallow-water reef areas.

Hard corals, and to a lesser extent, crustose coralline algae, are the primary structure builders creating topographic relief on Hawaiian reefs. Coral cover was highest at 20 m, and declined with increasing depth. The presence of coral at a site also became more variable at the deepest sites. While coral was found at all 10 m, 20 m, and 30 m sites, coral was absent at 41% of the 60 m sites, and no 60 m site had cover >1%. Though the three shallower depths had similar coral assemblages, *Porites lobata* was the only shallow-water species to extend into mesophotic depths, where most corals were deep-water species.

Temperature depth profiles showed the average water temperature at 60 m was significantly colder and more variable than at shallower sites. Mean temperature maximums tended to be similar across depths while temperature minimums decreased linearly with depth.

While environmental conditions at depth appear to be conducive to reduced coral bleaching, our data suggest deep reefs are not likely to be effective refugia for climate change in West Hawai‘i. Lack of common species across the depth range and the low cover of coral when present at 60 m, raise questions about the ability of this assemblage to serve as a significant larval source to reseed shallow reef areas. While the 30 m benthic assemblage appears to have fewer biological obstacles to serve as a refugia, the thermal conditions at this depth were not significantly different from those at 10 m. The 30 m assemblages may benefit from slightly lower thermal stress than shallower ones and therefore provide some refuge benefit, but this may not be sufficient to offset a serious and/or prolonged thermal event or long-term temperature increases expected under the current climate change trajectory. The study period did not encompass any shallow-water thermal stress events, so we were unable to empirically explore the temperature variation across depths during such an event.

Due to the challenges associated with visiting and collecting information at mesophotic depths, our understanding of mesophotic reefs, and especially their connectivity and importance to shallow-water coral reef ecosystems, is currently in its infancy. Assessing the adequacy of protection afforded to deep reefs is therefore difficult, but our data suggest that mesophotic ecosystems are sufficiently different from their shallow-water counterparts that they should receive special management attention. Current management of mesophotic ecosystems on West Hawai‘i appears to be primarily a collateral effect arising from the management of shallow-water ecosystems and/or specific fisheries, and is not an effort developed specifically with mesophotic ecosystems as their primary management target. Implementing effective management will likely require more information on the distribution, location, composition, and connectivity of mesophotic reefs to other deep-water ecosystems and their shallow-water counterparts. Hawai‘i’s “30 by 30” initiative presents a clear opportunity to develop and implement specific actions to protect and manage Hawai‘i’s mesophotic reefs.

2.0 Introduction

Scientific studies conducted on shallow-water (<30 m) coral reef fish assemblages and their habitat show that both are in a state of decline due to a number of anthropogenic impacts and management challenges (Pandolfi *et al.* 2003, Dulvy *et al.* 2004, Knowlton and Jackson 2008, Munday *et al.* 2008). However, fish habitat often extends deeper than the limit to which most scientific studies have been conducted, and thus relatively little is known about the importance of these deep reef communities to shallow-water fisheries that are often economically- and culturally-important to local communities in Hawai‘i.

In Hawai‘i, fishing is an important "way of life" and a culturally-significant activity for native Hawaiians. Many of the fisheries exploit predominately shallow-water reef fish populations via shore-based or in-water techniques (*e.g.*, spearfishing). Recent studies suggest fishing has caused decreases in the size and abundance of targeted species (Friedlander and DeMartini 2002, Williams *et al.* 2008, Friedlander *et al.* 2017), raising legitimate concerns that several are overfished (Nadon 2017). These declines have resulted in the introduction of the West Hawai‘i scuba spearfishing ban in 2013 and modifications of fishing regulations on Maui in 2014, and have served as important motivation for local communities to initiate community-led fisheries management through the State rule-making process.

Mesophotic coral reefs are coral communities in the deeper depths of the photic zone, typically between 30 and 150 meters in tropical and subtropical regions. This depth range falls below those typically accessed using conventional SCUBA, but above depths routinely explored by remotely operated vehicles (Pyle 1996, 2000). In Hawai‘i, mesophotic reefs lie sufficiently deep that impacts from anthropogenic stressors, such as fishing, are likely greatly reduced compared to their shallow-water (<30 m) counterparts. Mesophotic reefs may therefore act as a refuge for species heavily targeted in Hawai‘i, and could be an important source population for replenishing depleted shallow-water fisheries, either directly through migration up the reef slope (*e.g.*, adult spillover) or through heightened recruitment from deeper populations (*e.g.*, larval spillover). Improving our knowledge of the role deep reefs play in supporting shallow-water assemblages is critical to sustainable fisheries management. Understanding the structure and baseline condition of these areas is a high priority for fishing communities across Hawai‘i, as well as management agencies in the West Hawai‘i region. Due to their potential role as refugia, mesophotic reefs could also serve as reference areas to assess regional fishery management actions, such as the ban on SCUBA spearfishing along the west coast of Hawai‘i Island (West Hawai‘i) and the statewide ban on the use of small mesh nets. The large spatial extent of these bans makes it difficult to find appropriate shallow-water reference areas that would be helpful when assessing the effectiveness of management actions, but if mesophotic reefs have been a refuge from fishing, they could effectively fill this role.

In addition, mesophotic reefs may be more resistant to stressors associated with global climate change. Water temperatures on mesophotic reefs are cooler than shallow-water reefs and potentially less variable because atmospheric heat transfer and inputs of colder terrestrial freshwater are lower. As a result, ecosystem responses to climate change stressors, especially coral bleaching, could occur less frequently and/or with reduced severity. Anecdotal observations from closed circuit rebreather surveyors during the 2015 bleaching in West

Hawai‘i suggest deep reefs (≥ 30 m) experienced less bleaching than shallow ones, but rigorous quantitative data are not available. This higher resilience to climate stressors may result in higher quality habitat on mesophotic compared to shallow-water reefs in the future and may prove critical to achieving and maintaining sustainable ecosystem-based management for many economically and culturally important species.

During this study, The Nature Conservancy (TNC) partnered with Scripps Institution of Oceanography (SIO), NOAA Pacific Islands Fisheries Science Center, and the State of Hawai‘i Division of Aquatic Resources (DAR) to collect biological information from mesophotic reefs to assess their significance as refugia and their potential vulnerability to climate change stressors. We investigated the role of mesophotic reefs as refugia for species targeted by fishers and vulnerable to climate change impacts, and examined whether existing management actions were effectively incorporating mesophotic reefs into their strategies.

2.1 Problem Statement

Mesophotic reefs encompass almost two-thirds of the total depth range of coral reefs, yet remain largely unexplored (Pyle 2000, Feitoza *et al.* 2005). Mesophotic coral reefs likely have biological, physical and chemical connectivity with shallow-water reef ecosystems (Hinderstein *et al.* 2010), but the inter-relationship between these deep-water reefs and their shallow-water counterparts is still poorly understood, due to the logistical challenges of conducting work at mesophotic depths.

Large gaps in knowledge remain on fundamental aspects of mesophotic reef ecology, including patterns of community zonation, the role of natural and anthropogenic stressors in community change, and connectivity, both among mesophotic reefs areas and with their shallow-water counterparts. With the global decline of shallow-water coral reef environments, understanding the inter-relationships between mesophotic and shallow-water reefs has never been more urgent. Addressing these knowledge gaps to better inform management strategies is fundamental to coral reef conservation efforts globally.

Effective ecosystem-based management requires that the significant components of the ecosystem be explicitly considered and included in management efforts (Rooney *et al.* 2010). At present our knowledge of mesophotic reefs impairs the ability of managers to make adequately informed decisions about resource management, especially for shallow-water reef species targeted in the commercial and recreational fisheries.

3.0 Study Objectives

This study had four objectives:

- (1) Determine the potential of mesophotic reefs to act as refugia for fish species targeted by fishers, especially spearfishers;
- (2) Compare benthic structure (species composition and abundance) and the rate of coral bleaching between mesophotic and shallow-water reefs;
- (3) Examine the potential to use mesophotic reefs as a reference area for assessing the West Hawai'i SCUBA fishing ban, and;
- (4) Assess whether existing management strategies in West Hawai'i adequately protect mesophotic reefs.

4.0 Methods

For this project, divers used advanced diving technologies in the form of closed-circuit rebreathers (hereafter referred to as rebreathers). In recent decades, rebreathers have gained attention as a tool for conducting scientific research due to several advantages over traditional open-circuit SCUBA technologies. These advantages are particularly important for the extended range dive operations necessary to conduct work at mesophotic depths. First, rebreathers provide increased gas efficiency over open-circuit technologies by recycling the exhaled gas, removing carbon dioxide, and replacing metabolized oxygen in a closed loop system, thus reducing the amount of gas required during a dive. Second, rebreathers optimize no-decompression limits by reducing the amount of nitrogen in the breathing loop, thus reducing the risk of decompression sickness. In addition, the decompression risk for rebreathers can be further reduced by using combinations of mixed gases, such as Trimix. Third, because rebreathers are closed systems with few bubbles released, they are significantly quieter than typical of open-circuit technologies. This is particularly advantageous for conducting assessments of fishes where sound may affect their behavior (Lindfield *et al.* 2014).

Because rebreathers are considered advanced SCUBA technologies, their use requires specialized training before operation. For this project, all members of the research team completed the requisite training for the safe operation of rebreathers at these depths. All guidelines outlined by the American Academy of Underwater Sciences (AAUS) were followed. Data were collected for this project during two expeditions to West Hawai‘i, conducted between April 4-14, 2017 and the second the following year between April 12-29, 2018.

