ECOLOGY AND FISHING IMPACTS ON AQUARIUM FISHES ON MESOPHOTIC REEFS IN HAWAII

Final Report Year 2013-14

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Table of Contents

Summary

Reef fish community structure and habitat associations are well documented for shallow coral reefs (<20m) but are largely unknown in deeper extensions of reefs (mesophotic reefs; >30m). We examined reef fish community structure and benthic composition at depth intervals from 3-40m in West Hawaii. Reef fish species richness and abundance peaked between 12-20m. Fish community structure changed slowly with depth, with more than 85% of species observed at mesophotic depths also found in shallow reef habitats. Depth-related differences appear to be linked more closely with species' feeding behavior than with taxonomic structure, as the relative abundance of herbivorous fishes decreased and planktivorous fishes increased with depth. More than 51% of the variation in reef fish community structure was explained by depth, while only 17% was explained by differences in sites, indicating depth plays a predominant role in structuring communities. Habitat analyses show that coral cover peaks from 12-20m and deeper depths are dominated by sand and macroalgal cover. Peaks in coral cover correspond with peaks in reef fish richness and density, suggesting that changes in community composition with depth are likely a result of habitat structure and availability.

Introduction

Factors structuring reef fish communities have been researched extensively in the past 50 years, largely following the advent and widespread use of SCUBA diving (Sale 1991, Pyle 2000; Hixon 2011). Much of the spatial variation in reef fish community composition has been linked to habitat availability and complexity (Munday 2000, Almany 2004, Gratwicke and Speight 2005). In addition to habitat parameters, depth and associated abiotic gradients are also known to play a role in the community composition and abundance of reef fishes (McGehee 1994, Friedlander and Parrish 1998). While SCUBA diving has greatly enhanced the ability of researchers to understand reef fish dynamics, it has hindered scientific knowledge somewhat by limitations of bottom time allowed with increasing depth. As a result, the majority of knowledge of reef fishes and their habitats has been limited to depths of 20 meters or less yet coral reefs extend to depths in excess of 80 m in some areas (Maragos and Jokiel 1986, Khang and Maragos 2006, Menza et al. 2008, Reaka et al. 2008).

These deeper extensions of shallow coral reefs, or Mesophotic Coral Ecosystems (MCEs), have been understudied largely because of technological limitations of SCUBA. However, recent advances in diving and remote sensing technologies are now affording safer tools for exploration and documentation of these ecosystems (Pyle 1996, Pyle 2000, Lesser et al. 2009, Waddington et al. 2010). In the past ten years momentum has picked up exponentially for MCE research, largely due to recent advances in diving technology (TRIMIX SCUBA, rebreathers) and remote sensing (multibeam bathymetry, ROVs, AUVs). These recent studies have increased scientific understanding of MCE communities and their potential contributions to coral reef ecosystems, thus placing mesophotic reef environments on the map with coral reef management agencies as potential priority areas for research (Hinderstein et al. 2008, Khang et al. 2014).

The few ecological studies conducted on mesophotic reefs reveal general trends that support the premise of deep reefs as potentially substantial habitat (Brokovich et al. 2007, Lesser et al. 2009). Studies of mesophotic communities in the Caribbean and Red Sea reveal that coral cover is consistent through 50-60 m in depth (Goreau and Goreau 1973, Fricke and Schumacher 1983, Liddell and Ohlhorst 1988, Liddell et al. 1997, Bak et al. 2005). These findings suggest that extent of mesophotic reefs is much greater than expected and may provide significant habitat and possible refuge for shallow coral reef fishes (Bridge et al. 2013).

How coral reef communities change from shallow to mesophotic depths is not well understood (Slattery et al. 2011, VanOppen et al. 2011, Khang et al. 2014). Corals, fish and other organisms have been found from shallow to upper mesophotic zones; in the Caribbean nearly 80% of coral species occur to depths greater than 30m, while over 40% of coral species extend to 30+m in the Indo-Pacific (Bridge et al. 2013). Few studies to date have focused on MCE coral reef fish ecology. The majority of reef fish studies thus far have been conducted in the Caribbean and Red Sea, with Pacific Ocean sites greatly under-represented (Colin 1974, Thresher and Colin 1986, Pyle 2000, Feitzoa et al. 2005, Brokovich et al. 2007, 2008, 2010, Garcia-Sais 2010, Bryan et al. 2013, Bejarano et al. 2014, Schultz et al. 2014). To date, three studies have investigated reef fishes at mesophotic depths in Hawaii; two in the remote northwestern Hawaiian Islands (Parrish and Boland 2004, Kane et al. 2014), and one off of Maui in the main Hawaiian Islands (Boland and Parrish 2005). Thus, our understanding of reef fish abundance and community structure in the Hawaiian Archipelago from shallow to mesophotic depths is extremely limited, and in the majority of islands, completely absent.

The aims of this study were two-fold. First, we wanted to characterize coral reef fish distributions and their habitats along the entire depth range of continuous reefs on the island of Hawaii . Hawaii Island is the geologically youngest of all the islands in the archipelago with a steep bathymetric gradient and healthy coral reefs that extend continuously from shore to depths of approximately 40m. To accomplish our first goal we surveyed fish species and habitat distributions at standardized intervals from 3m to the lower extent of the continuous reef. Second, we sought to examine changes in reef fish species composition, abundance and trophic structure with depth to discern depth ranges of common shallow reef fishes and areas of potential transition to deeper species assemblages. Given the absence of quantitative reef fish data below 20m in Hawaii, this study provides the first baseline estimates for reef fishes in shallow mesophotic depths and sheds light on changes in community structure and function in this underrepresented region.

Materials and Methods

Study Sites

Initial observations of coral reef prevalence with depth in West Hawaii revealed that continuous reef was common from shore to depths of approximately 40 meters. Beyond 40m large sand flats occur to 60m depth or more, with habitat often re-emerging around 60-70m depth and patchily continuing to depths currently undetermined. As the primary aims of this study were to evaluate reef fish abundance and community structure along continuous reef habitat, survey depths were constrained to 40m or the beginning of large sand flat regions. Eleven sites were selected along West Hawaii's coastline in areas where continuous coral reef habitat occurs from shallow waters to at least 40 m within three general zones, North= north of Keahole Point, Central= Kailua-Kona region, South= south of Kealakekua bay (Figure 1).

Sampling Design

At each site, a stratified sampling design was employed to explore changes in reef fish abundance and community structure with depth. Concordant depth and bathymetric relief was sought at all sites to maintain consistency and reduce potential survey bias. Visual surveys of reef fish and benthic substrates were conducted on SCUBA at approximately ten meter depth intervals beginning at three meters and extending to 40 meters or the lower extent of continuous reef habitat within each site during July 2013 and July 2014. At each depth interval, three 25m transects were laid parallel to shore along the specified bathymetric depth contour, with each transect spaced a minimum of 5m apart. Visual fish surveys were conducted at each depth using a 25x4m belt transect method (Hill and Wilkinson 2004). Belt length, width and level of replication per depth (minimum n=3) were dictated by technical constraints resulting from the short bottom times allowed from using SCUBA at 40m depths (Brokovich et al. 2008; Sandin et al. 2008). Within each fish belt transect, all fishes were identified to species (Randall 2007), counted and sized to the nearest centimeter. Benthic survey data were collected at two of the three replicate transects within each depth by photographing a $0.25m^2$ quadrat every meter (n= 25 per transect) using an underwater camera equipped with a PVC photoquad framer and dual lighting system.

Data Analysis

A suite of univariate and multivariate analyses were used to examine the variation in reef fish species composition, abundance and trophic guilds among transects. Data transformations were applied as necessary but reported values in figures and tables are given as raw abundances unless otherwise noted. Trends in species diversity and reef fish abundance with depth were tested using a one-way ANOVA analysis (JMP 10.0, SAS Institute Inc., Cary, NC, 1989-2007). Post-hoc Tukey tests were performed to determine differences between depths for significant results. Trends in individual species abundance with depth were analyzed via one-way ANOVAs with post-hoc Tukey tests using square-root transformed data.

To assess potential changes in reef fish community structure with depth transects were averaged within each depth at each site to create a mean estimate per site/depth combination. A 2-D non-metric Multi-Dimensional Scaling (nMDS, Clarke 1993) was employed using the Bray-Curtis coefficient of similarity on square-root transformed fish abundance data (Primer v. 6.1.13, Primer-E). 2-D MDS scores were then tested using one-way and GLM ANOVAs to assess contributions of site, region and depth as factors structuring reef fish communities. Two-way crossed analysis of similarities (ANOSIM) tests were used to test for differences in species composition with depth, allowing for the fact that there may be site differences or regional differences (Primer v. 6.1.13, Primer-

E). For the pairwise ANOSIM tests a Bonferroni Correction (0.05/n tests) was used to correctly adjust significance levels. A one-way SIMPER analysis was conducted on fish abundance data to ascertain fish species responsible for similarities within each transect depth.

Changes in reef fish community structure were further examined by binning reef fish species into six broad trophic guilds (Randall 2007). Abundance of each trophic guild was then divided by the sum of fishes for each transect to obtain percentage estimates for each trophic guild. Comparisons of each trophic guild with depth were performed using one-way ANOVAs (JMP 10.0, SAS Institute Inc., Cary, NC, 1989-2007) with post-hoc Tukey tests to ascertain trends among significant results.

Benthic cover estimates were examined to determine changes in habitat with depth. Benthic photoquadrat samples were analyzed using CoralNet benthic image analysis (Beijbom et al. 2012). Within each photograph, fifty random points were placed and the biota directly underneath each point was identified to the lowest taxonomic classification possible (Fenner 2005, Huisman et al. 2007). Taxonomic identifications were then pooled to create the following descriptive habitat categories: Coral, Macroalgae, Turf Algae, Crustose Coralline Algae, and Sand. These categories were then summed by photo-quadrat and the percent cover data from each image was averaged to obtain one cover estimate per transect to correspond with fish transects. Log transformed benthic percent cover data for Turf, Sand, Coral, and Crustose Coralline Algae were compared across transect depths using one-way ANOVAs with post-hoc Tukey tests (JMP 10.0, SAS Institute Inc., Cary, NC, 1989-2007). Macroalgal data was analyzed using the non-parametric Wilcoxon Test and post-hoc Wilcoxon planned comparisons as equal variances could not be met for ANOVA comparisons (JMP 10.0, SAS Institute Inc., Cary, NC, 1989-2007).

Results

A total of 24,256 fishes were recorded from 147 species and 33 families within 182 transects at 11 sites along the West Hawaii coast. No overall major depth trends were apparent by fish family, as species abundance within families maintained relatively even richness with depth across pooled study sites (Table 1). Richness and density estimates for reef fish species exhibited similar trends with depth (Figure 1). Species richness was significantly higher at 12m and 21m depths than at 30m and 40m depths, while richness at 3m was not significantly different from either the 12m, 21m or 40 m depths (Fig. 2a, $F_{4,181}=10.52$, $p<0.0001$). Total fish abundance displayed similar trends with 12m, 21m depths significantly higher than 30m, 40m depths, but the 3m depth contour was not significantly different from either the 12m, 21m, or 30m abundances (Fig. 2b; $F_{4,181}=10.41$, $p<0.0001$).

Species distributions with depth varied greatly (ESM 1), with some species found at only a single transect depth and others found at all five transect depths (Table 2). Depth generalist species (observed at 4 or more depths, n=67) outnumbered depth specialist species (found at one or two contiguous depths, n=51). Depth specialists occurred at all transect depths and depth preferences were not concordant with genus or family (ESM 1). Approximately 50% of the depth specialist species can be classified as shallow specialists (only in the 3m and/or 12m depths) including *Caracanthus typicus* and *Melichthys niger*, while approximately 40% are classified as deep specialists (found only in the 30m and/or 40m depths) such as *Cirrhilabrus jordani* and *Pseudanthias bicolor* (Figure 3). Depth generalist species exhibited multiple trends with depth (Figure 4). Fifty-two percent of the 67 depth generalist species showed no significant changes in abundance with depth, while 16% of the depth generalists exhibited a hump-shaped distribution with depth, where abundances were lower at 3, 30 and 40m and higher at 12, 21m. Approximately 16% of the species significantly decreased with depth, while 12% significantly increased with depth. Similar to depth specialists, trends in depth generalist species do not appear to be a result of taxonomic classification (ESM 2).