4.1 Locations and Sites

After consultation with DAR, we selected 32 sites under varied management strategies along the Kona Coast of Hawai‘i Island for surveys (Figure 1, Appendix 1). To maximize diving safety and survey efficiency we restricted site selection to steep slope areas where all depth strata could be surveyed during one dive with only a modest decompression obligation remaining following the completion of data collection. To work across a range of fishery management strategies, we initially selected sites in the vicinity of three Marine Life Conservation Districts (MLCDs: Waialea Bay, Old Kona Airport, and Kealakekua Bay) and three Fishery Replenishment Areas (FRAs: Puakō, Kīholo, and Ka‘ūpūlehu), but some of these sites did not have suitably steep slopes to be safely surveyed leading us to select new sites near the MLCD at Kealakekua Bay and seven FRAs at Puakō, Kaloko-Honokōhau, Red Hill, Honaunau, Kona Paradise, Ho‘okena, and Miloli‘i. The selected FRAs have been under restricted gear management (primarily restrictions on nets and harvesting of selected fish species) for over 15 years to promote sustainable fishing of species important in the live fish aquarium trade. A total of 16 sites over two years were surveyed within these management areas. Sixteen additional sites were selected in “open” areas where fishing was permitted under the general State and West Hawai‘i regulations (DAR 2016). Each site was surveyed once, except for four sites (Kona_07, Kona_11, Kona_13, Kona_15), which were surveyed both in 2017 and 2018 to facilitate the deployment and retrieval of sea temperature recorders (STR). The specific location of each

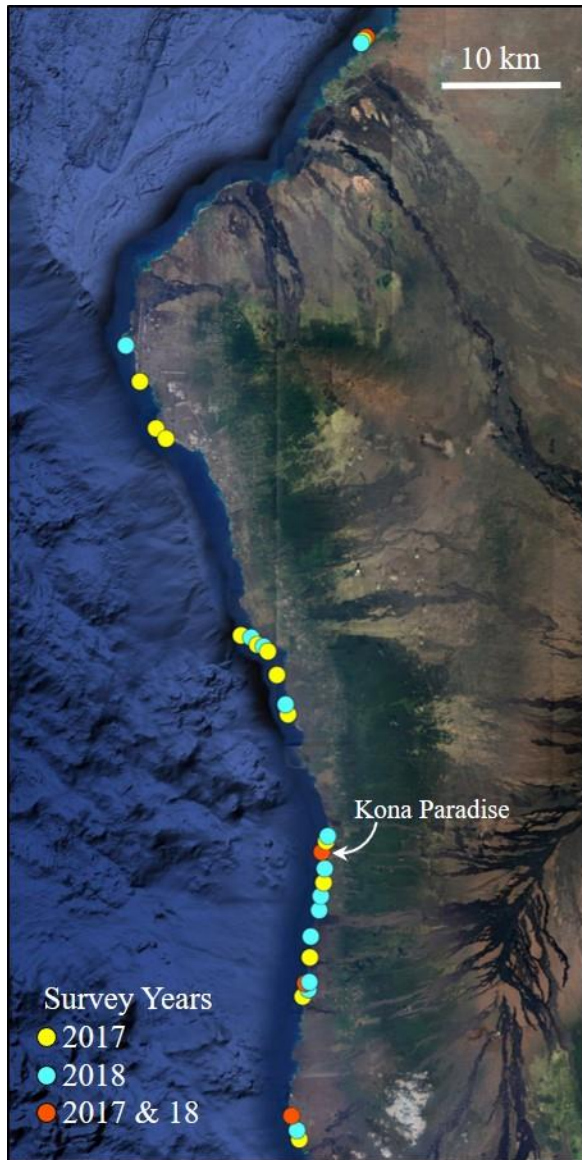


Figure 1. Sites surveyed in 2017, 2018 and both years. See Section 5.2 for a discussion of Kona_16 (Kona Paradise).

survey site within the different management areas was randomly generated using ArcGIS. At each site, transects at four discrete depth strata (10 m, 20 m, 30 m, and 60 m) were surveyed, with the deepest transect in the upper mesophotic reef zone.

4.2 Field Assessments

Boating Protocols

The survey team, comprised of five divers, navigated to each predetermined site using a Garmin GPS unit. Three divers were deployed and two remained onboard for diving safety precautions. Upon completion of the final transect (10 m), a member of the dive team deployed a surface buoy to mark the site location. The boat operator carefully navigated to the marker buoy and collected its coordinates using a handheld GPS.

Fish Surveys

Once on site, the three-member dive team descended directly to the deepest site (60 m), where divers established two transect start points approximately 5-10 m apart. From each start-point, a diver deployed a 25 m transect line along the depth contour, or along a predetermined compass heading if the bottom was flat. Transects were deployed parallel to each other.

All fish within or passing through a 5 m wide belt along each of the two transects were identified to species and sized into 5 cm bins (*i.e.*, 0-5 cm, >5-10 cm, >10-15 cm, etc.). Divers

moved slowly along the transects, usually taking between 8 and 12 minutes to complete each belt survey. All surveys were conducted by trained and calibrated divers with several years of experience employing this method.

Benthic Surveys

Information on the benthic composition, coral health, and topographic relief were collected using large-area imagery. Large-area imagery can be collected at a variety of spatial scales; for this study, we chose 2 x 25 m (50 m²) plots as the spatial sampling unit at each depth. Plots of this size were selected to ensure that sufficient benthic information was collected at each depth

without requiring significantly more time than required to conduct the fish surveys. Raw imagery was collected along the deeper of the two transects at each depth stratum and took approximately 20 minutes to complete.

Images were collected by a diver following directly behind the fish team along the deeper of the two transects. Imagery was collected using two Nikon D7000 16.2 megapixel DSLR still cameras mounted to a custom frame. The camera used to generate models was equipped with a wide-angle 18 mm focal length lens to ensure high overlap (>80%) among adjacent images. The second camera was equipped with a 55 mm focal length lens to capture images with ≤ 1 mm resolution to aid in ecological post-processing (Edwards *et al.* 2017). To obtain continuous coverage of the reef floor within the survey area, the diver operating the camera system would swim a swath on one side of the transect line, and then an overlapping swath focusing on the other side of the transect line on the way back to the transect origin. The diver would swim approximately 1.5 m above the benthos at a speed sufficient to maintain maximum overlap between adjacent images (5-7 m per min). Images were captured every second from each still camera using the built-in intervalometers, yielding approximately 600 individual images per camera per isobath. To provide scale and define the plane of projection for the resulting 3D model and orthoprojection, depth information was collected using three scale bars with depth gauges attached that were deployed inside the plot by the fish diver prior to imagery collection.

Technical Post-Processing of Raw Imagery

The first step in the generation of the orthoprojections was the creation of 3D point clouds from raw imagery. The details of the approach will not be addressed in detail here; they have been documented at length in previous publications (Fitzgibbon and Zisserman 1998, Burns *et al.* 2015, Naughton *et al.* 2015). Briefly, raw images were processed using the commercially available Structure-from-Motion (SfM) software Agisoft PhotoScan (Agisoft LLC., St. Petersburg, Russia). Agisoft was chosen as it is a comprehensively-evaluated and widely-used platform in both marine and terrestrial applications (Figueira *et al.* 2015, Nikolov and Madsen 2016). SfM determines point matches between multiple overlapping images to estimate camera positions, and the 3D locations of the points in the images are deduced through triangulation and refined by a process called bundle adjustment.

Ecological Post-processing of Large Imagery

Using the point cloud orthoprojections, a point-based visual identification approach was used to identify the benthic composition to the highest taxonomic resolution possible, usually to species. Working directly on the dense point cloud allowed the image analyst to rapidly reference to source images through an on-demand spot-view tool that provided access to all images used in the alignment of a given point in the model. This increased the analyst's ability to make detailed identifications with high confidence.

Topographic Relief

An index of rugosity was calculated using orthorectified and scaled 3D reconstruction along each transect area. Using the software program, Viscore, a profile of the three-dimensional

image was sliced along the transect area and the total length of the contour was measured. An index was calculated by dividing the length of the contour slice by the flat linear distance between the endpoints of the slice. For the resulting index, a value of one represents a flat surface with no topographic relief, and increasing values represent more topographically complex substratum.

Water Temperature and Oceanographic Data

Sea temperature recorders (STR) were deployed to collect oceanographic information on sea temperature fluctuations and the presence and frequency of internal waves. A STR was attached to the bottom at each depth at five survey sites (Kona_07, Kona_11, Kona_13, Kona_15, Kona_16) and one additional location (Kona_14 near Keahole Point) at which no biological surveys were conducted. Due to challenges during the 2018 dive at Kona_16, no biological surveys were conducted that year, but the STRs were successfully retrieved. The STRs collected temperature information every 15 minutes for four months (April 2017-August 2018).

4.3 Survey Design and Data Analysis

The survey design employed for this project had three factors:

- Depth: 10 m, 20 m, 30 m, and 60 m. The three shallowest depths lay within traditional scuba diving depths, while the deepest was within the upper mesophotic zone.
- Management strategy: Open and limited. Sites within “open” areas allow fishing under the current statewide and West Hawai‘i regulations (DAR 2016), which include a variety of species-specific size and take limits, seasonal closures, and gear restrictions. Sites within with “limited” management areas allow fishing under the current statewide and West Hawai‘i regulations, but with one or more additional restrictions (DAR 2016), *e.g.*, gear, species, or other take restrictions. In the West Hawai‘i area, most additional restrictions on fishing are associated with the live fish aquarium trade.
- Year: 2017 and 2018. Due to the time requirements to compile and process the photographic imagery, the collection of benthic information for 2018 was not completed in time for inclusion in this report.

For most analyses, species-level information was combined into higher taxonomic, trophic or other groupings, as relevant to address specific research questions. Trophic groupings for fish were based on a 5-level trophic designation and included: apex predators, piscivorous secondary consumers, non-piscivorous secondary consumers, planktivores, and herbivores. Target fish were comprised of several common fish species desirable for food, commercial activity, and/or cultural practices in Hawai‘i (see Williams *et al.* 2008) that were present within the survey area. A list of these species is available in Appendix 2. Benthic taxa were grouped into seven broad categories: hard coral, black coral, macroalgae, crustose coralline algae (CCA), turf, other biological organisms, and unconsolidated bottom. Group classifications for each benthic taxon appears in Appendix 3.

As appropriate, a multi-factor ANOVA or PEMANOVA was employed using depth, management strategy, and year (where appropriate) as factors. All factors were treated as

fixed. While four sites were visited in both 2017 and 2018, these repeated sites showed no temporal autocorrelation in total fish and target fish biomass, suggesting the spatial and temporal offset of the surveys were sufficient large to allow for these sites to be treated as independent in the analysis. Removing these four survey sites for one of the two sampling years also did not change the results. Prior to running an ANOVA, data were checked for normality and heteroscedasticity and transformed as needed (*i.e.*, fish biomass data were log+1 transformed). Any significant interaction term was investigated using graphical plots to assess the effect of the interaction on the interpretation of the individual factors. Variance partitioning of multivariate datasets was accomplished using redundancy analysis (RDA).

All analyses were conducted in R using the ‘vegan’ package (Oksanen *et al.* 2017). Final data were exported to Excel for graphing and figure generation. Follow-up PERMANOVA pairwise comparisons were conducted using the “pairwise.adonis()” function developed by Pedro Martinez Arbizu. All values are presented as mean \pm standard error of the mean (SEM) unless otherwise noted.

5.0 Results and Discussion

5.1 Mesophotic reefs as refugia for targeted fish species

Total fish and target fish biomass significantly declined with depth (Figure 2) and across survey years but showed no differences between management strategies (Table 1). The decline in fish biomass with depth was likely due to changes in habitat availability and quality, especially changes that caused a decrease in topographic relief. Fish biomass is generally correlated with benthic topography (Friedlander and Parrish 1998), and both total fish ($r=0.32$; $p=0.012$) and target fish ($r=0.24$; $p=0.050$) biomass were positively correlated with topographic relief in 2017. At all survey locations, topographic relief declined with depth, likely due to the decrease in the cover of structure-forming organisms such as coral, and a concurrent increase in unconsolidated substratum and hardbottom dominated by non-structure forming turf (see section 5.2).

The decline in fish biomass between survey years was expected; annual declines since 2015 have been observed on numerous West Hawai'i reefs (Minton *et al.* 2017a, 2018a, 2018b). The decline has been attributed primarily to the gradual “relaxation” of fish biomass following an unusually large fish recruitment event in 2014 (Talbot 2014) that resulted in a “spike” in fish abundance and biomass on West Hawai'i reefs (Minton *et al.* 2018a). However, our data suggest declines between survey years were not constant across depths; the magnitude of the decline in total fish biomass was smaller at deep compared to shallow sites (Figure 2). Two possible, non-exclusive explanations include: (1) the 2014 recruitment pulse occurred primarily in the shallow-water fish assemblage and elevated its biomass more relative to the deep-water fish assemblage, and/or (2) fish biomass has declined more quickly in shallow-water compared to deep-water fish assemblages.

Unfortunately, without pre-2014 data for the mesophotic fish assemblage, our study cannot provide much insight into the first potential explanation. Kane and Tissot (2017) conducted mesophotic surveys as deep as 50 m on West Hawai'i between 2013 and 2015, but their study did not examine annual changes in fish biomass, and they provided no annual biomass-by-depth breakdowns. However, their work may be able to provide the information necessary to better examine the effect of the 2014 fish recruitment event on the mesophotic fish assemblage. While our data do not provide definitive evidence to assess the second explanation, they have the potential to provide insight into the factors contributing to the magnitude of decline observed at the different depths, *i.e.*, fishing effects and changes in habitat quality. Unfortunately, the in-depth exploration necessary to address this question was beyond the scope of this effort.

Fish trophic structure also varied significantly across depth and between survey years (Table 2). The biomass of herbivores and, to a lesser extent, non-piscivorous secondary consumers declined with depth (Figure 3), whereas apex predator biomass appeared to increase. Biomass of piscivorous secondary consumers and planktivores showed no clear pattern, although planktivore biomass may be increasing with depth. Consistent with other findings in Hawai'i (Kosaki *et al.* 2012, Kahng 2014, Kane and Tissot 2017), the mesophotic fish assemblage at West Hawai'i is more carnivore-dominated than its shallow-water counterpart. This change in trophic structure is also consistent with changes in the composition of the substratum (see section 5.2).

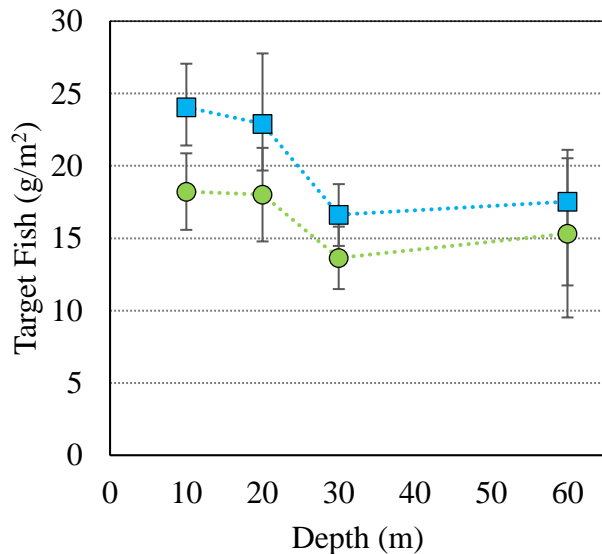
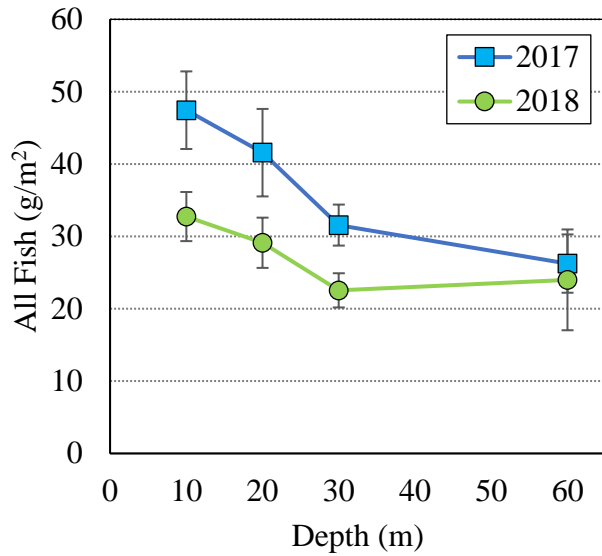


Figure 2. Total fish and target fish biomass by depth in 2017 and 2018.

Unconsolidated sediment increased with depth, replacing macroalgae and turf-covered hard bottom and causing a reduction in topographic relief. The observed changes in fish trophic structure would be consistent with a “flattened” reef and a shift in the composition of benthic primary producers.

While not statistically significant, data suggest that some differences in trophic structure may exist between management strategies. Unfortunately, no conclusions can be clearly drawn from our data, but they suggest sites in open areas may have slightly greater apex, herbivore, and secondary predator biomass than sites within areas with limited management (Figure 3). This trend is not consistent with other studies and is likely associated with differences in the benthic composition found between management strategies (see section 5.2), but additional information would be needed before drawing a robust conclusion.

A total of 156 taxa in 32 families were observed over the two years of surveys (Appendix 4). The fish assemblage showed a gradual change with depth, so while the 60 m fish assemblage was the least similar to those at shallower depths, all assemblages had a high degree of similarity (Table 3), suggesting considerable overlap in species composition and relative biomass. Similar

gradual changes in the fish assemblage have been observed elsewhere, including West Hawai‘i, where Kane and Tissot (2017) noted a 78% overlap in fish species between shallow and upper mesophotic reefs.

The majority of fish species occurred over a wide depth range (Appendix 4). Almost 40% of the taxa were observed at all survey depths, and 60% were observed at three of four survey depths. Only 27% of taxa were observed at a single depth, and most of these were “rare,” accounting for only a small percentage of the total fish biomass at that depth. Notable exceptions were *Abudefduf abdominalis* and *Kyphosus* sp. which were common at and restricted to 10 m, *Caranx ignobilis* at 30 m, and *Caranx lugubris* at 60 m. Of the 40 taxa that were observed at only one

Table 1. ANOVA results for the effect of depth (10 m, 20 m, 30 m, and 60 m), management strategy (open and limited), and survey year (2017 and 2018) on total fish and target fish biomass.

<i>Total Fish Biomass</i>	df	SS	F-value	p
Depth (d)	2	3.5164	11.1	<0.001
Management (m)	2	0.0568	0.2	0.836
Year (y)	1	1.5873	10.0	0.002
d*m	1	0.0589	0.4	0.544
d*y	1	0.1401	0.9	0.349
m*y	1	0.1011	0.6	0.426
d*m*y	1	0.0637	0.4	0.527
Residual	135	21.4199		

<i>Target Fish Biomass</i>	df	SS	F-value	p
Depth (d)	2	1.5040	6.3	0.002
Management (m)	2	0.0792	0.3	0.719
Year (y)	1	1.2738	10.6	0.001
d*m	1	0.0000	0.0	0.998
d*y	1	0.1217	1.0	0.315
m*y	1	0.0094	0.1	0.780
d*m*y	1	0.0690	0.6	0.449
Residual	135	16.1613		

Table 2. PERMANOVA results examining the effect of depth (10 m, 20 m, 30 m, and 60 m), management strategy (open and limited), and survey year (2017 and 2018) on the trophic structure of the fish assemblage.

<i>Trophic Structure</i>	df	SS	F-value	P
Depth (d)	1	3.954	13.1	0.005
Management (m)	1	0.429	1.4	0.075
Year (y)	1	1.749	12.5	0.005
d*m	1	0.272	0.9	0.632
d*y	1	0.366	1.2	0.179
m*y	1	0.267	0.9	0.632
d*m*y	1	0.312	1.0	0.433
Residual	135	40.761		

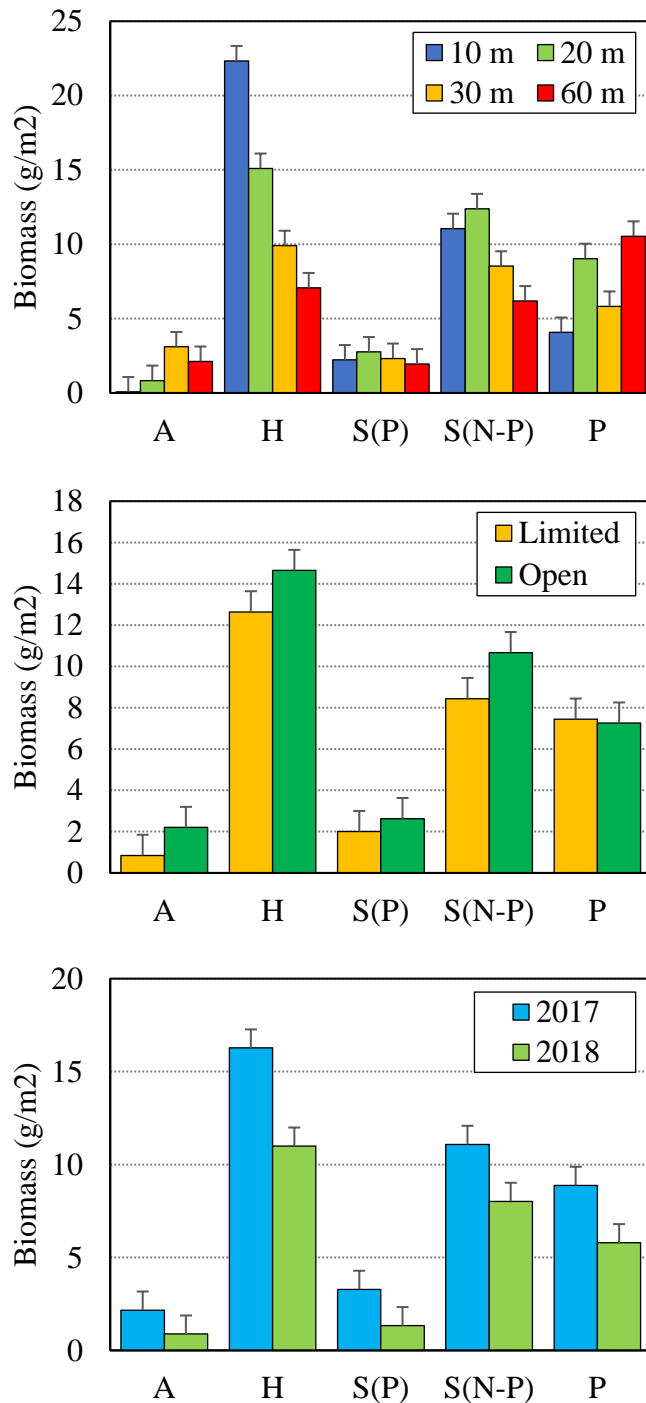


Figure 3. Biomass of five trophic groups by depth, management strategy and survey year. A=apex predators, H=herbivores, S(P)=piscivorous secondary consumers, S(N-P)=non-piscivorous secondary consumers, P=planktivores.

depth, 18 were observed only at 60 m, and represented taxa that have been observed in mesophotic assemblages elsewhere in Hawai'i (Pyle *et al.* 2016).