The community structure of reef fishes transition gradually with depth (Figure 5). Shallow reef fish communities are more distinct, while deeper communities have more similarity, particularly at the 30 and 40m depths. Two-way crossed ANOSIMs were employed on square root transformed fish abundance data to determine the significance of differences in species assemblages between sites and depths. Results indicated significance of both site and depth in structuring communities (2-way ANOSIM, site R=0.166, p=0.018; depth R=0.515, p=0.001). Two-way crossed ANOSIMS showed stronger spatial influence when sites were grouped into regional designations (north, central, south) and depth maintained strong significance (2-way ANOSIM, region R=0.241, p=0.003; depth R=0.561, p=0.001). Pairwise ANOSIMs between geographic regions indicated northern sites were significantly different than central and southern sites, while there were no differences between central and southern sites (Bonferroni corrections P<0.017; North-South R=0.29, P=0.003; North-Central R=0.326, P=0.003; Central-South R=0.128, P=0.098). Pairwise ANOSIMs between depths revealed significant differences between nearly all depth pairings except for 30, 40m, 21, 30m and 12, 21m pairings (Table 3; Bonferroni corrections P<0.0045; 30, 40m R=0.031, P=0.353; 21, 30m R=0.322, P=0.032;12, 21m R=0.209, P=0.041). R values for differences in species structure between 3m and all other depths were strong, as well as differences between 12m and 30, 40m depths (Table 3).

Univariate analyses of MDS axis scores were congruent with ANOSIM results. Axis 1(x-axis) revealed depth and region were significant factors structuring the spread of reef fish communities yet interactions between depth and region were not significant (ANOVA Model: $F_{14,53}$=16.76, P<0.0001; Depth: $F_{4,53}$=56.05, P<0.0001; Region: $F_{2,53}$=3.59, P=0.037; Depth*Region: $F_{8,53}$=1.22, P=0.313). Axis 2 (y-axis) was structured by a combination of regional and site variation (1-way ANOVA Region: $F_{2,53}$=6.65, P<0.003; Site: $F_{10,53}$=2.19, P<0.038). Post-hoc Tukey tests supported differences by region with Northern sites significantly differing from Central and Southern sites, but no significant differences between Central and Southern sites. Post-hoc Tukey tests for site variation did not follow any obvious trend, with the exception of Kiholo (North) and 3-Caves (South) having the least amount of similarities with other sites.

SIMPER tests reveal shifts in dominant species with depth. Surgeonfishes, damselfishes and wrasse dominate assemblages at most depths and are most abundant at mid-depths (Table 4). Species similarities within each depth were concordant among depths; 3m depths were 53% similar between transects, 12m were 60%, 21m were 52%, 30m were 40% and 40m were 44% similar between transects. *Chromis leucura* was characteristic of mesophotic depths, while the majority of the 30 and 40m depths were still dominated by shallow fish species (Table 4). Depth-related differences appear to be linked more closely with species' feeding guilds than with taxonomic structure, with increasing dominance of planktivorous fishes with depth. Trophic structure analyses indicate herbivore, corallivore and omnivore abundances significantly decreased with depth (Figure 6; Herbivore $F_{4,53}$=4.26, p=0.005; Corallivore $F_{4,53}$=8.43, p<0.001; Omnivore $F_{4,53}$=2.84, p=0.034). Planktivorous fishes significantly increased with depth ($F_{4,53}$=2.70, p=0.041). Invertebrate feeding fishes had statistically significant differences between depths, with higher abundances at 30m and lower abundances at 12m, with all other depths having non-significant differences ($F_{4,53}$=3.07, p=0.025). Piscivorous fish abundances did not differ significantly with depth, indicating a low but even abundance at all depths surveyed (Piscivore $F_{4,53}$=0.83, p=0.513).

Reef complexity appears to decrease at deeper depths (Figure 7). Habitat analyses reveal significant increases in sand and macroalgal cover with depth (Figure 8; ANOVA; Sand: $F_{4,117}$=25.03, p<0.001; Wilcoxon; Macroalgae Chi Square_4=33.91, p<0.001). Coral cover was lower at shallow and deep depths, and had highest percent cover at 12, 21m depths ($F_{4,117}$=24.77 p<0.001). Crustose coralline algae was significantly higher at 3m but did not differ from 12-40m (CCA $F_{4,117}$=6.84, p<0.001). Turf algae cover did not significantly change with depth (ANOVA; $F_{4,117}$=2.17, p=0.076).

Discussion

The reef fish community structure in West Hawaii transitioned gradually with increasing depth. Multivariate ordination showed sequential grouping from 3-40m (Figure 5), and indicated that mesophotic communities (30,40m depths) were less distinct and displayed more variability than at shallower depths. While these communities showed distinct groupings in ordination space, the community structure was largely comprised of similar species (Table 4). More than half of the 147 species observed on transects were found at 3 or more of the transect depths, indicating that the majority of fishes' ranges encompass variations in depth of 20 meters or more.

Coral reef fishes are considered to be highly specialized and exhibit narrow home ranges, usually determined by availability of microhabitats or habitat patches (Sale 1977, Munday 2000, Gratwicke and Speight 2005, Wilson et al. 2008). Specific habitat associations and ontogenetic repartitioning of shallow fish species have been studied extensively (Adams and Ebersole 2002, Lecchini and Galzin 2005, DeMartini and Anderson 2007), but to date few studies have investigated non-ontogenetic shifts in habitat associations, especially with depth. The large depth ranges inhabited (30+ meters) by almost one-third of species observed in this study suggests that many of these small reef fishes may alter microhabitat associations based on availability of habitats at different depths. One example from this study is the distribution of *Chaetodon multicinctus* (Table 4). *C. multicinctus* is typically found on coral-rich reefs in less than 20m depth as it feeds primarily on polyps from the corals *Porites compressa* and *Pocillopora meandrina* (Randall 2007), but was commonly observed during our surveys at 30-40m depths where coral cover was extremely low and their two favored corals were absent. The persistence of common shallow coral reef fish species at mesophotic depths indicates the adaptability of highly specialized fishes to multiple environments and possible shifts in dietary preferences.

Depth was a significant factor structuring reef fish communities. Analysis of community similarities reveal over 52% of variation between fish assemblages was due to differences in depth, while only 17% was explained by differences between sites and 24% explained by geographic region. These results suggest that central and southern West Hawaii reef fish communities maintain consistency along West Hawaii within any particular depth profile, but change considerably between surveyed depths, while reef fish communities in the northern West Hawaii region maintain somewhat different communities from more southern sites but exhibit similar trends with depth. It is likely that changes in species richness and abundance are a result of changes in habitat at various depths, and not just of depth itself (Colin 1974). The steep slope of West Hawaii's reefs show maxima in reef fish species richness and density between 12-21 meters, with declines in both abundance and richness at shallower and deeper depths (Figure 2). It is interesting to note that fish richness and density in mesophotic reef areas (30m or 40m) were statistically similar to the 3m depths, indicating that depth itself is not necessarily a driving factor of reef fish species prevalence.

The richness and density maxima found here are shallower than other shallow/mesophotic studies from the Caribbean and Red Sea. Observations in Puerto Rico, Western Australia and Israel indicate reef fish species richness maxima at 25-30 meters, while fish densities decreased sharply below 30m in Puerto Rico and Western Australia and maintained consistent to shallow depths in Israel (Puerto Rico: Garcia-Sais 2010, Bejarano 2014; Western Australia: Fitzpatrick et al. 2012; Israel: Brokovich et al. 2008). West Hawaii's reefs are characterized by healthy stands of the branching coral *Porites compressa* from 10-25m depth (Dollar 1982, Jayewardene et al. 2009). West Hawaii is fairly protected from swell and wind waves relative to other locations in the Hawaiian Archipelago and tropical reefs in general. The calm waters of West Hawaii thus allow for fragile branching corals such as *P. compressa* to flourish in more shallow waters than other locations. Both above and below these depths, coral cover is reduced and shifts from branching morphologies to lobe or plate morphologies (Figure 7; Dollar 1982, Jayewardene et al. 2009). Numerous studies have documented the relationship between reef complexity and fish species richness and abundance in shallow waters (Syms and Jones 2000, Almany 2004). It is likely that reef fish richness and density maxima observed at 12-21m are related to the shallower occurrence of *P. compressa* and increased habitat complexity that it provides. It is important to note though that reef fish in West Hawaii have not been quantified below 40 meters, so it is possible that richness and density may differ at these deeper depths.

Some changes in reef fish community structure may not be due to habitat. While the abundance of macroalgae increases with depth, abundances of herbivorous fishes decrease with depth (Figures 6,8). Decreasing herbivorous fish abundances in mesophotic depths was first reported at Enewetak in the 1980s, yet has received scant attention until recently (Thresher and Colin 1986). This pattern has been confirmed in the Red Sea, Caribbean, and northwestern Hawaiian Islands, even though edible macroalgae was found to increase with depth at most of these locations (Brokovich et al. 2008, Brokovich et al. 2010, Garcia-Sais 2010, Kosaki et al. 2012, Bejarano et al. 2014). The trend of increased abundances of zooplanktivorous fishes at mesophotic depths is also supported at many locations worldwide (Thresher and Colin 1986, Brokovich et al. 2008, Garcia-Sais 2010, Kosaki et al. 2012, Bejarano et al. 2014).

Mechanisms behind the decrease in herbivores and increase in zooplanktivores with depth are currently unknown. Grazing pressure is reduced in mesophotic depths as compared to shallow regions even though palatable algae exists (Brokovich et al. 2010, Khang et al. 2010). While herbivore abundances have been positively correlated with temperature (Floeter et al. 2005), the only mesophotic study of herbivory suggests this is not the case (Brokovich et al. 2010). Additionally, the increase in zooplanktivorous fish abundance has been hypothesized to result from higher zooplankton abundances and more nutrient rich water at depth (Khang et al. 2010) yet the only study to evaluate zooplankton abundances at mesophotic depths report negligible abundances (Rodriguez-Jerez 2004). It is also noted that water clarity is increased in mesophotic depths, indicating plankton abundances may be decreased (R. Pyle, personal communication). More investigations are needed to confirm or refute possible mechanisms underlying these observed trophic shifts.

Accumulating baseline information on mesophotic coral reefs is imperative to enhance both general knowledge and predictive modeling capabilities for coral reef fishes. While habitat complexity is one of the main drivers of reef fish community composition in shallow waters, additional forces beyond habitat appear to gain importance with depth. Changes in reef fish trophic structure with depth do not follow correlations between fish trophic groups and habitats observed in shallow waters (Choat 1991, Hughes et al. 2007, Brokovich et al. 2010, Bejarano et al. 2014). It is therefore important to consider differential drivers of community structure with depth in future modeling efforts for population and community structure of reef fishes. In addition, the interplay between shallow and mesophotic reefs is poorly understood (Lesser et al. 2009, Khang et al. 2010, Khang et al. 2014). It is plausible that mesophotic reefs contribute to the richness and productivity of shallow reefs and thus warrant inclusion in future modeling efforts.