We found little evidence to support that deeper reefs on West Hawai'i are acting as refugia for fish from fishing pressure. In our survey design, evidence for a depth refugia would have appeared as a significant depth by management interaction, indicating that shallow-water fishing outside of the protected areas had resulted in lower fish populations compared to inside, but that this difference would have disappeared at mesophotic depths. Unfortunately, our study was complicated by lack of suitable survey sites in and near management areas that would have provided the best possible test of this hypothesis (*i.e.*, MLCDs). Except for a single site (Kealakekua Bay), all management areas included in this study allowed for some fishing to occur, and in some cases, placed only minor limitations on fishing effort or gear. Many of the protected areas on West Hawai'i were developed to manage the live fish aquarium trade, and other studies have shown that West Hawai'i areas with limited management (*i.e.*, FRAs) appear to provide few benefits to the fish assemblage as a whole or to those species targeted by non-aquarium trade fishers. The management areas in West Hawai'i have shown positive benefits for *Zebrasoma flavescens* (Williams *et al.* 2009). Looking specifically at this species, we found it occurred at all depths, but could detect no difference between management strategies (ANOVA, $F_{1,136}=1.72$, $p=0.191$) or evidence that mesophotic reefs provided a fishing refugia (ANOVA, $F_{3,136}=0.42$, $p=0.742$). Unfortunately, it is difficult to draw

Table 3. Similarity matrix (Bray-Curtis) among fish assemblages at 10, 20, 30, and 60 m. Values represent mean similarity across all sites and survey years.

	10 m	20 m	30 m	60 m
10 m	-			
20 m	72%	-		
30 m	65%	74%	-	
60 m	50%	59%	67%	-

conclusions from the single MLCD we were able to include in our study.

While we did not find compelling evidence that mesophotic reefs were significant refugia from fishing across all trophic groups, they may provide some benefits for certain species. Apex predator biomass was higher at deep (30 and 60 m) compared to shallow (10 and 20 m) sites. While *Caranx melampygus* was the only apex predator observed shallower than 30 m in these surveys, most other apex predators have previously been recorded from shallow reefs in Hawai‘i (Randall 2007, Pyle *et al.* 2016). However, even though apex predator biomass was higher at deep compared to shallow sites in West Hawai‘i, it was still low compared to areas with little or no fishing, *e.g.*, the Northwestern Hawaiian Islands (Friedlander and Demartini 2002, Minton *et al.* 2017b). Most of these species are prized by fishers and tend to have high mobility, allowing them to range onto shallow reefs where they are vulnerable to harvest. This high mobility would likely reduce any potential refuge benefits provided by mesophotic reefs.

Likewise, high similarity between mesophotic and shallow-water fish assemblages suggest the potential for deep reefs to serve as a general refugia. However, abundance (Kane and Tissot 2017) and biomass at depth are significantly lower than on shallow-water reefs, raising concerns about the ability of mesophotic fish assemblages to serve as significant source populations for larval production or post-settlement immigration into shallow-water reef areas.

5.2 Benthic structure and coral bleaching rates along depth gradients

Benthic structure significantly changed with depth and by management strategy (Table 4). The benthic structure at 60 m was different from that at 10 m and 20 m, mostly due to an increase in unconsolidated bottom at depth, and an associated decrease in structure-forming organisms

Table 4. PERMANOVA results examining the effect of depth (10 m, 20 m, 30 m, and 60 m), and management strategy (open and limited) on the benthic structure. Benthic data were available only for the 2017.

<i>Benthic Cover</i>	df	SS	F-value	P
Depth (d)	1	1.316	26.5	0.005
Management (m)	1	0.892	17.9	0.005
d*m	1	0.153	3.1	0.060
Residual	68	3.382		

(Figure 4). At 60 m sites, >40% of the bottom was composed of unconsolidated substratum (*i.e.*, sand and rubble), and 92% of the bottom was covered by sand, rubble, and “non-structure forming” turf. Topographic relief declined from 1.67 ± 0.08 to 1.29 ± 0.03 , indicating a flattening of the substratum, a phenomenon associated with decreased fish abundance and biomass (Alvarez-Filip *et al.* 2009).

Our analysis identified one unusual 60 m site: Kona_16, known locally as “Kona Paradise” (Figure 4). Unlike most deep reef sites, Kona Paradise had no unconsolidated bottom, and was dominated by CCA, turf, and the red algae *Peyssonnelia* spp. Kane and Tissot (2017), who conducted 50 m surveys in the same vicinity, specifically identified Kona Paradise as having high fish species richness relative to other deep reef locations. While our 60 m site at Kona Paradise did not have the highest species richness among our 60 m sites, it was well above the average for 60 m sites during both survey years.

Sites in areas open to fishing had significantly greater turf and less unconsolidated substratum, whereas coral and other biological organisms tended to have similar cover between the management strategies (Figure 5). The presence of similar cover of structure-forming organisms between management strategies, suggests that sites inside and outside areas with limited management likely had similar quality as habitat for most fish species, a conclusion supported by finding little difference in the fish assemblage structure between management strategies (see section 5.1).

These differences associated with depth and management strategies were potentially complicated by a (nearly) significant depth by management interaction. After examination of interaction plots (see Figure 5), this interaction did not appear to alter the interpretation of the general trends for either factor, but instead provided “nuance” to the differences in benthic structure across depths and management strategies. For example, cover of turf was similar between management strategies on shallow reefs (Figure 5), but diverged with depth so that turf cover on deep reefs was higher at sites open to fishing compared to those with limited management. Macroalgae cover was higher on shallow reef sites open to fishing than those with limited management but converged to a similar cover at depth.

Hard corals, and to a lesser extent, crustose coralline algae, are the primary structure builders creating topographic relief on Hawaiian reefs. Coral cover was highest at 20 m (Figure 5), where *Porites lobata* and *P. compressa* dominated the assemblage. Coral cover then declined with

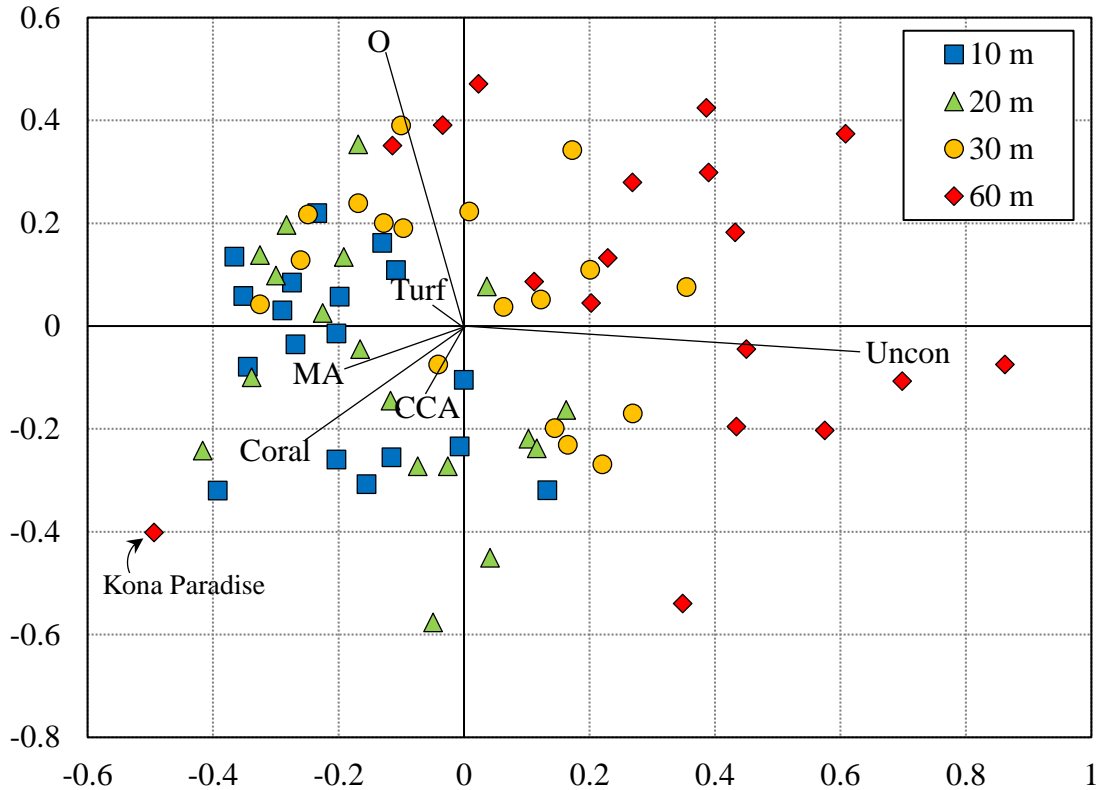


Figure 4. NMDS of benthic cover by groups for assemblages at 10 m, 20 m, 30 m, and 60 m depth on West Hawai‘i. MA = macroalgae, CCA = crustose coralline algae, Uncon = unconsolidated bottom, O = other benthic organisms. See text for discussion of Kona Paradise.

increasing depth, until total coral cover was <1% at 60 m. The presence of coral at a site also became more variable. At all 10 m, 20 m, and 30 m sites coral was present, even if the cover was low. In contrast, at 41% of the 60 m sites (7 of 17 sites) coral was entirely absent, and no site had cover >1%. While overall coral richness was similar at all depth, ranging from 5-7 species¹, average coral richness at a site declined with depth, dropping from 2.9 ± 0.3 coral species at 10 m to 1.9 ± 0.2 at 60 m (Figure 5). Species composition also changed with depth (Figure 6), with marked differences in the assemblage structure between shallow (10 m, 20 m, and 30 m) and deep (60 m) sites. Common shallow-water species such as *P. compressa*, *Montipora capitata*, and *M. patula*, gave way to corals more generally found at mesophotic depths, e.g., *Leptoseris* spp. and *Leptastrea* spp.

¹Collecting coral richness information from photographs generally underestimates true richness compared to *in situ* data collection. Unfortunately, *in situ* data is not yet practical at mesophotic depths. The amount of underestimation in photographs is generally positively correlated with topographic relief (*i.e.*, corals cannot be seen in photographs when occurring in holes or underneath ledges or other organisms), suggesting any underestimations here will be greater in shallow compared to deep communities.