The mesophotic zone of coral reefs has typically been defined as beginning in 30 meters and extending to the lower distributional limit of light-dependent coral reef communities (Hinderstein et al. 2010, Khang et al. 2010). While the lower limits are biologically based, the upper limits of MCEs were originally designated by limitations of traditional SCUBA diving (30-40m; Khang et al. 2014). This classification has sometimes led to the assumption that mesophotic reefs are distinct ecosystems, separate from the more shallow reefs that have been well documented. This study highlights that while technically in the

MCE range, the 30 and 40m fish communities are extensions of the more shallow reefs, with more than 85% of the fish species observed at 30 or 40 meters depth typically associated with shallow waters. Our data does corroborate the few other mesophotic fish studies in that these shallow MCE regions act as transition zones between shallow and deep fish communities (Brokovich et al. 2008, Garcia-Sais 2010, Bejarano et al. 2014). Sixteen species of deep reef fishes were recorded at the 30, 40m depths, indicating that the reef fish community begins transitioning to deeper adapted species at these depths.

The extension of common shallow reef fish communities into mesophotic depths yields insight for current and future coral reef management initiatives in Hawaii and elsewhere. Given the reported decline of shallow coral reefs and bleak outlooks for their future, the occurrence of common shallow reef fishes at mesophotic depths has important conservation implications (Hoegh-Guldberg 1999, Pandolfi 2002, Bongaerts et al. 2010, Bridge et al. 2013). Recent investigations in Okinawa found healthy corals at upper mesophotic depths that were considered locally extinct in the shallow waters (Sinniger et al. 2013). As shallow reefs continue to decline due to local and global stressors, mesophotic reefs may become increasingly important habitat and refuge space for impacted shallow reef organisms, yet many coral reef policies only consider coral reef habitat in less than 20-30m of water (Riegl and Piller 2003, Bridge et al. 2013). As this research and others suggest, MCEs contain valuable habitat for commercially and recreationally important species and warrant consideration in future management and conservation planning.

Education and Outreach Activities

Posters**:**

Bogeberg MA, Kane CN, Tissot BN, Walsh W. 2013. Aquarium fish use of upper mesophotic coral reefs in West Hawaii. Poster session presented at: Western Society of Naturalists Meeting. 2013 Nov 7-10. Oxnard, CA.

Kane CN, Bogeberg MA, Tissot BN. 2014. Refuge in the deep: shallow coral reef fishes utilize mesophotic reef habitats in West Hawaii. Poster presented at: 2014 Ocean Sciences Meeting. 23-28 February 2014, Honolulu, HI.

Talks**:**

Tissot, BN. 2014. 2014. Managing Nemo: Conservation and Conflict in the Marine Aquarium Trade. Moss Landing Marine Laboratory, Moss Landing, CA.

Tissot, BN. 2014. 2014. Managing Nemo: Conservation and Conflict in the Marine Aquarium Trade. Sequoia Park Zoo, Eureka, CA.

Bogeberg MA, Kane CN, Tissot BN. 2014. Habitat Associations of yellow tang (*Zebrasoma flavescens*) from shallow to upper mesophotic corals reefs (3-40 m) in west

Hawaii. Contributed talk: Western Society of Naturalists Meeting. 2014 Nov 13-16. Tacoma, WA.

Kane CN, Bogeberg MA, Tissot BN. 2014. Shifts in coral reef fish community structure along a 40m depth gradient in west Hawaii. Contributed talk: Western Society of Naturalists Meeting. 2014 Nov 13-16. Tacoma, WA.

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Literature Cited

Adams AJ and JP Ebersole. 2002. Use of back-reef and lagoon habitats by coral reef fishes. *Mar Ecol Prog Ser* 228: 213-226.

Almany GR. 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 131(1): 105-113.

Bak RPM. G Nieuwland, EH Meesters. 2005. Coral reef crisis in deep and shallow reefs: 30 years of constancy and change in reefs of Curacao and Bonaire. *Coral Reefs* 24: 475-479.

Beijbom O, PJ Edmunds, DI Kline, GB Mitchell, and D Kriegman. 2012. Automated annotation of coral reef survey images. *IEEE Conference on Computer Vision and Pattern Recognition (CVPR)*, Providence, Rhode Island, June, 2012.

Bejarano I, RS Appeldoorn, and M Nemeth. 2014. Fishes associated with mesophotic coral ecosystems in La Parguera, Puerto Rico. *Coral Reefs* DOI 10.1007/s00338-014-1125-6

Boland RC and FA Parrish. 2005. A description of fish assemblages in the black coral beds off Lahaina, Maui, Hawaii. Pacific Science 59(3): 411-420.

Bongaerts P. T Ridgway, EM Sampayo, and O Hoegh-Guldberg. 2010a. Assessing the 'deep reef refugia' hypothesis: focus on Caribbean reefs. *Coral Reefs* 29: 309-327.

Bridge TCL, TP Hughes, GM Guinotte and P Bongaerts. 2013. Call to protect all coral reefs. *Nature Climate Change* 3: 528-530.

Brokovich E. S Einbinder, S Kark, N Shashar and M Kiflawi. 2007. A deep nursery for juveniles of the zebra angelfish *Genicanthus caudovittatus*. *Environ. Biol. Fish* 80: 1-6.

Brokovich E. S Einbinder, N Shashar, M Kiflawi, and S Kark. 2008. Descending to the twilight-zone: changes in coral reef fish assemblages along a depth gradient down to 65 m. *Mar Ecol Prog Ser* 371: 253-262.

Brokovich E, I Ayalon, S Einbinder, N Segev, Y Shaked, A Genin, S Kark, M Kiflwai. 2010. Grazing pressure on coral reefs decreases across a wide depth gradient in the Gulf of Aqaba, Red Sea. *Mar Ecol Prog Ser* 399:69-80.

Bryan DR. K Kilfoyle, RG Gilmore Jr. and RE Spieler. 2013. Characterization of the mesophotic reef fish community in south Florida, USA. *J. Appl. Ichthyol*. 29(2013): 108-117.

Choat JH. 1991. The biology of herbivorous fishes on coral reefs. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, CA, p 120−155.

Clarke KR. 1993. Nonparametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18: 117-143.

Colin PL. 1974. Observation and collection of deep reef fishes off the coasts of Jamaica and Honduras. *Mar Biol* 24(1): 29-38.

DeMartini EE and TW Anderson. 2007. Habitat associations and aggregation of recruit fishes on Hawaiian coral reefs. *Bull Mar Sci* 81(1): 139-152.

Dollar SJ. 1982. Wave stress and coral community structure in Hawaii. *Coral Reefs* 1: 71-81.

Feitzoa BM. RS Rosa, and LA Rocha. 2005. Ecology and zoogeography of deep-reef fishes in northeastern Brazil. *Bull. Mar. Sci.* 76(3): 725-742.

Fenner D. 2005. *Corals of Hawaii: A field guide to the hard, black, and soft corals of Hawaii and the northwest Hawaiian Islands, including Midway*. Mutual Publishing, LLC, Honolulu, HI. 144 pp.

Fitzpatrick BM, ES Harvey, AJ Heyward, EJ Twiggs, J Colquhoun. Habitat specialization in tropical continental shelf demersal fish assemblages. *PLoS ONE* 7(6): e39634. Doi:10.1371/journal.pone.0039634

Floeter SR, MD Behrens, CEL Ferreira, MJ Paddack and MH Horn. 2005. Geographical gradients of marine herbivorous fishes: patterns and processes. *Mar Biol.* 147(6): 1435-1447.

Fricke HW and H Schumacher. 1983. The depth limit of Red Sea stony corals: an ecophysiological problem (a deep diving survey by submersible). *Mar Biol* 4: 163-194.

Garcia-Sais JR. 2010. Reef habitats and associated sessile-benthic and fish assemblages across a euphotic-mesophotic depth gradient in Isla Desecheo, Puerto Rico. *Coral Reefs* 29: 277-288.

Gratwicke B and MR Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J. Fish Bio 66*: 650-667.

Hill J and C Wilkinson. 2004. Methods for ecological monitoring of coral reefs. Version 1. Australian Institute of Marine Science, Townsville AUS. 117pp.

Hinderstein LM, JCA Marr, FA Martinez, MJ Dowgiallo, KA Puglise, D Zawada, and R Pyle. 2010. Introduction to mesophotic coral ecosystems: Characterization, ecology, and management. *Coral Reefs* 29: 247-251.

Hixon, M.A. 2011. 60 years of coral reef fish ecology: past, present, future. *Bull. Mar. Sci* 87(4): 727-765.

Hoegh-Guldberg O. 1999. Climate change, coral bleaching and the future of the world's coral reefs. *Mar Freshw Res* 50:839-866.

Hughes TP, DR Bellwood, CS Folke, LJ McCook, JM Pandolfi. 2007. No-take areas, herbivory and coral reef resilience. *Trends Ecol Evol* 22: 1−3

Huisman JM, IA Abbott, CM Smith. 2007. *Hawaiian Reef Plants*. University of Hawaii Sea Grant College Program, Honolulu, HI. 264 pp.

Jayewardene D, MJ Donahue, C Birkeland. 2009. Effects of frequent fish predation on corals in Hawaii. *Coral Reefs* 28: 499-506.

Kane C, R Kosaki, D Wagner. 2014. High levels of mesophotic reef fish endemism in the Northwestern Hawaiian Islands. *Bull Mar Sci* 90(2): 693-703.

Kahng SE and JE Maragos. 2006. The deepest zooxanthellate, scleractininan corals in the world? *Coral Reefs* 25: 254.

Khang SE, JR Garcia-Sais, HL Spalding, E Brokovich, D Wagner, E Weil, L Hinderstein, and RJ Toonen. 2010. Community ecology of mesophotic coral reef ecosystems. *Coral Reefs* 29: 255-275.

Khang SE, JM Copus and D Wagner. 2014. Recent advances in the ecology of mesophotic coral ecosystems (MCEs). *Current Opinion in Environmental Sustainability* 7: 72-81.

Kosaki RK, C Kane, RL Pyle. 2012. Trophic structure of mesophotic fish assemblages in the northwestern Hawaiian Islands. *12th International Coral Reef Symposium:* Cairns, AUS 2012: 9C.

Lecchini D and R Galzin. 2005. Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). *Mar Biol* 147: 47-58.

Lesser MP. M Slattery and JJ Leichter. 2009. Ecology of mesophotic coral reefs. *J. Exp. Mar. Biol. Ecol.* 375: 1-8.

Liddell WD and SL Ohlhurst. 1988. Hard substrata community patterns, 1-120m, North Jamaica. *Palaios* 3: 413-423.

Liddell WD. WE Avery and SL Ohlhurst. 1997. Patterns of benthic community structure, 10-250m, the Bahamas. *Proc. 8th Int. Coral Reef Symp.* Vol 1 pp 437-442.

Maragos JE and P Jokiel. 1986. Reef corals of Johnston Atoll – one of the World's most isolated reefs. *Coral Reefs* 4: 141-150.

McGehee MA. 1994. Correspondence between assemblages of coral reef fishes and gradients of water motion, depth and substrate size off Puerto Rico. *Mar Ecol Prog Ser* 105: 243-255.

Menza, C. M. Kendall and S. Hile. 2008. The deeper we go the less we know. *Rev. Biol. Trop.* 56(1): 11-24

Munday PL. 2000. Interactions between habitat use and patterns of abundance in coral-dwelling fishes. *Environ. Biol Fishes* 58: 355-369.

Pandolfi JM. 2002. Coral community dynamics at multiple scales. *Coral Reefs* 21:13-23.

Parrish FA and RC Boland. 2004. Habitat and reef-fish assemblages of banks in the Northwestern Hawaiian Islands. *Mar Biol* 144: 1065-1073.

Pyle RL. 1996. How much coral reef biodiversity are we missing? *Global Biodiversity* 6(1): 3-7.

Pyle RL. 2000. Assessing undiscovered fish biodiversity on deep coral reefs using advanced self-contained diving technology. *Mar. Tech. Soc. J.* 34(4): 82-91.

Randall JE. 2007. *Reef and shore fishes of the Hawaiian Islands.* Sea Grant College Program, University of Hawaii, Honolulu Hawaii. pp. 546.