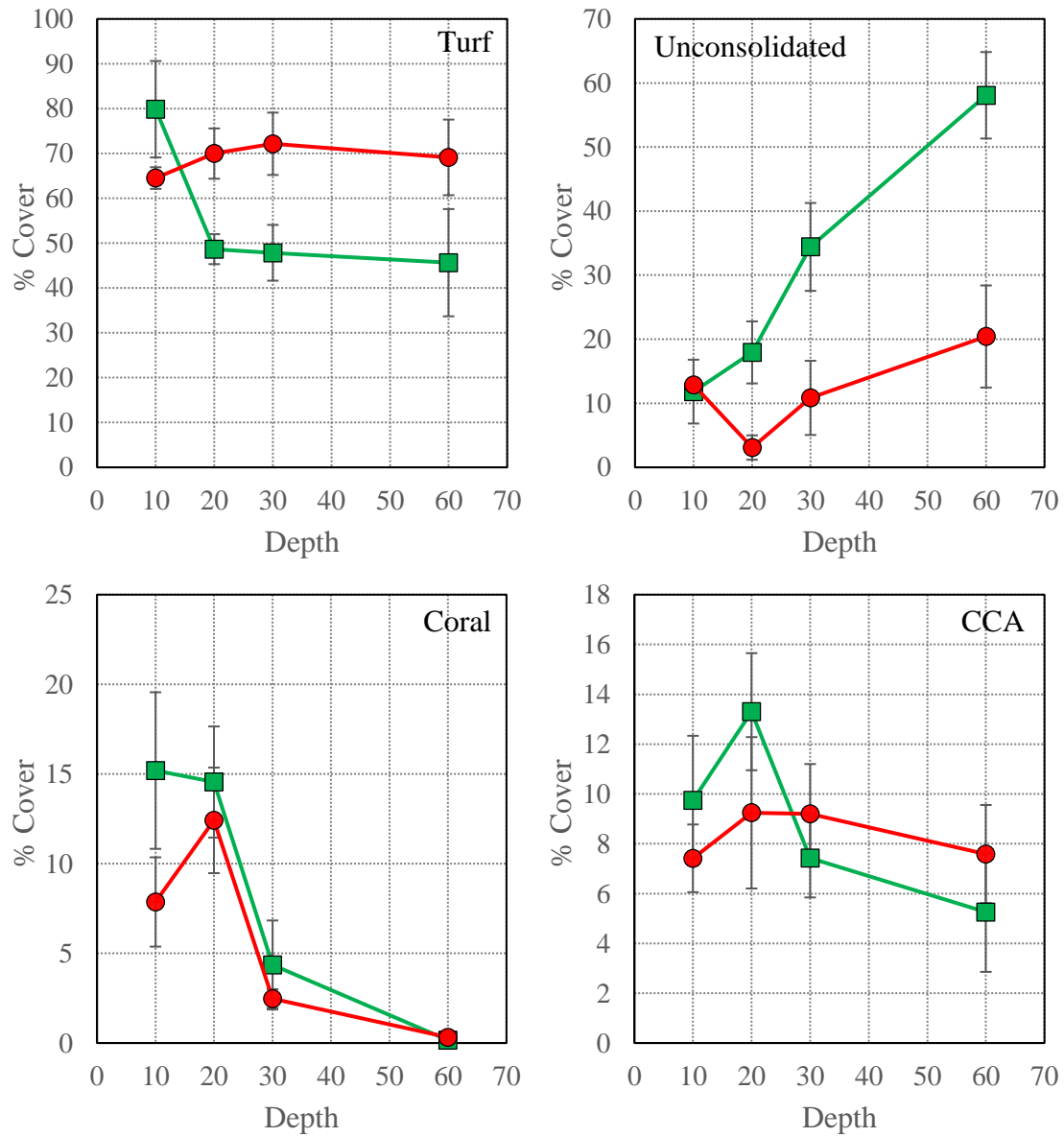


Figure 5 (con't on next page). Change in benthic groups, topographic relief, and coral richness at sites open to fishing (red circles) and with limited management (green squares). Error bars are SEM (error bars not visible are smaller than the size of the marker)

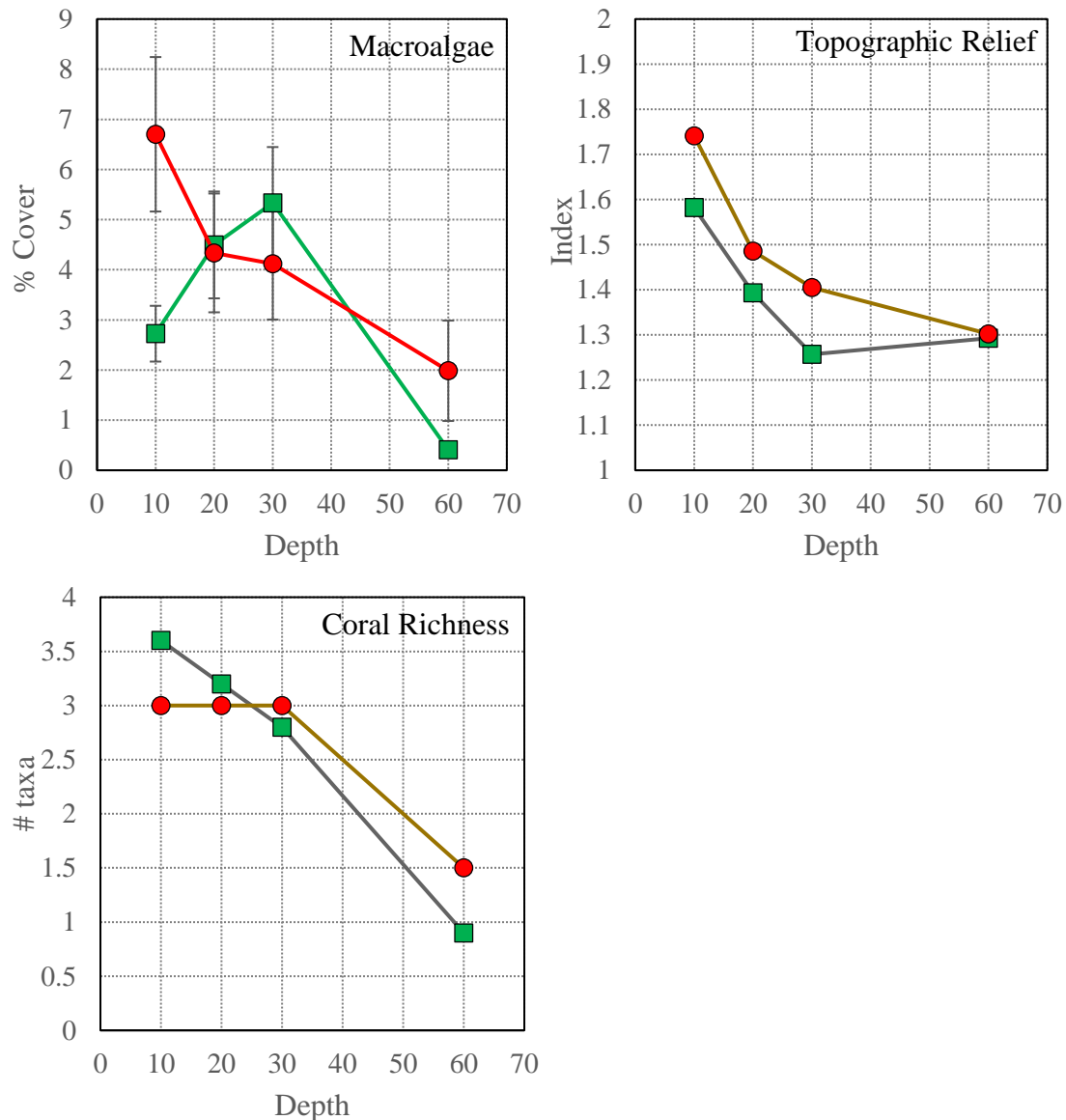


Figure 5 (con't). Change in benthic groups, topographic relief, and coral richness at sites open to fishing (red circles) and with limited management (green squares). Error bars are SEM (error bars not visible are smaller than the size of the marker).

Corals are particularly susceptible to the environmental changes expected to result from climate change. Prolonged periods of elevated ocean temperatures can trigger coral bleaching, and if a thermal event is sufficiently large and/or long-lasting, it can result in a mass coral bleaching event, during which multiple coral species experience bleaching simultaneously on a reef. A mass coral bleaching occurred on West Hawai'i reefs in 2015, and resulted in a ~50% decline in coral cover (Kramer *et al.* 2016, Maynard *et al.* 2016, Minton *et al.* 2017a).

Glynn (1996) first suggested that mesophotic reefs may provide a refugia from climate change effects because they are less affected by thermal stress events, as well as other natural (*e.g.*, storm-driven waves) and anthropogenic (*e.g.*, fishing) stressors. Under this hypothesis, corals on

mesophotic reefs should experience lower bleaching prevalence and mortality than corals on shallow reefs. The 2015 mass coral bleaching event in West Hawai‘i was a missed opportunity to examine bleaching prevalence simultaneously on shallow and mesophotic reefs. As part of this project, we attempted to document thermal stress on corals, but bleaching prevalence was too low to reliably document in 2017, so no rigorous assessment was possible.

	10 m	20 m	30 m	60 m
PLOB	100	94	100	44
PCOM	69	94	81	
MCAP	63	25	31	
MPAT	38	13	13	
Por sp.	6			
Poc sp.	6			6
PMEA	6			
PVAR		6		6
Coral sp.			6	
Leptoseris				13
Cycloseris				6
Leptastrea				6

Figure 6. Coral cover with depth. The number inside each depth bar represent percent of sites (out of 16) at which the species was present. Color represent mean percent cover within that depth range: white=0%, light grey= >0-0.05%, medium grey= >0.05-1%, dark grey = >1-5%, black = >5-10%

Temperature depth profiles showed the average water temperature at 60 m was significantly colder than at the three shallower sites, which did not differ (Figure 7). Most interestingly, however, the variability in temperature over the deployment period was greatest at 60 m, and this variability seemed to result from lower minimum temperatures at depth. Mean temperature maximums were more similar across the depths than were temperature minimums. These findings are consistent with other recent studies of mesophotic reefs in the Pacific and Caribbean (Englebert *et al.* 2017, Baldwin *et al.* 2018). This higher variability in temperature at depth may create conditions conducive to lower bleaching response (McClanahan *et al.* 2007, Safaie *et al.* 2018).

While environmental conditions at depth appear to be conducive to reduced coral bleaching, our data suggest deep reefs are not likely to be effective refugia for climate change on West Hawai‘i. Of the common shallow reef coral species, only *Porites lobata* was observed at 60 m, and the distribution was patchy. *P. lobata* was observed at only 44% of our deep reef sites, and when present, *P. lobata* cover was low (<1%), raising questions about the ability of this population to serve as a significant larval source to reseed shallow reef areas. In addition, recent studies showing depth partitioning in coral symbionts (Bongaerts *et al.* 2013, Pochon *et al.* 2015) that

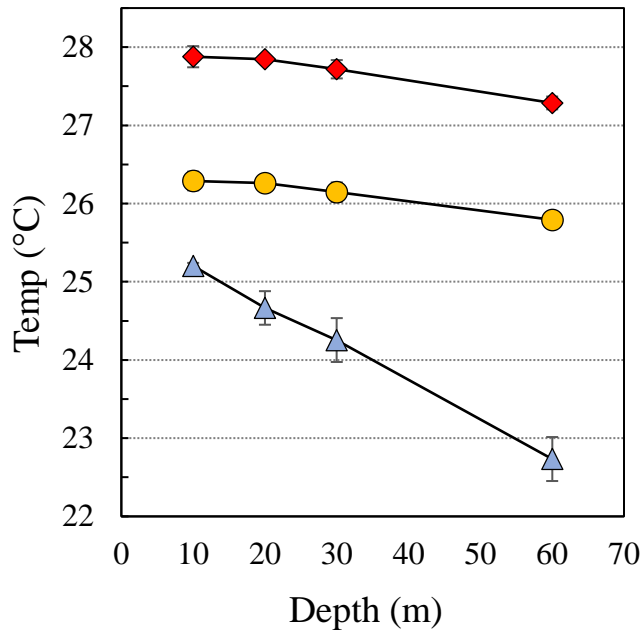


Figure 7. Mean (●), minimum (▲) and maximum (◆) temperature by depth.

assemblage, etc.), the thermal conditions at this depth were not significantly different from those at 10 m. While the 30 m assemblage may benefit from slightly lower thermal stress than shallower ones and therefore provide some refuge benefit, this may not be sufficient to offset a serious and/or prolonged thermal event or long-term temperature increases expected under the current climate change trajectory. The study period did not encompass any shallow-water thermal stress events, so we were unable to empirically explore the temperature variation across depths during such an event.