Reaka ML, PJ Rodgers and AU Kudla. 2008. Patterns of biodiversity and endemism on Indo-West Pacific coral reefs. *Proc Natl Acad Sci* USA 105: 11474-11481

Riegl B and WE Piller. 2003. Possible refugia for reefs in times of environmental stress. *Int J Earth Sci* 92: 520-531.

Rodriguez-Jerez Z. 2004. *Zooplankton communities of Isla Desecheo and adjacent waters of Mona Passage.* MS Thesis, Department of Marine Sciences, University of Puerto Rico. 85pp.

Sale PF. 1977. Maintenance of high diversity in coral reef fish communities. *Am Nat* 111(978): 337-359.

Sale PF. 1991. Ecology of coral reef fishes. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, San Diego, CA. pp 1-11.

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, et al. 2008. Baselines and degradation of coral reefs in the northern Line Islands. *PLoS ONE* 3(2): e1548. doi:10.1371/journal.pone.0001548

Schultz AL, HA Malcolm, DJ Bucher, M Linklater, SDA Smith. 2014. Depth and medium-scale spatial processes influence fish assemblage structure of unconsolidated habitats in a subtropical marine park. *PLoS ONE* 9(5): e96798. doi:10.1371/journal.pone.0096798.

Sinniger F, M Morita, S Harii. 2013. “Locally extinct” coral species *Seriatopora hystrix* found at upper mesophotic depths in Okinawa. *Coral Reefs* 32: 153.

Slattery M, MP Lesser, D Brazeau, MD Stokes, JJ Leichter. 2011. Connectivity and stability of mesophotic coral reefs. *J Exp Mar Biol Ecol* 408: 32-41.

Syms C and GP Jones. 2000. Habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81(10): 2714-2729.

Thresher RE and PL Colin. 1986. Trophic structure, diversity and abundance of fishes of the deep reef (30–300 m) at Enewetak, Marshall Islands. *Bull Mar Sci* 38: 253–272.

VanOppen MJH, P Bongaerts, JN Underwood, LM Peplow, TF Coopers. 2011. The role of deep reefs in shallow reef recovery: an assessment of vertical connectivity in a brooding coral from west and east Australia. *Mol Ecol* 20: 1647-1660.

Waddington KI. JJ Meeuwig, SN Evans, and LM Bellchambers. 2010. Assessment of the benthic biota of a deep coastal ecosystem by remote and in situ sampling techniques. *Mar. Fresh. Res.* 61: 1164-1170.

Wilson SK, SC Burgess, AJ Cheal, M Emslie, R Fisher, I Miller, NVC Polunin HPA Sweatman. 2008. Habitat utilization by coral reef fish: implications for specialists vs. generalists in a changing environment. *J Animal Ecol* 77: 220-228.

List of Tables

Table 1: Total species richness by family at each transect depth.

Family	3m	12m	21m	30m	40m
Acanthuridae	16	18	14	12	10
Apogonidae	1	1	1	1	1
Aulostomidae	1	1	1	1	1
Balistidae	5	4	3	4	4
Blennidae	4	3	1	2	0
Bothidae	1	0	0	0	0
Caracanthidae	1	1	0	0	0
Carangidae	1	2	1	0	3
Chaetodontidae	9	10	11	9	11
Cirrhitidae	3	3	3	2	1
Congridae	0	0	0	0	1
Gobidae	0	0	0	1	1
Holocentridae	2	7	7	3	4
Kyphosidae	1	0	0	0	0
Labridae	14	12	15	15	14
Lethrinidae	0	0	1	0	1
Lutjanidae	1	1	2	1	4
Malacanthidae	0	0	1	0	0
Monocanthidae	4	3	2	2	0
Mullidae	5	5	4	5	5
Muraenidae	3	2	1	1	3
Ostraciidae	1	1	1	1	2
Pinguipedidae	0	0	0	0	1
Pomacanthidae	0	3	2	2	3
Pomacentridae	8	12	10	8	6
Priacanthidae	1	0	0	0	0
Scaridae	5	5	6	6	2
Scorpaenidae	2	0	0	1	0
Serranidae	1	1	1	2	3
Sphyraenidae	1	0	0	0	0
Synodontidae	0	1	1	1	1
Tetradontidae	2	1	1	4	4
Zanclidae	1	1	1	1	1

Table 2: Number of species observed from one to five depths, indicating the proportion of depth specialists (found at only one or two contiguous depths) to depth generalists (found at four or more depths).

# Depths	# Species	% of Total
1	34	23%
2	24	16%
3	22	15%
4	30	20%
5	37	25%

Table 3: ANOSIM results for similarities in species presence between pairs of depths. Significant p-value after Bonferroni Correction (0.05/n): $p<0.0045$.

Depth Groups (m)	R	P
3, 12	0.53	0.001
3, 21	0.821	0.001
3, 30	0.9	0.001
3, 40	0.969	0.001
12, 21	0.209	0.041
12, 30	0.747	0.001
12, 40	0.852	0.001
21, 30	0.322	0.032
21, 40	0.473	0.001
30, 40	0.031	0.353

Table 4: SIMPER results for reef fish species responsible for ≥75% of the similarities within each transect depth. Fishes in bold indicate mesophotic species. Note increasing proportion of zooplanktivorous fishes with depth.

Depth	Species	Family	Trophic Guild	Avg. Abund.	Sim/SD	Cumulative %
3m	*Thalassoma duperrey*	Labridae	Invertivore	15.44	6.72	13.18
	Chromis vanderbilti	Pomacentridae	Zooplanktivore	30.91	2.17	26.12
	Acanthurus nigrofuscus	Acanthuridae	Herbivore	20.34	2.62	38.56
	Zebrasoma flavescens	Acanthuridae	Herbivore	7.84	1.89	46.39
	Ctenochaetus strigosis	Acanthuridae	Herbivore	10.11	0.99	52.19
	Paracirrhites arcatus	Cirrhitidae	Invertivore	4.45	1.57	57.10
	Stegastes fasciolatus	Pomacentridae	Herbivore	3.13	1.63	61.78
	Halichoeres ornatissimus	Labridae	Invertivore	2.10	5.17	66.25
	Gomphosus varius	Labridae	Invertivore	1.46	1.76	69.39
	Chaetodon quadrimaculatus	Chaetodontidae	Corallivore	0.88	2.05	72.05
	Plectroglyphidodon johnstonianus	Pomacentridae	Corallivore	1.08	0.94	74.44
	Sufflamen bursa	Balistidae	Invertivore	0.66	1.24	76.45
12m	*Chromis agilis*	Pomacentridae	Zooplanktivore	34.46	3.36	13.29
	Ctenochaetus strigosis	Acanthuridae	Herbivore	19.71	4.16	24.28
	Zebrasoma flavescens	Acanthuridae	Herbivore	15.44	4.35	33.97
	Acanthurus nigrofuscus	Acanthuridae	Herbivore	12.53	1.90	41.69
	Chromis vanderbilti	Pomacentridae	Zooplanktivore	25.60	0.97	49.28
	Thalassoma duperrey	Labridae	Invertivore	6.30	3.90	55.54
	Chaetodon multicintus	Chaetodontidae	Corallivore	5.81	3.92	61.39
	Paracirrhites arcatus	Cirrhitidae	Invertivore	4.49	1.66	65.54
	Plectroglyphidodon johnstonianus	Pomacentridae	Corallivore	2.31	5.51	69.19
	Pseudochelinus evanidus	Labridae	Invertivore	2.56	1.05	71.81
	Pseudochelinus octotaenia	Labridae	Invertivore	1.19	1.41	74.08
	Halichoeres ornatissimus	Labridae	Invertivore	0.96	1.72	76.09
21m	*Chromis agilis*	Pomacentridae	Zooplanktivore	40.58	1.53	13.59
	Ctenochaetus strigosis	Acanthuridae	Herbivore	14.67	3.16	25.14
	Zebrasoma flavescens	Acanthuridae	Herbivore	13.40	2.78	36.01
	Chaetodon multicintus	Chaetodontidae	Corallivore	3.92	5.08	42.39
	Thalassoma duperrey	Labridae	Invertivore	3.53	2.90	48.35
	Pseudochelinus evanidus	Labridae	Invertivore	4.97	1.20	52.86
	Acanthurus nigrofuscus	Acanthuridae	Herbivore	2.66	0.94	56.44
	Forcipiger flavissimus	Chaetodontidae	Invertivore	1.23	2.90	59.83
	Chlorurus sordidus	Scaridae	Herbivore	1.66	1.37	62.98
	Naso lituratus	Acanthuridae	Herbivore	1.00	3.72	66.12
	Centropyge potteri	Pomacanthidae	Herbivore	1.35	1.31	68.98
	Parupeneus multifasciatus	Mullidae	Invertivore	0.90	1.80	71.68
	Pseudochelinus octotaenia	Labridae	Invertivore	1.00	1.19	73.60

	Chaetodon ornatissimus	Chaetodontidae	Corallivore	0.56	1.16	75.37
30m	*Pseudochelinus evanidus*	Labridae	Invertivore	9.24	2.62	17.53
	Chromis leucura	Pomacentridae	Zooplanktivore	10.69	0.66	27.11
	Chromis agilis	Pomacentridae	Zooplanktivore	8.41	0.96	35.69
	Thalassoma duperrey	Labridae	Invertivore	1.96	2.49	43.86
	Acanthurus nigrofuscus	Acanthuridae	Herbivore	2.69	1.51	51.46
	Zebrasoma flavescens	Acanthuridae	Herbivore	2.96	2.25	58.55
	Chaetodon multicintus	Chaetodontidae	Corallivore	1.00	1.24	62.37
	Parupeneus multifasciatus	Mullidae	Invertivore	0.74	1.24	65.98
	Naso lituratus	Acanthuridae	Herbivore	0.55	1.24	69.29
	Sufflamen bursa	Balistidae	Invertivore	0.62	0.92	72.44
	Centropyge fisheri	Pomacanthidae	Herbivore	1.25	0.80	75.46
40m	*Chromis agilis*	Pomacentridae	Zooplanktivore	10.76	1.39	11.73
	Pseudochelinus evanidus	Labridae	Invertivore	5.43	2.70	22.91
	Thalassoma duperrey	Labridae	Invertivore	2.79	8.01	32.22
	Chromis leucura	Pomacentridae	Zooplanktivore	8.07	0.84	40.31
	Sufflamen bursa	Balistidae	Invertivore	1.23	4.38	46.00
	Acanthurus nigrofuscus	Acanthuridae	Herbivore	2.37	1.52	51.59
	Ctenochaetus strigosis	Acanthuridae	Herbivore	1.90	0.88	56.70
	Zebrasoma flavescens	Acanthuridae	Herbivore	1.54	1.15	61.46
	Forcipiger flavissimus	Chaetodontidae	Invertivore	0.96	1.06	65.28
	Chaetodon multicintus	Chaetodontidae	Corallivore	0.55	1.67	68.77
	Xanthicthys auromarginatus	Balistidae	Zooplanktivore	1.35	0.84	71.85
	Parupeneus multifasciatus	Mullidae	Invertivore	0.50	1.22	74.65
	Chromis verater	Pomacentridae	Zooplanktivore	1.64	0.51	77.00