5.3 Mesophotic reefs as reference area to West Hawaii SCUBA fishing ban

Spears have been shown to be among the most efficient fishing gear in Hawai‘i, having among the highest catch per unit effort and the ability to target a wide a range of species, including many that are not easily caught using other gear (Giddens 2012, Koike *et al.* 2015, TNC unpub. data). The efficiency of conventional spearfishing is limited primarily by the ability of fisher to hold their breath, and the depth to which they can free dive while breath-holding. More recently, spearfishers have used scuba equipment to increase their efficiency and extend the depth range over which they operate. Due to its efficiency, scuba spearfishing has emerged as a significant threat to many species (*e.g.*, parrotfish), and potentially contributing to their overharvest. As a result, scuba spearfishing has been banned by many local governments (see Walsh 2013 for a review). While still legal in most of Hawai‘i, DAR implemented a scuba spearfishing ban in 2013 for the entirety of the West Hawai‘i Regional Fishery Management Area (WHRFMA).

could affect individual competitiveness and survival, and the importance of self-seeding on shallow-water reefs (Concepcion *et al.* 2014, Bongeaerts *et al.* 2017) raise further questions about the potential role of mesophotic reefs as a propagule source for shallow-water ones. Finally, *P. lobata* is among the most temperature tolerant coral species in Hawai‘i, and likely the least susceptible to climate change effects, making it the coral species least in need of a thermal refugia. Thermally susceptible species such as *Montipora capitata* and *Pocillopora meandrina* were not observed at depth (Figure 6), and thus would gain no refuge benefit from mesophotic reefs.

While 30 m benthic assemblages appear to have fewer biological obstacles to serving as a refugia (*e.g.*, shares many species, fewer symbiont differences, higher abundance/cover of coral than 60 m

Monitoring the effectiveness of this management action presents a significant challenge in that suitable reference locations are not readily available within the West Hawai‘i area. A reference area is necessary to help establish causation between the management action (*e.g.*, the scuba spearfishing ban) and any changes in the condition of the marine resources. Because the scuba spearfishing ban covers the entirety of the West Hawai‘i coast, a reference area would need to be situated outside the geographical area, which would likely subject it to different regional conditions, and may result in an area with a dissimilar fish assemblage.

The fish assemblage in the upper mesophotic areas of West Hawai‘i may potentially serve as a better reference area for monitoring the scuba spearfishing ban than a shallow-water reef area in a different geographical region. These mesophotic reefs lie within the geographical region and share a reasonably high similarity with the shallow-water assemblage. Due to their depths, they historically have been below the limits of most, if not all, scuba spearfishers. Several of the key shallow-reef taxa harvested by spear are also present at 60 m (Table 5), with several forming a relatively large percentage of the total biomass of the mesophotic fish assemblage. *Naso hexacanthus*, parrotfishes as a group, *Myripristis* spp., and *Monotaxis grandoculis*, ranked 1st, 6th, 9th and 22nd (out of 92 taxa) in their contribution to total fish biomass at 60 m.

However, while mesophotic reefs have the potential to serve as viable reference areas, they are not ideal. Many of the key target species are not present or are relatively rare at 60 m. Our data also suggest that the mesophotic fish assemblage may experience different regional and/or ecological processes or are responding differently to regional processes than shallow-water ones. If true, mesophotic reefs would not fulfill the primary role of a reference site. This concern could likely be mitigated by using the fish assemblage at a shallower depth, but one still below conventional scuba limits (*e.g.*, 45-50 m). Regardless, these upper mesophotic reefs may prove a better option than selecting an area outside of the West Hawai‘i geographic area.

Table 5. Ten most commonly harvested taxa using spear and their relative biomass at 60 m. The harvest list was compiled from recreational spearfishing catch data from Puakō (Giddens 2012) and from the State of Hawai‘i’s commercial fishery reporting for spearfishing landings from West Hawai‘i for the years 2012 and 2013 (DAR, Department of Land and Natural Resources).

Species	60 m
Parrotfish	4.39%
<i>Octopus</i> spp.	-
<i>Naso hexacanthus</i>	17.04%
<i>Ctenochaetus strigosus</i>	0.84%
<i>Monotaxis grandoculis</i>	1.23%
<i>Myripristis</i> spp.	3.15%
<i>Acanthurus triostegus</i>	0
<i>Naso lituratus</i>	0.52%
<i>Acanthurus achilles</i>	0
<i>Mulloidichthys flavolineatus</i>	0.07%

5.4 Assessing effectiveness of management strategies and mesophotic reefs

Currently, no actions specifically designed to manage mesophotic reefs have been implemented on West Hawai‘i. Marine management has focused predominantly on shallow-water marine resources, especially coral reef fishes and their habitat. In West Hawai‘i, a network of marine managed areas provides varying levels of protection to over 35% of the coastline (IUCN 2009).

The West Hawai‘i Regional Fishery Management Area (WHRFMA) encompasses nearly the entirety of the West Hawai‘i coast. The WHRFMA offers some additional restrictions on species that can be taken (*e.g.*, sharks, rays, kona crabs, etc.) and gear that can be used (*e.g.*, scuba spearfishing), but otherwise allows fishing similar to “open” areas around the state. The WHRFMA likely contains much, if not all, of the available mesophotic reef habitat available on West Hawai‘i.

Within the WHRFMA are smaller MLCDs, FRAs, FMAs, and Netting Restricted Areas that provide additional protections (Table 6). Many of these smaller protected areas extend into waters that could include mesophotic reefs, but it is not clear how much mesophotic reef actually exists within the boundaries of this network of protected areas. During this project, several protected areas had to be dropped from our survey design because they either (1) lacked suitable hardbottom habitat (*i.e.*, did not possess mesophotic reef) or (2) the hardbottom available was not on a sufficiently steep slope to allow divers to safely survey four depths in a single dive.

Table 6. Management areas on West Hawai‘i.

Protected Area	Level of Protection	Mesophotic Depths	Mesophotic Reef
Hookena	FRA	Yes	Yes
Kaloko-Honokōhau	FRA/FMA	Yes	Yes
Kaohe (Kona Paradise)	FRA	Yes	Yes
Ka‘ūpūlehu	FRA/FMA	Yes	Yes
Kealakekua Bay	MLCD	Yes	Yes
Kīholo Bay	FMA	No	No
Lapakahi	MLCD	No	No
Miloli‘i	FRA/FMA	Yes	Yes
Napoo-Honaunau	FRA	Yes	Yes
North Kailua-Keahou	FRA	Yes	No
North Kohala	FRA	Yes	No
Old Airport	MLCD	No	No
Papawai Bay	FMA	Yes	Yes
Puakō-‘Anaeho‘omalu	FRA/FMA	Yes	Yes
Red Hill	FRA	Yes	Yes
Waialea Bay	MLCD	No	No
West Hawai‘i Regional (WHRFMA)	FMA	Yes	Yes

Differences between benthic assemblages at depth inside and outside protected areas raise concerns about the effectiveness of the current network of management areas. While extensive mesophotic area lies within the broader WHRFMA, specifically designated MLCDs, FRAs, and FMAs appear to contain less hardbottom at depth compared to sites outside these areas. Hardbottom is the primary habitat requirement for most coral reef species. Even with this difference, cover of deep-water corals did not differ between management strategies, suggesting the availability of hardbottom may not be a limiting factor (Figure 5). Coral richness was lower at sites inside protected areas than outside, suggesting that while the network of protected areas may include sufficient hardbottom, the habitat as a whole may be of “lower quality” for at least some mesophotic corals.

Due to the challenges associated with visiting and collecting information at mesophotic depths, our understanding of mesophotic reefs, and especially their connectivity and importance to shallow-water coral reef ecosystems, is currently in its infancy. Assessing the adequacy of protection afforded to deep reefs is therefore difficult, but our data suggest that mesophotic ecosystems are sufficiently different from their shallow-water counterparts that they should receive special management attention. Current management of mesophotic ecosystems appears to be primarily a collateral effect arising from the management of shallow-water ecosystems and/or specific fisheries (*e.g.*, bottomfish restricted fishing areas), and is not an effort developed specifically with mesophotic ecosystems as their primary management target. Implementing effective management will likely require more information on the distribution, location, composition, and connectivity of mesophotic reefs to other deep-water ecosystems and their shallow-water counterparts. Hawai‘i’s “30 by 30” initiative (State of Hawai‘i 2016), a commitment to effectively manage 30% of Hawai‘i’s marine resources by 2030, presents a clear opportunity to develop and implement specific actions to protect and manage Hawai‘i’s mesophotic reefs.

5.5 Sharing Study Results

In an effort to ensure that managers, communities, and scientists have the most comprehensive information possible, we have and will continue to disseminate our findings to State (DAR) and Federal (NOAA) agencies and local communities statewide, where it can be used to inform management strategies at multiple levels. To date, information from the first year of this project was shared via a presentation at the IEA Symposium (December 2017), and the authors are preparing a manuscript for peer-reviewed publication. In addition, findings from this study were shared with the participants of two 30 by 30 spatial planning workshops convened by DAR and TNC, which helped participants refine the depth strata included in the development of management recommendations.

6.0 Future Work

TNC would like to further investigate mesophotic reefs as a refugia for fishing and other nearshore stressors. This study focused on mesophotic reefs in close spatial proximity to shallow-water reefs (*i.e.*, steep slopes). While this would likely facilitate connectivity, the proximity to areas experiencing high fishing pressure may also reduce the potential refugia benefits of these mesophotic reefs, especially for some highly mobile target species (*i.e.*, the steep slopes that facilitated diver movement during the study may also facilitate regular fish movement along the same depth gradient, exposing fish to fishing pressure in shallow waters). Given the findings of this study, less steep slopes may provide more refugia benefit than steep slopes for two reasons: 1) more suitable reef habitat may be available per linear length of coastline, and 2) a large distance between the mesophotic and shallow-water reefs, where fishing pressure may be high could reduce the probability of the take of mobile target species.

In addition, the potential role of reefs between 30 m and 50 m deep to serve as climate refugia warrants further investigation. While the temperature profile of 30 m reefs was similar to those of 10 m and 20 m reefs during this study, thermal stress events on coral reefs are often associated with clear, calm weather that leads to thermal stratification of the water column, with higher temperatures in shallower waters. Closer examination of temperature profiles and the responses of corals in future thermal stress events would provide of more direct test of the ability of mid-depth reefs to provide refugia of cooler water to in these specific circumstances.