List of Figures

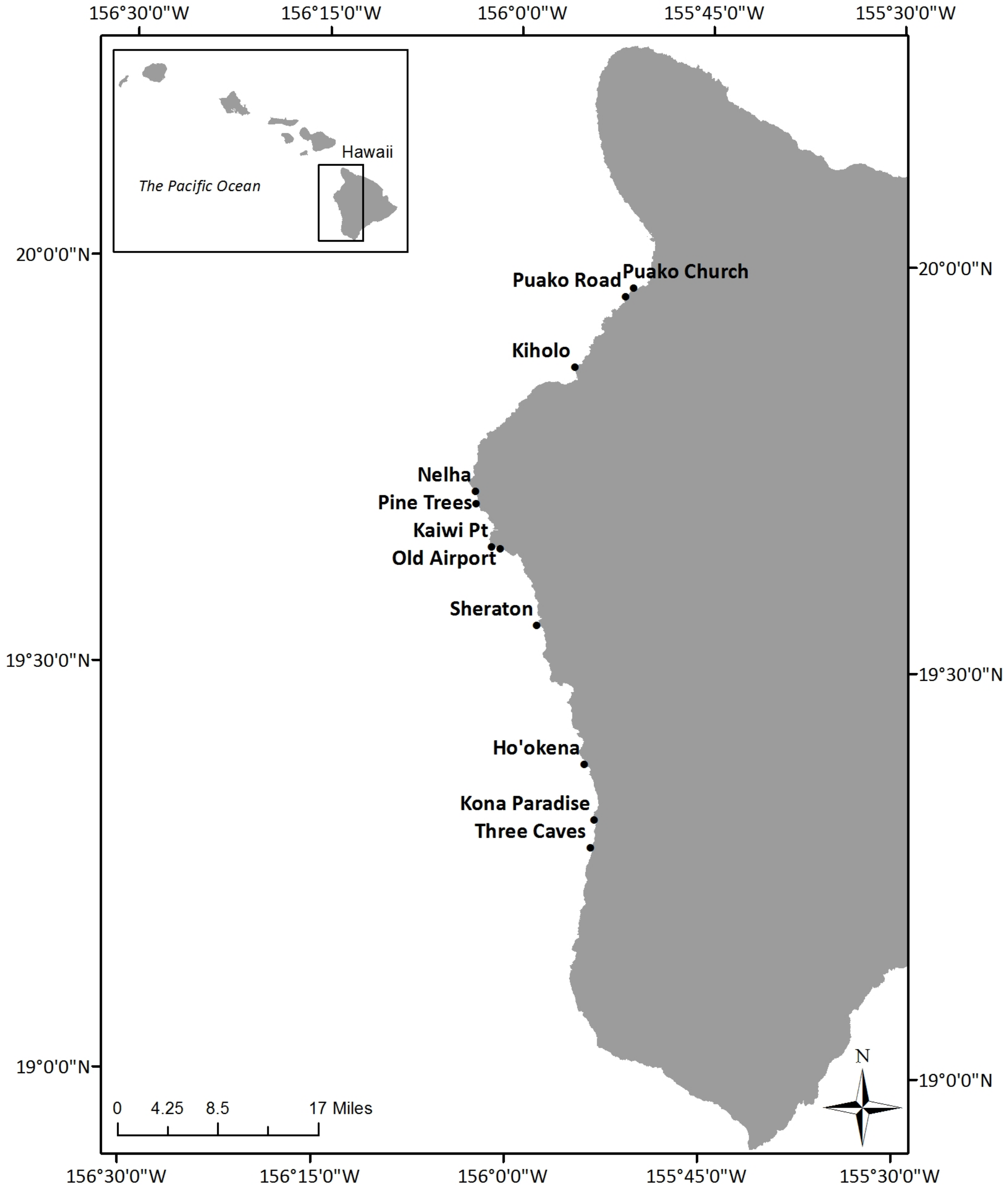

Figure 1: Location of study sites in West Hawaii. Eleven sites were selected based on continuous habitat from 3-40+ meters depth.

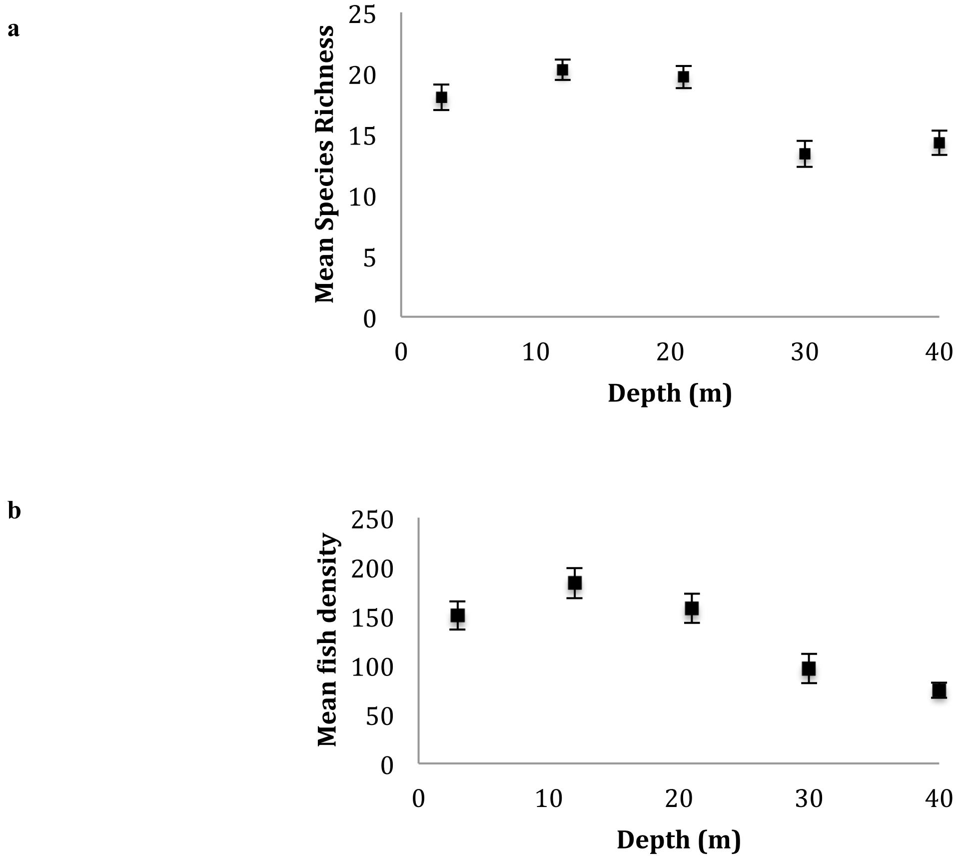

Figure 2: Changes in a) species richness and b) number of fishes per $100m^2$ at each transect depth. Error bars indicate ± 1 SE.

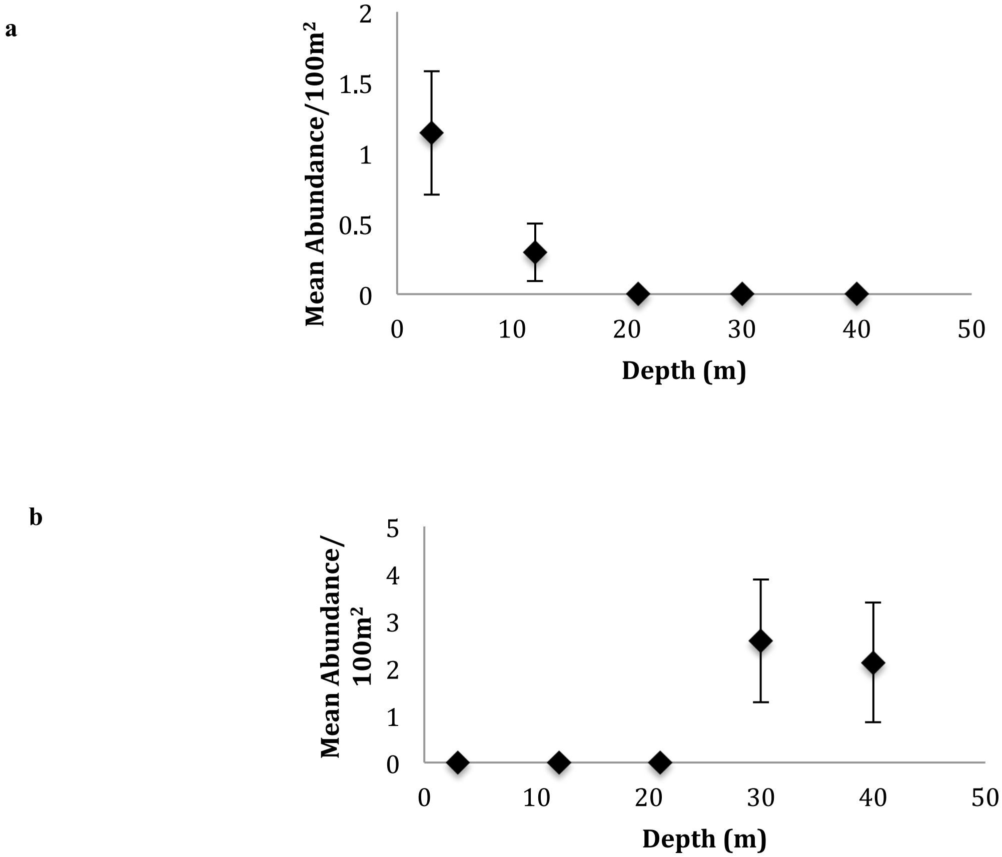

Figure 3: Examples of differing species abundance patterns (mean ± SE) with depth for “depth specialist” fishes found at only one or two depths. a) Shallow specialist (*Caracanthus typicus*), 26 species were found only in the 3 and/or 12m depths, b) Deep specialist (*Cirrhilabrus jordani*), 21 species were found only in the 30 and/or 40m depths.

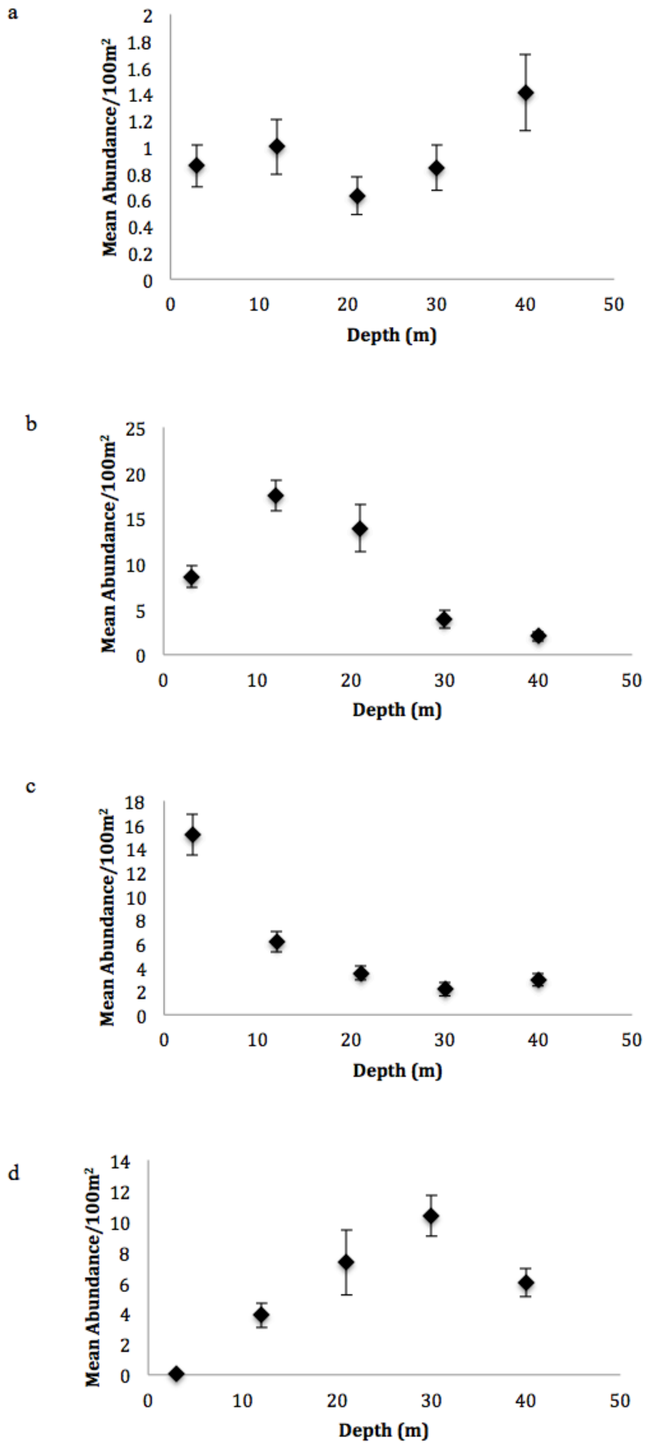

Figure 4: Examples of differing species abundance patterns (mean ± SE) with depth for "depth generalist" fishes found at four or five depths. a) Non-significant depth pattern (*Sufflamen bursa*), accounting for 52% of depth generalist species; b) Hump-shaped distribution with depth (*Zebrasoma flavescens*), accounting for 16% of generalist species; c) Decreasing abundance with depth (*Thalassoma duperrey*), accounting for 16% of generalist species; and d) Increasing pattern with depth (*Pseudochelinus evanidus*), accounting for 12% of generalist species.