7.0 Acknowledgements

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Appendix 1: Survey Site Metatdata

Site	Year Surveyed	Management	Latitude	Longitude
KONA_01	2017	Open	19.65512	-156.03185
KONA_02	2017	FRA	19.49052	-155.95955
KONA_03	2017	FMA	19.64696	-156.02347
KONA_04	2017	Open	19.48314	-155.94582
KONA_05	2017	FRA	19.45911	-155.92921
KONA_06	2017	FRA	19.4277	-155.9198
KONA_07	2017-2018	Open	19.10771	-155.91631
KONA_11	2017-2018	FRA	19.96745	-155.85503
KONA_12	2017	FMA	19.96476	-155.85773
KONA_13	2017-2018	FRA	19.22413	-155.90276
KONA_14	2017	Open	19.23424	-155.90106
KONA_15	2017-2018	Open	19.31821	-155.8911
KONA_16	2017	MLCD	19.47783	-155.93689
KONA_17	2017	Open	19.2938	-155.88957
KONA_18	2017	FRA	19.32677	-155.88748
KONA_19	2017	Open	19.08904	-155.90976
KONA_20	2017	Open	19.20297	-155.90704
KONA_21	2017	FRA	19.69245	-156.04565
KONA_101	2018	FRA	19.43561	-155.92186
KONA_102	2018	FRA	19.33088	-155.88611
KONA_103	2018	Open	19.25084	-155.90033
KONA_104	2018	Open	19.27185	-155.8933
KONA_105	2018	Open	19.21459	-155.90143
KONA_106	2018	Open	19.28311	-155.89194
KONA_107	2018	FRA	19.30494	-155.88859
KONA_108	2018	FRA	19.4888	-155.95103
KONA_109	2018	Open	19.48167	-155.94058
KONA_110	2018	Open	19.20869	-155.90224
KONA_111	2018	Open	19.09615	-155.91162
KONA_112	2018	Open	19.72115	-156.05766
KONA_113	2018	FRA	19.69256	-156.04572
KONA_116	2018	FRA	19.96271	-155.85945

Appendix 2: Target fish species

Fish species comprising the seven resource species groups prized by fishers and the non-resource group used in this report. Groups are modified from Williams *et al.* (2008).

<u>Resource Groups</u>	
<u>Surgeonfishes (Acanthuridae)</u>	<u>Apex</u>
Achilles tang	Smalltoothed jobfish
Ringtail surgeonfish	Green jobfish
Eyestripe surgeonfish	All jacks
Whitebar surgeonfish	All big-eyes
Bluelined surgeonfish	All barracudas
Orangeband surgeonfish	
Convict tang	<u>Goatfishes (Mullidae)</u>
Yellowfin surgeonfish	All
<i>Ctenochaetus</i> spp.	
<i>Naso</i> spp.	<u>Parrotfishes (Scaridae)</u>
	All
<u>Wrasses (Labridae)</u>	
Hawaiian hogfish	<u>Soldier/Squirrelfishes (Holocentridae)</u>
Cigar wrasse	<i>Myripristis</i> spp.
Yellowstriped coris	Saber squirrelfish
Yellowtail Coris	Tahitian squirrelfish
Iniistius spp.	
Ringtail wrasse	<u>Others</u>
Old woman wrasse	Milkfish
Surge wrasse	Stocky hawkfish
	Bigeye emperor
	<u>Non-resource</u>
Brown surgeonfish	Fourspot butterflyfish
Goldrim surgeonfish	Teardrop butterflyfish
Multiband butterflyfish	<i>Plectroglyphidodon</i> spp.
Ornate butterflyfish	<i>Stegastes</i> spp.
All wrasses, except those listed above	
All hawkfishes, except stocky hawkfish	
All triggerfishes, except planktivorous species	

Appendix 3: Group classifications for benthic taxa

Name	Family/Group	Benthic Category
Black Coral	Black Coral	Black Coral
CCA	CCA	CCA
CCA, disease	CCA	CCA
<i>Cycloseris</i> sp.	Fungiidae	Hard Coral
<i>Leptastrea</i> sp.	Faviidae	Hard Coral
<i>Leptoseris</i> sp.	Agariciidae	Hard Coral
<i>Montipora capitata</i>	Acroporidae	Hard Coral
<i>Montipora patula</i>	Acroporidae	Hard Coral
<i>Pavona varians</i>	Agariciidae	Hard Coral
<i>Pocillopora meandrina</i>	Pocilloporidae	Hard Coral
<i>Pocillopora</i> spp.	Pocilloporidae	Hard Coral
<i>Porites compressa</i>	Poritidae	Hard Coral
<i>Porites lobata</i>	Poritidae	Hard Coral
<i>Porites lobata</i> (massive)	Poritidae	Hard Coral
<i>Porites</i> spp. (massive)	Poritidae	Hard Coral
Unknown <i>Pavona</i> (massive)	Agariciidae	Hard Coral
Unknown table coral	Coral	Hard Coral
<i>Asparagopsis</i> sp.	Rhodophyta	Macroalgae
Black crust	Black crust	Macroalgae
Brown Macroalgae	Phaeophyta	Macroalgae
<i>Caulerpa</i> sp.	Chlorophyta	Macroalgae
<i>Codium</i> sp.	Chlorophyta	Macroalgae
<i>Dictyota</i> sp.	Phaeophyta	Macroalgae
<i>Halimeda</i> sp.	Chlorophyta	Macroalgae
<i>Lobophora variegata</i>	Phaeophyta	Macroalgae
<i>Microdictyon</i> sp.	Chlorophyta	Macroalgae
<i>Neomeris</i> sp.	Chlorophyta	Macroalgae
<i>Padina</i> sp.	Phaeophyta	Macroalgae
<i>Peyssonnelia</i> sp.	Rhodophyta	Macroalgae
Red Macroalgae (fleshy)	Rhodophyta	Macroalgae
Red Macroalgae (calcareous)	Rhodophyta	Macroalgae
<i>Turbinaria</i> sp.	Phaeophyta	Macroalgae
<i>Ulva</i> sp.	Chlorophyta	Macroalgae
<i>Valonia</i> sp.	Chlorophyta	Macroalgae
Bryozoan	Sessile Invertebrate	Other
Cyanobacteria	Cyanobacteria	Other
Limestone	Abiotic	Other

Name	Family/Group	Benthic Category
Octocoral	Octocoral	Other
Sponge	Sessile Invertebrate	Other
Tunicate	Sessile Invertebrate	Other
Zoanthid	Sessile Invertebrate	Other
Turf	Turf	Turf
Rubble, with CCA	Unconsolidated	Unconsolidated
Sand	Unconsolidated	Unconsolidated
Rubble, with turf	Unconsolidated	Unconsolidated

Appendix 4: Depth distribution of fish

Depth distribution of 149 fish species observed during surveys on West Hawai‘i. Numbers in grey box are percent of the species biomass that occurs at the depth and % total biomass is the percent of the total biomass across all depths comprised by the species. Dark grey cells highlight the depth at which the greatest biomass for the species occurred. Empty and unshaded cells represent no individuals observed at that depth during any survey. Note: 156 fish taxa were observed during the surveys, but for seven species (e.g., six species of eel and *Decapterus macarellus*), no biomass estimates were obtained due to challenges in accurately sizing individuals.

Taxon	Family	10 m	20 m	30 m	60 m	%Total Biomass
<i>Zembrasoma flavescens</i>	Acanthuridae	47.8	27.5	19.8	5.0	7.7
<i>Naso lituratus</i>	Acanthuridae	49.1	36.0	13.2	1.7	6.2
<i>Ctenochaetus strigosus</i>	Acanthuridae	44.4	37.8	14.2	3.7	4.1
<i>Acanthurus dussumieri</i>	Acanthuridae	29.3	22.2	19.4	29.1	3.8
<i>Melichthys niger</i>	Balistidae	73.8	24.9	1.3		3.5
<i>Ctenochaetus hawaiiensis</i>	Acanthuridae	36.7	27.3	22.8	13.2	3.4
<i>Cephalopholis argus</i>	Serranidae	36.3	35.6	23.4	4.6	2.7
<i>Sufflamen bursa</i>	Balistidae	30.2	25.0	23.7	21.2	2.7
<i>Acanthurus blochii</i>	Acanthuridae	73.0	6.3		20.7	2.5
<i>Acanthurus olivaceus</i>	Acanthuridae	38.4	29.7	23.3	8.6	2
<i>Melichthys vidua</i>	Balistidae	36.6	19.2	26.7	17.4	1.6
<i>Kyphosus species</i>	Kyphosidae	57.2	24.0	18.8		1.5
<i>Acanthurus nigrofuscus</i>	Acanthuridae	55.6	23.8	18.4	2.2	1.2
<i>Thalassoma duperrey</i>	Labridae	54.4	23.0	14.5	8.0	1
<i>Abudefduf abdominalis</i>	Pomacentridae	100.0				0.4
<i>Chromis vanderbilti</i>	Pomacentridae	82.1	17.3	0.5		0.4
<i>Halichoeres ornatissimus</i>	Labridae	70.2	22.9	6.9		0.3
<i>Balistes polylepis</i>	Balistidae	67.4		16.3	16.3	0.3
<i>Paracirrhites arcatus</i>	Cirrhitidae	39.1	53.1	7.5	0.3	0.3
<i>Kyphosus bigibbus</i>	Kyphosidae	100.0				0.2
<i>Acanthurus nigroris</i>	Acanthuridae	93.9	1.6	4.4		0.2

Taxon	Family	10 m	20 m	30 m	60 m	%Total Biomass
<i>Mulloidichthys flavolineatus</i>	Mullidae	81.1	0.8	10.6	7.5	0.2
<i>Calotomus carolinus</i>	Scaridae	66.4	24.6	9.0		0.2
<i>Naso unicornis</i>	Acanthuridae	64.8	18.0		17.2	0.2
<i>Gomphosus varius</i>	Labridae	54.6	32.7	3.9	8.7	0.2
<i>Canthigaster jactator</i>	Tetraodontidae	50.3	19.5	24.1	6.1	0.2
<i>Abudefduf vaigiensis</i>	Pomacentridae	100.0				0.1
<i>Cantherhines dumerilii</i>	Monacanthidae	100.0				0.1
<i>Chaetodon quadrimaculatus</i>	Chaetodontidae	71.0	2.3		26.7	0.1
<i>Acanthurus leucopareius</i>	Acanthuridae	58.2	30.6	7.2	4.0	0.1
<i>Acanthurus triostegus</i>	Acanthuridae	100.0				<0.1
<i>Chaetodon lunulatus</i>	Chaetodontidae	100.0				<0.1
<i>Cirrhitops fasciatus</i>	Cirrhitidae	100.0				<0.1
<i>Cirrhitus pinnulatus</i>	Cirrhitidae	100.0				<0.1
<i>Cirripectes vanderbilii</i>	Blenniidae	100.0				<0.1
<i>Plagiotremus ewaensis</i>	Blenniidae	100.0				<0.1
<i>Pervagor spilosoma</i>	Monacanthidae	93.2		6.8		<0.1
<i>Pervagor aspricaudus</i>	Monacanthidae	89.7	5.2	5.2		<0.1
<i>Stegastes marginatus</i>	Pomacentridae	85.7	7.1	7.1		<0.1
<i>Plectroglyphidodon imparipennis</i>	Pomacentridae	83.3			16.7	<0.1
<i>Acanthurus achilles</i>	Acanthuridae	76.5	23.5			<0.1
<i>Chaetodon unimaculatus</i>	Chaetodontidae	66.7	33.3			<0.1
<i>Ostracion meleagris</i>	Ostraciidae	62.5	12.5	12.5	12.5	<0.1
<i>Stethojulis balteata</i>	Labridae	51.2	37.2	11.6		<0.1
<i>Pseudocheilinus tetrataenia</i>	Labridae	46.5	33.3	14.7	5.5	<0.1
<i>Chlorurus spilurus</i>	Scaridae	31.3	47.8	18.6	2.3	4.4
<i>Monotaxis grandoculis</i>	Lethrinidae	34.6	37.3	18.4	9.6	2.6
<i>Myripristis berndti</i>	Holocentridae	4.4	46.8	23.2	25.6	2.3
<i>Oxycheilinus unifasciatus</i>	Labridae	20.2	33.2	19.5	27.1	2