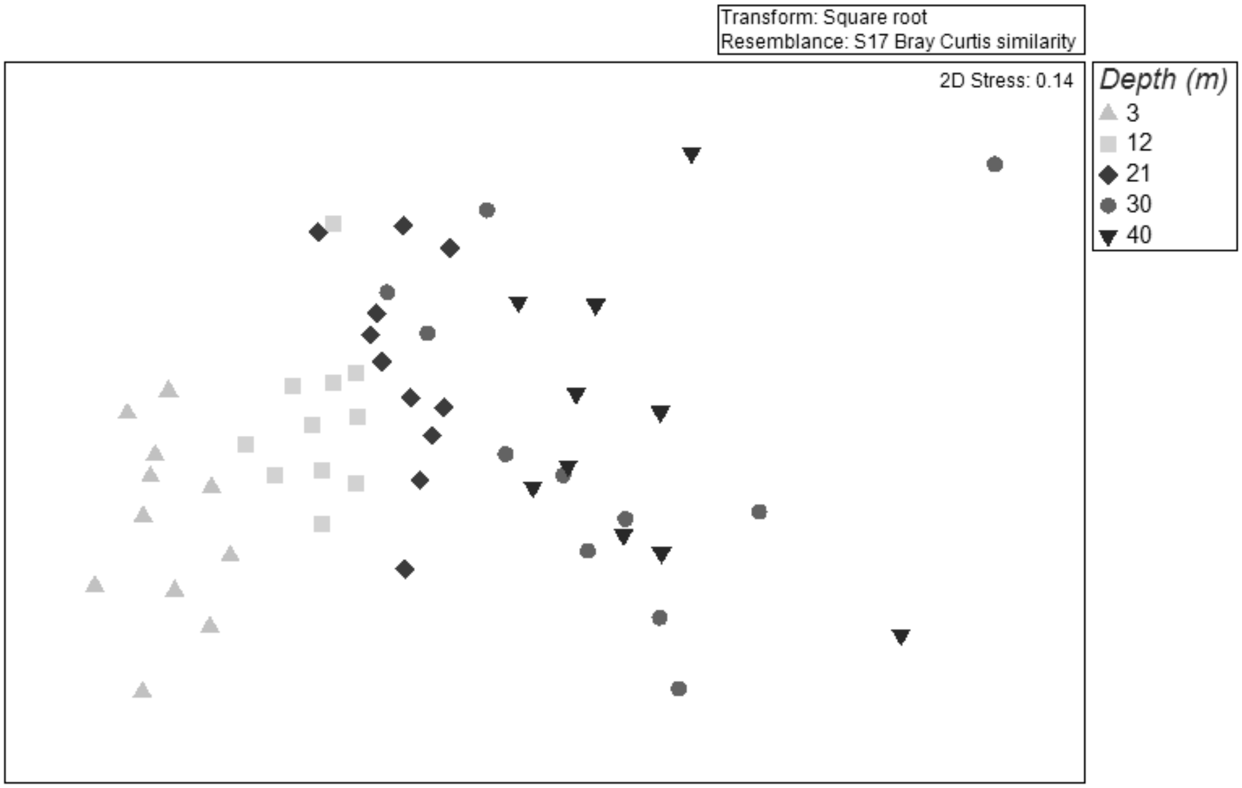

Figure 5: nMDS ordination of square-root transformed fish community structure at eleven sites in West Hawaii from 3-40m.

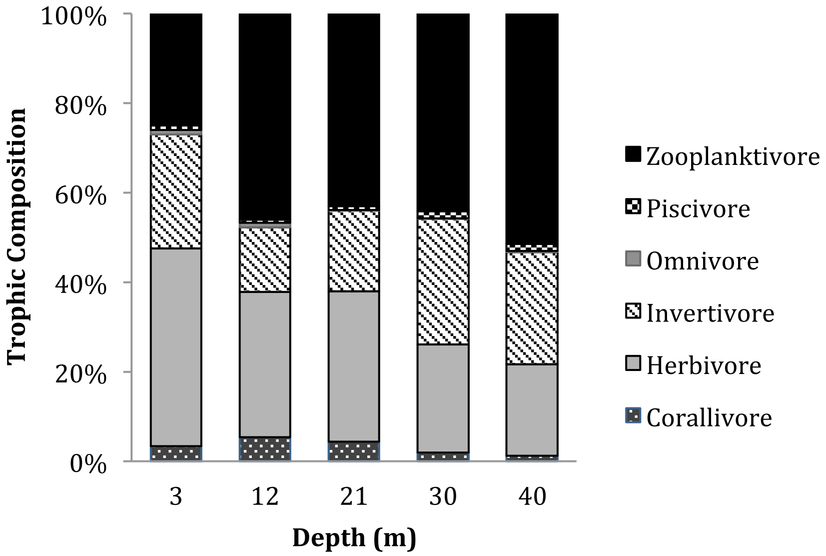

Figure 6: Mean proportion of reef fish trophic guilds per 100m^2 at each transect depth.

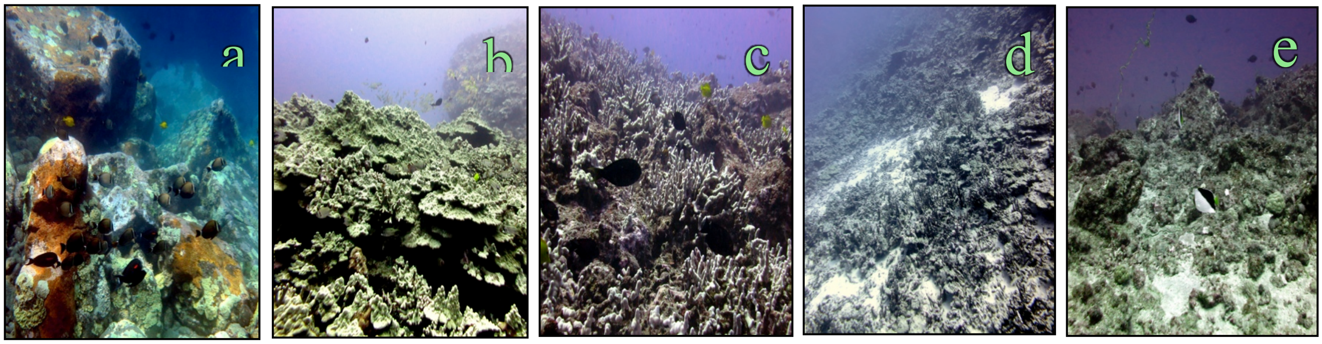

Figure 7: Coral reef habitat at a) 3m; b) 12m; c) 21m; d) 30m; and e) 40m. Note decrease in coral cover and complexity in deep habitats, which mostly contained coral rubble and rock outcroppings.

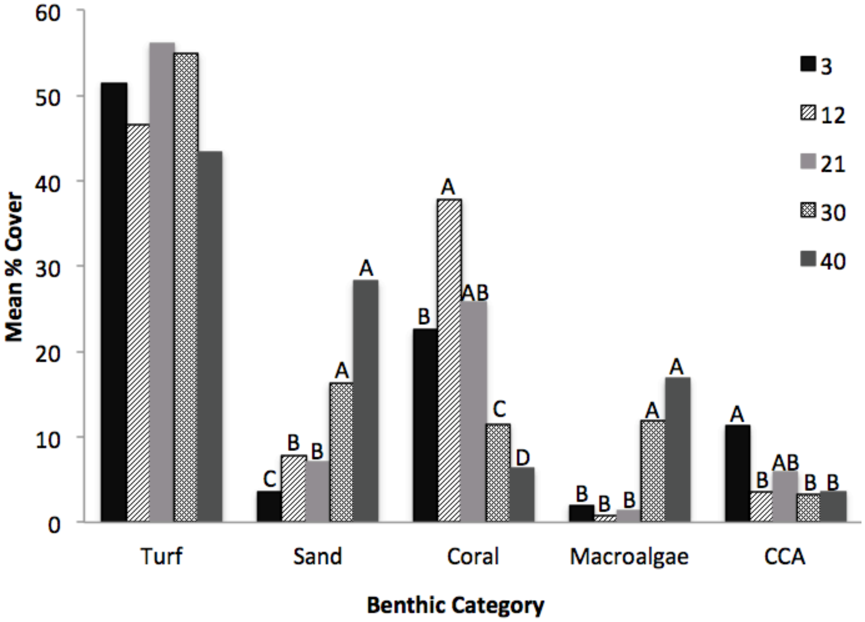

Figure 8: Mean percent cover by transect of prominent benthic categories along depth gradient. Letters indicate significant differences between depths within each category.

Supplementary Material:

ESM 1: Abundance of fishes at each transect depth recorded from eleven locations along West Hawaii. Grey shaded columns indicate mesophotic depths. Species in bold indicate fish species recorded only at mesophotic depths. MD =mean density, SE=standard error.

			3m		12m		21m		30m		40m	
Species	**Trophic Group**	**Family**	**MD**	**SE**	**MD**	**SE**	**MD**	**SE**	**MD**	**SE**	**MD**	**SE**
Abudefduf abdominalis	Zooplanktivore	Pomacentridae	0.91	0.66	0.49	0.36	0.34	0.34	0.00	0.00	0.00	0.00
Abudefduf vaigiensis	Zooplanktivore	Pomacentridae	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Acanthurus achilles	Herbivore	Acanthuridae	0.26	0.13	0.16	0.07	0.05	0.05	0.00	0.00	0.00	0.00
Acanthurus blochii	Herbivore	Acanthuridae	0.11	0.09	0.05	0.04	0.03	0.03	0.00	0.00	0.00	0.00
Acanthurus dussimieri	Herbivore	Acanthuridae	0.20	0.15	0.30	0.17	0.08	0.04	0.08	0.06	0.26	0.11
Acanthurus guttatus	Herbivore	Acanthuridae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acanthurus leucopareius	Herbivore	Acanthuridae	3.83	2.08	0.05	0.04	0.11	0.11	0.08	0.08	0.00	0.00
Acanthurus nigricans	Herbivore	Acanthuridae	0.20	0.13	0.11	0.05	0.16	0.09	0.13	0.11	0.00	0.00
Acanthurus nigrofuscus	Herbivore	Acanthuridae	22.11	3.53	13.62	2.42	4.37	0.91	3.00	0.66	3.29	0.71
Acanthurus nigroris	Herbivore	Acanthuridae	0.74	0.64	0.22	0.14	0.42	0.24	0.74	0.64	0.00	0.00
Acanthurus olivaceous	Herbivore	Acanthuridae	0.97	0.61	0.73	0.23	0.92	0.29	0.61	0.17	0.65	0.17
Acanthurus thompsoni	Zooplanktivore	Acanthuridae	0.00	0.00	0.16	0.16	1.45	0.67	0.11	0.11	0.76	0.53
Acanthurus triosteges	Herbivore	Acanthuridae	0.31	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Acanthurus xanthopterus	**Herbivore**	**Acanthuridae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.05**	**0.05**	**0.09**	**0.06**
Anampses chrysocephalus	Invertivore	Labridae	0.00	0.00	0.00	0.00	0.16	0.12	0.16	0.16	0.15	0.12
Aphareus furca	Piscivore	Lutjanidae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03
Apolemichthys arcuatus	Invertivore	Pomacanthidae	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.12	0.09
Aprion virenscens	Piscivore	Lutjanidae	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.03	0.03	0.03
Arothron hispidus	**Omnivore**	**Tetradontidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**	**0.00**	**0.00**
Aulotomus chinensis	Piscivore	Aulostomidae	0.20	0.07	0.27	0.09	0.37	0.10	0.11	0.05	0.06	0.04
Bodianus albotaneatus	Invertivore	Labridae	0.00	0.00	0.03	0.03	0.05	0.04	0.08	0.04	0.18	0.08
Bothus mancus	Invertivore	Bothidae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Bryaninops yongei	**Unknown**	**Gobidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**

Calotomus carolinus	Herbivore	Scaridae	0.03	0.03	0.05	0.04	0.11	0.05	0.11	0.08	0.00	0.00
Cantherhines dumerilli	Corallivore	Monocanthidae	0.06	0.04	0.03	0.03	0.00	0.00	0.03	0.03	0.00	0.00
Cantherhines sandwichensis	Omnivore	Monocanthidae	0.00	0.00	0.03	0.03	0.05	0.04	0.00	0.00	0.00	0.00
Cantherhines verecundus	Herbivore	Monocanthidae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Canthigaster amboinensis	Herbivore	Tetradontidae	0.23	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.03
Canthigaster coronata	**Herbivore**	**Tetradontidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.13**	**0.08**	**0.24**	**0.11**
Canthigaster epilampra	**Herbivore**	**Tetradontidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.08**	**0.06**	**0.29**	**0.13**
Canthigaster jactator	Herbivore	Tetradontidae	1.14	0.26	0.84	0.18	0.32	0.10	0.45	0.13	0.79	0.17
Caracanthus typicus	Unknown	Caracanthidae	1.14	0.44	0.30	0.20	0.00	0.00	0.00	0.00	0.00	0.00
Caranx melampygus	Piscivore	Carangidae	0.26	0.18	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Centropyge fisheri	Herbivore	Pomacanthidae	0.00	0.00	0.03	0.03	1.03	0.38	2.79	0.83	0.79	0.30
Centropyge potteri	Herbivore	Pomacanthidae	0.00	0.00	1.05	0.29	1.76	0.34	0.68	0.23	0.82	0.24
Cephalopholis argus	Piscivore	Serranidae	0.11	0.07	0.24	0.11	0.37	0.11	0.11	0.08	0.21	0.13
Chaetodon auriga	Invertivore	Chaetodontidae	0.17	0.09	0.27	0.22	0.03	0.03	0.00	0.00	0.06	0.06
Chaetodon kleinii	Zooplanktivore	Chaetodontidae	0.00	0.00	0.00	0.00	0.39	0.13	0.61	0.18	0.71	0.21
Chaetodon lunula	Invertivore	Chaetodontidae	2.00	1.80	0.46	0.33	0.08	0.06	0.11	0.07	0.18	0.10
Chaetodon lunulatus	Corallivore	Chaetodontidae	0.06	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Chaetodon miliaris	Zooplanktivore	Chaetodontidae	0.00	0.00	0.00	0.00	0.13	0.09	0.03	0.03	0.35	0.23
Chaetodon multicintus	Corallivore	Chaetodontidae	1.37	0.35	5.95	0.72	4.11	0.48	1.32	0.25	0.65	0.17
Chaetodon ornatissimus	Corallivore	Chaetodontidae	0.57	0.17	0.68	0.16	0.71	0.18	0.21	0.09	0.06	0.06
Chaetodon quadrimaculatus	Corallivore	Chaetodontidae	1.00	0.21	0.24	0.11	0.03	0.03	0.00	0.00	0.00	0.00
Chaetodon tinkerii	**Omnivore**	**Chaetodontidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**	**0.18**	**0.10**
Chaetodon unimaculatus	Corallivore	Chaetodontidae	0.14	0.08	0.14	0.07	0.08	0.06	0.08	0.08	0.00	0.00
Chlorurus perspicillatus	Herbivore	Scaridae	0.00	0.00	0.00	0.00	0.03	0.03	0.03	0.03	0.00	0.00
Chlorurus sordidus	Herbivore	Scaridae	1.54	0.72	0.81	0.38	1.89	0.47	1.50	0.80	0.62	0.32
Chromis agilis	Zooplanktivore	Pomacentridae	0.49	0.37	35.46	8.29	55.03	11.05	13.68	5.03	13.85	3.81
Chromis hanui	Zooplanktivore	Pomacentridae	0.06	0.06	2.24	0.57	1.87	0.85	1.42	0.66	0.94	0.39
Chromis leucura	Zooplanktivore	Pomacentridae	0.00	0.00	0.08	0.06	1.55	0.91	31.71	11.3	12.82	3.94

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Chromis ovalis	Zooplanktivore	Pomacentridae	0.06	0.06	2.22	2.16	0.05	0.05	1.18	1.18	0.26	0.26
Chromis vanderbilti	Zooplanktivore	Pomacentridae	43.06	10.37	37.81	8.90	12.84	8.26	0.16	0.16	0.00	0.00
Chromis verater	Zooplanktivore	Pomacentridae	0.00	0.00	0.05	0.05	0.61	0.58	0.03	0.03	4.18	1.63
Cirrhilabrus jordani	**Zooplanktivore**	**Labridae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**2.58**	**1.30**	**2.12**	**1.27**
Cirrhitops fasciatus	Invertivore	Cirrhitidae	0.03	0.03	0.03	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Cirripectes vanderbilti	Herbivore	Blennidae	0.14	0.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Coris gaimard	Invertivore	Labridae	0.57	0.25	0.32	0.16	0.21	0.09	0.21	0.11	0.12	0.06
Ctenochaetus hawaiiensis	Herbivore	Acanthuridae	0.43	0.20	1.05	0.41	0.74	0.16	0.26	0.11	0.62	0.38
Ctenochaetus strigosis	Herbivore	Acanthuridae	15.54	4.46	21.32	2.17	16.18	2.15	3.87	1.48	2.56	0.73
Dascyllus albisella	Zooplanktivore	Pomacentridae	0.00	0.00	0.30	0.20	1.08	0.44	0.66	0.39	0.59	0.31
Decapterus macarellus	Zooplanktivore	Carangidae	0.00	0.00	0.19	0.16	0.13	0.13	0.00	0.00	0.18	0.18
Dendrochirus barberi	Invertivore	Scorpaenidae	0.14	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Diodon hystrix	Invertivore	Tetradontidae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Elagatis bipinnulata	**Zooplanktivore**	**Carangidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Exallias brevis	Corallivore	Blennidae	0.06	0.04	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Forcipiger flavissimus	Invertivore	Chaetodontidae	0.71	0.17	0.73	0.17	1.34	0.21	1.21	0.36	1.29	0.29
Forcipiger longirostris	Invertivore	Chaetodontidae	0.20	0.10	0.38	0.13	0.71	0.25	0.16	0.08	0.03	0.03
Gnatholepis anjerensis	**Zooplanktivore**	**Gobidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**	**0.00**	**0.00**
Gomphosus various	Invertivore	Labridae	1.69	0.36	0.59	0.16	0.18	0.08	0.26	0.17	0.00	0.00
Gorgasia hawaiiensis	**Zooplanktivore**	**Congridae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.24**	**0.24**
Gymnothorax flavimarginatus	Piscivore	Muraenidae	0.03	0.03	0.03	0.03	0.00	0.00	0.03	0.03	0.09	0.06
Gymnothorax melatremus	Piscivore	Muraenidae	0.20	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Gymnothorax meleagris	Piscivore	Muraenidae	0.09	0.05	0.03	0.03	0.03	0.03	0.00	0.00	0.03	0.03
Gymnothorax rueppellii	**Piscivore**	**Muraenidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Halichoeres ornatissimus	Invertivore	Labridae	2.17	0.44	1.08	0.22	0.32	0.11	0.42	0.27	0.15	0.07
Hemitaurichthys polylepis	Zooplanktivore	Chaetodontidae	0.00	0.00	0.81	0.81	0.26	0.19	0.00	0.00	0.82	0.82
Hemitaurichthys thompsoni	Zooplanktivore	Chaetodontidae	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00

Heniochus diphreutes	**Zooplanktivore**	**Chaetodontidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.06**	**0.06**
Iniistius pavo	**Invertivore**	**Labridae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Kyphosus sandwicensis	Herbivore	Kyphosidae	0.06	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Labroides phthirophagus	Invertivore	Labridae	0.09	0.05	0.86	0.18	0.68	0.16	0.16	0.06	0.24	0.10
Lutjanis fulvus	**Invertivore**	**Lutjanidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Lutjanus kasmira	Invertivore	Lutjanidae	0.00	0.00	0.03	0.03	3.68	3.68	0.00	0.00	0.44	0.23
Macropharyngodon geoffery	Invertivore	Labridae	0.51	0.37	0.00	0.00	0.03	0.03	0.18	0.14	0.03	0.03
Malacanthus brevirostris	Invertivore	Malacanthidae	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.00	0.00	0.00
Melichthys niger	Omnivore	Balistidae	1.11	0.37	1.97	0.82	0.00	0.00	0.00	0.00	0.00	0.00
Melichthys vidua	Herbivore	Balistidae	0.11	0.09	0.19	0.09	0.29	0.13	0.21	0.09	0.18	0.08
Monotaxis grandoculus	Invertivore	Lethrinidae	0.00	0.00	0.00	0.00	0.11	0.08	0.00	0.00	0.09	0.06
Mulloidichthys flavolineatus	Invertivore	Mullidae	0.09	0.09	0.19	0.19	0.00	0.00	0.50	0.28	0.29	0.20
Mulloidichthys vanicolensis	Invertivore	Mullidae	0.03	0.03	0.05	0.05	1.63	1.16	0.00	0.00	0.00	0.00
Myripristis berndtii	Zooplanktivore	Holocentridae	0.06	0.06	0.08	0.05	0.26	0.17	0.00	0.00	0.09	0.09
Myripristis chryseres	Zooplanktivore	Holocentridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Myripristis kuntee	Zooplanktivore	Holocentridae	0.03	0.03	0.84	0.50	0.84	0.29	0.08	0.06	0.03	0.03
Naso brevirostris	Zooplanktivore	Acanthuridae	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Naso hexacanthus	Zooplanktivore	Acanthuridae	0.00	0.00	3.73	2.72	0.92	0.52	0.00	0.00	0.41	0.30
Naso lituratus	Herbivore	Acanthuridae	0.80	0.28	0.95	0.23	1.11	0.23	0.71	0.20	0.32	0.09
Naso unicornis	Herbivore	Acanthuridae	0.17	0.10	0.05	0.05	0.00	0.00	0.00	0.00	0.29	0.24
Neoniphon sammara	Invertivore	Holocentridae	0.00	0.00	0.03	0.03	0.11	0.06	0.03	0.03	0.00	0.00
Novaculichthys taeniourus	Invertivore	Labridae	0.00	0.00	0.00	0.00	0.05	0.04	0.00	0.00	0.00	0.00
Ostracion meleagris	Invertivore	Ostraciidae	0.20	0.09	0.11	0.08	0.05	0.04	0.05	0.04	0.09	0.06
Ostracion whitleyi	**Invertivore**	**Ostraciidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Oxychelinus bimaculatus	**Invertivore**	**Labridae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**	**0.29**	**0.17**
Oxychelinus unimaculatus	Piscivore	Labridae	0.14	0.08	0.32	0.13	0.37	0.10	0.24	0.11	0.15	0.07
Paracirrhites arcatus	Invertivore	Cirrhitidae	5.89	1.36	5.46	0.98	1.55	0.42	0.47	0.25	0.09	0.05
Paracirrhites forsteri	Invertivore	Cirrhitidae	0.31	0.13	0.32	0.10	0.13	0.07	0.03	0.03	0.00	0.00