Taxon	Family	10 m	20 m	30 m	60 m	%Total Biomass
<i>Myripristis kuntze</i>	Holocentridae	13.2	74.4	6.6	5.9	1.2
<i>Chromis agilis</i>	Pomacentridae	12.5	53.5	30.1	3.8	1.1
<i>Hemitaurichthys thompsoni</i>	Chaetodontidae	15.9	67.4	15.8	0.9	1
<i>Mulloidichthys vanicolensis</i>	Mullidae	1.9	80.9	10.8	6.4	0.7
<i>Chaetodon ornatissimus</i>	Chaetodontidae	43.4	49.4	5.0	2.2	0.7
<i>Chaetodon multicinctus</i>	Chaetodontidae	34.3	49.5	12.4	3.8	0.4
<i>Chaetodon auriga</i>	Chaetodontidae	16.3	67.0	5.6	11.1	0.3
<i>Centropyge potteri</i>	Pomacanthidae	10.4	56.0	27.8	5.7	0.3
<i>Hemitaurichthys polylepis</i>	Chaetodontidae	35.3	41.0	21.4	2.3	0.3
<i>Dascyllus albisella</i>	Pomacentridae	0.0	56.7	37.9	5.4	0.2
<i>Neoniphon sammara</i>	Holocentridae		50.8	0.8	48.4	0.2
<i>Paracirrhites forsteri</i>	Cirrhitidae	29.5	41.2	29.4		0.2
<i>Parupeneus insularis</i>	Mullidae	28.5	45.4	3.4	22.7	0.1
<i>Chromis ovalis</i>	Pomacentridae		100.0			0.1
<i>Fistularia commersonii</i>	Fistulariidae	6.3	69.9	23.8		0.1
<i>Acanthurus nigricans</i>	Acanthuridae	16.6	68.7	14.7		0.1
<i>Plectroglyphidodon johnstonianus</i>	Pomacentridae	23.3	65.0	11.7		0.1
<i>Aluterus scriptus</i>	Monacanthidae	32.1	47.5	15.5	4.9	0.1
<i>Aulostomus chinensis</i>	Aulostomidae	36.8	44.8	17.8	0.6	0.1
<i>Pseudocheilinus octotaenia</i>	Labridae	29.9	36.8	31.1	2.3	0.1
<i>Chaetodon lineolatus</i>	Chaetodontidae		100.0			<0.1
<i>Chromis acares</i>	Pomacentridae		100.0			<0.1
<i>Myripristis amaena</i>	Holocentridae		100.0			<0.1
<i>Novaculichthys taeniourus</i>	Labridae		100.0			<0.1
<i>Sargocentron diadema</i>	Holocentridae		100.0			<0.1
<i>Zembrasoma veliferum</i>	Acanthuridae		100.0			<0.1
<i>Thalassoma ballieui</i>	Labridae	2.7	97.3			<0.1
<i>Centropyge loriculus</i>	Pomacanthidae	10.0	80.0	10.0		<0.1

Taxon	Family	10 m	20 m	30 m	60 m	%Total Biomass
<i>Coris venusta</i>	Labridae	8.4	65.5	26.2		<0.1
<i>Labroides phthirophagus</i>	Labridae	18.7	62.4	9.5	9.4	<0.1
<i>Pseudojuloides cerasinus</i>	Labridae	8.2	59.8	29.3	2.7	<0.1
<i>Ostorhinchus maculiferus</i>	Apogonidae		55.2		44.8	<0.1
<i>Acanthurus thompsoni</i>	Acanthuridae	3.2	30.1	34.7	32.0	3.2
<i>Scarus rubroviolaceus</i>	Scaridae	29.3	21.5	36.0	13.3	3.1
<i>Parupeneus multifasciatus</i>	Mullidae	21.8	20.5	35.7	22.0	1.9
<i>Bodianus albotaeniatus</i>	Labridae	0.1	49.5	31.2	19.2	1.2
<i>Caranx ignobilis</i>	Carangidae			100.0		0.9
<i>Zanclus cornutus</i>	Zanclidae	31.0	21.6	38.3	9.1	0.7
<i>Aphareus furca</i>	Lutjanidae	8.6	16.8	40.5	34.0	0.7
<i>Chromis leucura</i>	Pomacentridae		1.4	72.1	26.5	0.6
<i>Forcipiger flavissimus</i>	Chaetodontidae	22.7	26.1	30.3	20.9	0.5
<i>Coris gaimard</i>	Labridae	28.0	21.4	36.2	14.3	0.4
<i>Pseudocheilinus evanidus</i>	Labridae	7.2	28.5	56.3	8.1	0.3
<i>Kyphosus sandwicensis</i>	Kyphosidae		27.8	72.2		0.3
<i>Sargocentron tiera</i>	Holocentridae	29.9		53.4	16.8	0.2
<i>Chromis hanui</i>	Pomacentridae	19.8	14.9	62.6	2.7	0.1
<i>Centropyge fisheri</i>	Pomacanthidae	2.6	17.0	76.5	3.9	0.1
<i>Chaetodon kleinii</i>	Chaetodontidae		35.4	40.9	23.8	0.1
<i>Plagiotremus goslinei</i>	Blenniidae	49.1		50.9		<0.1
<i>Macropharyngodon geoffroy</i>	Labridae	3.5		96.5		<0.1
<i>Synodus ulae</i>	Synodontidae			66.7	33.3	<0.1
<i>Synodus species</i>	Synodontidae			97.5	2.5	<0.1
<i>Apogon kallopterus</i>	Apogonidae			100.0		<0.1
<i>Gunnellichthys curiosus</i>	Microdesmidae			100.0		<0.1
<i>Oxycheilinus bimaculatus</i>	Labridae			100.0		<0.1
<i>Pterois sphex</i>	Scorpaenidae			100.0		<0.1

Taxon	Family	10 m	20 m	30 m	60 m	%Total Biomass
<i>Naso hexacanthus</i>	Acanthuridae	10.4	19.8	12.9	57.0	6.5
<i>Lutjanus kasmira</i>	Lutjanidae	4.1	18.5	37.7	39.8	2.7
<i>Aprion virescens</i>	Lutjanidae			46.8	53.2	1.3
<i>Caranx melampyus</i>	Carangidae	10.3	15.2	14.7	59.8	1.2
<i>Xanthichthys auromarginatus</i>	Balistidae	15.4	14.6	24.1	45.9	1.1
<i>Chromis verater</i>	Pomacentridae	5.7	1.4	3.1	89.7	1
<i>Naso brevirostris</i>	Acanthuridae	4.5	24.3		71.3	1
<i>Forcipiger longirostris</i>	Chaetodontidae	16.7	22.6	26.2	34.5	0.7
<i>Scarus psittacus</i>	Scaridae	23.5	26.2	13.2	37.1	0.6
<i>Parupeneus cyclostomus</i>	Mullidae	31.9	0.1	12.6	55.5	0.5
<i>Caranx lugubris</i>	Carangidae				100.0	0.4
<i>Scarus dubius</i>	Scaridae			4.4	95.6	0.3
<i>Chaetodon lunula</i>	Chaetodontidae	27.4	20.5	12.6	39.4	0.2
<i>Sargocentron spiniferum</i>	Holocentridae	10.8	14.6	25.4	49.1	0.2
<i>Chlorurus perspicillatus</i>	Scaridae	6.6		14.4	79.0	0.2
<i>Chaetodon miliaris</i>	Chaetodontidae	6.0	12.0	10.0	72.0	0.1
<i>Apolemichthys arcuatus</i>	Pomacanthidae				100.0	0.1
<i>Heniochus diphreutes</i>	Chaetodontidae				100.0	0.1
<i>Lutjanus fulvus</i>	Lutjanidae				100.0	0.1
<i>Seriola dumerili</i>	Carangidae				100.0	0.1
<i>Chaetodon tinkeri</i>	Chaetodontidae		3.6	29.7	66.7	0.1
<i>Parupeneus pleurostigma</i>	Mullidae		8.4	36.6	55.0	0.1
<i>Sufflamen fraenatus</i>	Balistidae			48.8	51.2	0.1
<i>Apogon species</i>	Apogonidae				100.0	<0.1
<i>Bothus species</i>	Bothidae				100.0	<0.1
<i>Callionymus comptus</i>	Callionymidae				100.0	<0.1
<i>Cheilio inermis</i>	Labridae				100.0	<0.1
<i>Cirrhilabrus jordani</i>	Labridae				100.0	<0.1

Taxon	Family	10 m	20 m	30 m	60 m	%Total Biomass
<i>Gnatholepis caurensis hawaiiensis</i>	Gobiidae				100.0	<0.1
Gobiidae species	Gobiidae				100.0	<0.1
<i>Malacanthus brevirostris</i>	Malacanthidae				100.0	<0.1
<i>Myripristis chryseres</i>	Holocentridae				100.0	<0.1
<i>Neoniphon aurolineatus</i>	Holocentridae				100.0	<0.1
<i>Parapercis schauinslandi</i>	Pinguipedidae				100.0	<0.1
<i>Pseudanthias bicolor</i>	Serranidae				100.0	<0.1
<i>Ptereleotris heteroptera</i>	Microdesmidae				100.0	<0.1
<i>Anampses chrysocephalus</i>	Labridae			30.0	70.0	<0.1
<i>Sargocentron xantherythrum</i>	Holocentridae		32.4	0.2	67.3	<0.1
<i>Canthigaster coronata</i>	Tetraodontidae			35.0	65.0	<0.1
<i>Pristiapogon kallopterus</i>	Apogonidae		22.6	23.8	53.6	<0.1
<i>Canthigaster epilampra</i>	Tetraodontidae		16.3	32.5	51.2	<0.1
<i>Acanthurus xanthopterus</i>	Acanthuridae	50.0		50.0		0.1
<i>Synodus variegatus</i>	Synodontidae			50.0	50.0	<0.1
<i>Coris flavovittata</i>	Labridae		50.0		50.0	<0.1