Parapercis schauinslandii	**Invertivore**	**Pinguipedidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Parupeneus cyclostomus	Piscivore	Mullidae	0.09	0.06	0.05	0.04	0.24	0.15	0.03	0.03	0.26	0.12
Parupeneus insularis	Invertivore	Mullidae	0.11	0.05	0.03	0.03	0.24	0.14	0.03	0.03	0.15	0.10
Parupeneus multifasciatus	Invertivore	Mullidae	0.34	0.10	0.70	0.25	1.03	0.21	1.11	0.40	0.68	0.16
Parupeneus pleurostigma	**Invertivore**	**Mullidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.11**	**0.05**	**0.09**	**0.09**
Pervagor aspricadus	Omnivore	Monocanthidae	0.03	0.03	0.11	0.08	0.03	0.03	0.03	0.03	0.00	0.00
Pervagor spilosoma	Omnivore	Monocanthidae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Plagiotremus ewaensis	Piscivore	Blennidae	0.26	0.13	0.08	0.05	0.08	0.06	0.05	0.05	0.00	0.00
Plagiotremus goslinei	Piscivore	Blennidae	0.17	0.10	0.00	0.00	0.00	0.00	0.03	0.03	0.00	0.00
Plectrogliphodon johnstonianus	Corallivore	Pomacentridae	1.63	0.40	2.49	0.46	1.32	0.31	0.24	0.14	0.00	0.00
Plectroglyphidodon imparipennis	Zooplanktivore	Pomacentridae	0.69	0.22	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Priacanthus meeki	Piscivore	Priacanthidae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Pristiapogon kallopterus	Zooplanktivore	Apogonidae	0.06	0.04	0.14	0.08	0.53	0.16	0.16	0.16	0.21	0.11
Pseudanthias bicolor	**Zooplanktivore**	**Serranidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.82**	**0.82**
Pseudanthias hawaiiensis	**Zooplanktivore**	**Serranidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.08**	**0.08**	**0.06**	**0.06**
Pseudochelinus evanidus	Invertivore	Labridae	0.09	0.05	3.89	0.81	7.32	2.11	10.37	1.33	6.03	0.93
Pseudochelinus octotaenia	Invertivore	Labridae	0.17	0.09	1.59	0.25	1.71	0.43	0.32	0.10	0.06	0.04
Pseudochelinus tetrataenia	Invertivore	Labridae	0.14	0.07	0.35	0.19	0.08	0.04	0.00	0.00	0.00	0.00
Pseudojuloides ceracinus	Invertivore	Labridae	0.00	0.00	0.00	0.00	0.53	0.30	0.95	0.53	0.50	0.28
Rhinecanthus rectangulatus	Omnivore	Balistidae	0.20	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Sargocentron diadema	Invertivore	Holocentridae	0.00	0.00	0.08	0.05	0.18	0.14	0.03	0.03	0.44	0.44
Sargocentron spiniferun	Invertivore	Holocentridae	0.00	0.00	0.03	0.03	0.05	0.05	0.00	0.00	0.03	0.03
Sargocentron tiere	Invertivore	Holocentridae	0.00	0.00	0.03	0.03	0.03	0.03	0.00	0.00	0.00	0.00
Sargocentron xantherythrum	Invertivore	Holocentridae	0.00	0.00	0.03	0.03	0.37	0.24	0.00	0.00	0.00	0.00
Scarus dubius	Herbivore	Scaridae	0.06	0.04	0.05	0.04	0.11	0.08	0.47	0.26	0.00	0.00
Scarus psittacus	Herbivore	Scaridae	1.00	0.55	0.03	0.03	0.32	0.17	0.61	0.36	0.00	0.00
Scarus rubroviolaceus	Herbivore	Scaridae	0.06	0.06	0.14	0.10	0.05	0.04	0.16	0.11	0.03	0.03

Scorpaenopsis diabolus	**Piscivore**	**Scorpaenidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**	**0.00**	**0.00**
Sebastapistes coniorta	Invertivore	Scorpaenidae	0.09	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Seriola dumerili	**Piscivore**	**Carangidae**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.03**	**0.03**
Sphyraena barracuda	Piscivore	Sphyraenidae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Stegastes fasciolatus	Herbivore	Pomacentridae	3.60	0.82	0.54	0.34	0.03	0.03	0.00	0.00	0.00	0.00
Stethojulis balteata	Invertivore	Labridae	0.91	0.23	0.30	0.11	0.16	0.06	0.16	0.10	0.00	0.00
Sufflamen bursa	Invertivore	Balistidae	0.86	0.16	1.00	0.21	0.63	0.14	0.84	0.17	1.41	0.29
Sufflamen fraenatum	Invertivore	Balistidae	0.20	0.20	0.00	0.00	0.00	0.00	0.08	0.04	0.12	0.06
Synodus sp.	Piscivore	Synodontidae	0.00	0.00	0.11	0.06	0.03	0.03	0.08	0.06	0.06	0.04
Thalassoma balleui	Invertivore	Labridae	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Thalassoma duperrey	Invertivore	Labridae	15.17	1.75	6.14	0.86	3.50	0.56	2.13	0.54	2.94	0.51
Thalassoma trilobatum	Invertivore	Labridae	0.54	0.51	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wrasse unidentified	Unknown	Labridae	0.06	0.06	0.03	0.03	0.00	0.00	0.00	0.00	0.00	0.00
Xanthichthys auromarginatus	Zooplanktivore	Balistidae	0.00	0.00	0.19	0.12	0.58	0.40	0.24	0.09	2.65	0.87
Zanclus cornutus	Invertivore	Zanclidae	0.20	0.08	0.32	0.16	0.29	0.12	0.24	0.11	0.21	0.11
Zebrasoma flavescens	Herbivore	Acanthuridae	8.57	1.23	17.51	1.69	13.89	2.61	3.92	1.02	2.03	0.52
Zebrasoma veliferum	Herbivore	Acanthuridae	0.09	0.06	0.08	0.08	0.00	0.00	0.00	0.00	0.00	0.00

ESM 2: Depth trends for species found at four or more transect depths.

Species	**Trophic Guild**	**Family**	**F**	**P**	**Decreases**	**Increases**	**Hump**
Acanthurus leucopareius	Herbivore	Acanthuridae	8.56	0.0001	x		
Acanthurus nigrofuscus	Herbivore	Acanthuridae	18.72	0.0001	x		
Chaetodon ornatissimus	Corallivore	Chaetodontidae	5.01	0.0008	x		
Chromis vanderbilti	Zooplanktivore	Pomacentridae	18.35	0.0001	x		
Gomphosus various	Invertivore	Labridae	13.89	0.0001	x		
Halichoeres ornatissimus	Invertivore	Labridae	13.52	0.0001	x		
Paracirrhites arcatus	Invertivore	Cirrhitidae	24.63	0.0001	x		
Paracirrhites forsteri	Invertivore	Cirrhitidae	4.15	0.003	x		
Scarus psittacus	Herbivore	Scaridae	2.55	0.041	x		
Stethojulis balteata	Invertivore	Labridae	8.32	0.0001	x		
Thalassoma duperrey	Invertivore	Labridae	26.82	0.0001	x		
Centropyge fisheri	Herbivore	Pomacanthidae	11.21	0.0001		x	
Centropyge potteri	Herbivore	Pomacanthidae	8.34	0.0001		x	
Chromis hanui	Zooplanktivore	Pomacentridae	4.16	0.003		x	
Chromis leucura	Zooplanktivore	Pomacentridae	14.09	0.0001		x	
Chromis verater	Zooplanktivore	Pomacentridae	8.55	0.0001		x	
Pseudochelinus evanidus	Invertivore	Labridae	20.87	0.0001		x	
Scarus dubius	Herbivore	Scaridae	2.61	0.037		x	
Xanthichthys auromarginatus	Zooplanktivore	Balistidae	8.74	0.0001		x	
Acanthurus thompsoni	Zooplanktivore	Acanthuridae	3.91	0.005			x
Aulotomus chinensis	Piscivore	Aulostomidae	2.70	0.032			x
Chaetodon multicintus	Corallivore	Chaetodontidae	28.61	0.0001			x
Chromis agilis	Zooplanktivore	Pomacentridae	16.83	0.0001			x
Ctenochaetus strigosis	Herbivore	Acanthuridae	22.03	0.0001			x
Labroides phthirophagus	Invertivore	Labridae	8.88	0.0001			x

Myripristis kuntee	Zooplanktivore	Holocentridae	4.41	0.002	x
Plectrogliphodon johnstonianus	Corallivore	Pomacentridae	17.92	0.0001	x
Pristiapogon kallopterus	Zooplanktivore	Apogonidae	3.54	0.008	x
Pseudochelinus octotaenia	Invertivore	Labridae	17.53	0.0001	x
Zebrasoma flavescens	Herbivore	Acanthuridae	25.19	0.0001	x
Acanthurus dussimieri	Herbivore	Acanthuridae	0.98	0.421	
Acanthurus nigricans	Herbivore	Acanthuridae	0.84	0.502	
Acanthurus nigroris	Herbivore	Acanthuridae	0.63	0.643	
Acanthurus olivaceous	Herbivore	Acanthuridae	0.11	0.979	
Bodianus albotaneatus	Invertivore	Labridae	2.11	0.081	
Calotomus carolinus	Herbivore	Scaridae	1.01	0.404	
Canthigaster jactator	Herbivore	Tetradontidae	3.13	0.016	
Cephalopholis argus	Piscivore	Serranidae	2.05	0.0889	
Chaetodon auriga	Invertivore	Chaetodontidae	1.46	0.217	
Chaetodon lunula	Invertivore	Chaetodontidae	1.14	0.342	
Chaetodon unimaculatus	Corallivore	Chaetodontidae	1.00	0.401	
Chlorurus sordidus	Herbivore	Scaridae	1.50	0.2056	
Chromis ovalis	Zooplanktivore	Pomacentridae	0.58	0.679	
Coris gaimard	Invertivore	Labridae	0.77	0.544	
Ctenochaetus hawaiiensis	Herbivore	Acanthuridae	1.99	0.098	
Dascyllus albisella	Zooplanktivore	Pomacentridae	2.19	0.072	
Forcipiger flavissimus	Invertivore	Chaetodontidae	1.63	0.169	
Forcipiger longirostris	Invertivore	Chaetodontidae	2.91	0.0226	
Gymnothorax flavimarginatus	Piscivore	Muraenidae	0.71	0.586	
Gymnothorax meleagris	Piscivore	Muraenidae	1.11	0.353	
Macropharyngodon geoffery	Invertivore	Labridae	1.26	0.287	
Melichthys vidua	Herbivore	Balistidae	0.47	0.754	
Mulloidichthys flavolineatus	Invertivore	Mullidae	1.16	0.332	
Myripristis berndtii	Zooplanktivore	Holocentridae	1.04	0.386	

Naso lituratus	Herbivore	Acanthuridae	2.27	0.064
Ostracion meleagris	Invertivore	Ostraciidae	0.86	0.487
Oxychelinus unimaculatus	Piscivore	Labridae	1.41	0.234
Parupeneus cyclostomus	Piscivore	Mullidae	1.29	0.273
Parupeneus insularis	Invertivore	Mullidae	1.12	0.35
Parupeneus multifasciatus	Invertivore	Mullidae	1.75	0.141
Pervagor aspricadus	Omnivore	Monocanthidae	0.67	0.61
Plagiotremus ewaensis	Piscivore	Blennidae	1.91	0.112
Sargocentron diadema	Invertivore	Holocentridae	0.67	0.612
Scarus rubroviolaceus	Herbivore	Scaridae	0.43	0.789
Sufflamen bursa	Invertivore	Balistidae	1.64	0.166
Synodus sp.	Piscivore	Synodontidae	0.87	0.484
Zanclus cornutus	Invertivore	Zanclidae	0.08	0.987