Bull Mar Sci. 96(4):577–591. 2020
https://doi.org/10.5343/bms.2019.0031

research paper

Comparing mesophotic and shallow reef fish assemblages in the ʻAuʻau Channel, Hawaii: fish size, feeding guild composition, species richness, and endemism

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Date Submitted: 22 February, 2019.
Date Accepted: 20 April, 2020.
Available Online: 21 April, 2020.

ABSTRACT.—Mesophotic (30–150 m) reef fish assemblages in the ʻAuʻau Channel, between the Hawaiian Islands of Maui and Lanai, were compared visually with neighboring shallow (<30 m depth) reef fish assemblages for differences in structure. Between 2007 and 2011, approximately 7000 mesophotic and 4000 shallow reef fishes were identified, sized (standard length), and assigned to seven foraging guilds. The shallow water zone had more species than the mesophotic zone (99 vs 80, respectively). Mesophotic planktivores and two herbivore species were significantly larger than their shallow reef counterparts. Shallow reef fish assemblages had a higher Chao1 estimated species richness for herbivores and corallivores but not the other five foraging guilds. The differences between mesophotic and shallow fish assemblages indicate that both have unique communities of high conservation importance.

Mesophotic Coral Ecosystems (MCEs) are among the most understudied coral ecosystems in the world because they occur at depths historically neglected by researchers working in the tropics and subtropics (Pyle 1996). Globally, MCEs range between 30 and 150 m, with the shallower depth defined by the limit of conventional scientific scuba diving and the deeper depth limited by the corals' ability to photosynthesize (Hinderstein et al. 2010, Kahng et al. 2010).

While MCE fish assemblages have been regarded as a transitional fauna between shallow-reef and deep-reef communities (Brokovich et al. 2008), there is increasing evidence that they are unique and ecologically important (Fukunaga et al. 2016, Coleman et al. 2018, Rocha et al. 2018). In particular, MCEs contain newly discovered fish species (Pyle 1996, Pyle et al. 2008), have high endemism rates (Kane et al. 2014, Kosaki et al. 2017), provide refugia for commercially-harvested and nontargeted species (Tenggardjaja et al. 2014, Lindfield et al. 2016), and support spawning aggregations (Beets and Friedlander 1999). Little is known about the ecological drivers structuring the composition and diversity of these assemblages relative to shallow-water fauna. Despite growing research on mesophotic reef fishes in the last decade, their management is hindered by limited knowledge about their community structure, feeding guild composition, species diversity, and endemism (Pyle et al. 2008, Hinderstein et al. 2010).

Hawaii's shallow reef fish communities are characterized by relatively low species richness (612 species) and high endemism (20%; Randall 2007). These patterns, resulting from Hawaii's geographic isolation, allow for few colonizing species, but promote local adaptation and speciation (Briggs and Bowen 2013). In most tropical reefs around the world, herbivorous fishes represent the largest feeding guild, both in abundance and weight (Ogden and Lobel 1978). While this pattern holds in Hawaii, top predators are most prevalent in areas with no fishing pressure, such as the Northwestern Hawaiian Islands (NWHI; Friedlander and DeMartini 2002, Holzwarth et al. 2006, Friedlander et al. 2010). Ecological effects of fishing are strongly felt in the Main Hawaiian Islands (MHI), but vary regionally. For instance, shallow-water reef fish assemblages of west Maui show some effects of fishing, with low piscivore abundance and generally smaller fishes compared to lesser fished areas in Lanai (Williams et al. 2008). Thus, these results suggest that shallow-water areas of the ʻAuʻau Channel, located between the islands of Maui and Lanai, might be impacted to an intermediate extent (Williams et al. 2008).

Because the mesophotic realm lies in relatively inaccessible waters, it has been considered less impacted by anthropogenic activities, including fishing (Bejarano et al. 2010, Garcia-Sais 2010), and has been considered a refuge from local anthropogenic impacts and climate change (Bongaerts et al. 2010, Lindfield et al. 2016). Hawaii's ʻAuʻau Channel MCE fish assemblages would be expected to resemble those from unfished shallow reefs rather than shallow-water fished areas (Friedlander and DeMartini 2002, Williams et al. 2008). MCE fishes should be larger than nearshore shallow reef fish assemblages.

This study compared reef fish assemblages from the MCE (30–150 m) and shallow reef (<30 m) depths in the ʻAuʻau Channel, using four ecosystem metrics: fish size distribution (body length), feeding guild composition, species richness, and endemism.

Methods

Study Site.—The study site was located in the ʻAuʻau Channel between the islands of Maui and Lanai in the MHI and bounded within the following polygon: 20°58.045, –156°41.047; 20°53.735, –156°51.890; 20°45.205, –156°49.586; and 20°47.931, –156°37.061. The maximum seafloor depth is approximately 250 m, with 480 km^2 between 30 and 150 m deep (J Rooney, NOAA PIFSC, pers comm; Costa et al. 2015). The bottom of the ʻAuʻau Channel is heterogeneous, with six dominant substrate types: large beds of *Halimeda* algae, sandy bottom, *Montipora* coral and *Microdictyon* algal fields, hard pavement, *Leptoseris* coral beds, and coral rubble (Costa et al. 2015). Shallow reef habitat occurs along the shorelines of the two islands (Maui, Lanai) bordering the channel. While the shallow waters are actively fished at both islands, human impacts on the fish populations are believed to be less at Lanai due to the smaller human population, difficult access to shorelines, and larger body sizes and higher biomass of fishes found there (Williams et al. 2008).

Table 1. Survey methods used in this study, showing survey effort and number of fishes recorded. SCUBA = self contained underwater breathing apparatus, TOAD = towed optical assessment device, SUB = Pisces IV or V Submersible.

Survey method	Number of surveys	Depth range (m)	Survey length (m)	Survey width (m)	Total area surveyed (m^2)	Total number of fishes
Shallow reef SCUBA	27	3–24	15–75	4–15	10,806	4,204
Mesophotic TOAD	14	53–136	296–3,854	22	225,646	997
Mesophotic SUB	29	64–110	153–833	6	46,360	6,052
Mesophotic SCUBA	9	48–83	25	2	500	48

Survey Methods.—This study relied on archived data, collected by the National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NOAA/NMFS) in the ʻAuʻau Channel between 2007 and 2011. Mesophotic data were collected using three distinct survey platforms: a Towed Optical Assessment Device (TOAD), the submersibles Pisces IV and V (SUB), and mixed gas SCUBA diving (SCUBA). The Coral Reef Ecosystems Program (CREP) of the Pacific Island's Fisheries Science Center (PIFSC), National Marine Fisheries Service (NMFS) collected the shallow reef data using SCUBA (CREP PIFSC 2015).

Visual surveys of fish assemblages and substrate cover were conducted using strip transects and standing point counts of various widths and distances, dependent on the survey platform (Table 1). All fishes encountered during surveys were identified to genus, and most to species (91.3%), and classified in one of seven functional groups (Table 2). Fish size (standard length) was visually estimated to the nearest centimeter. The TOAD and SUBs had two or more lasers spaced a specific distance apart to aid in length estimation (Kelley et al. 2005, Rooney et al. 2010). Mesophotic and shallow reef divers relied on previous experience and visual calibration techniques (Boland and Parrish 2005, Heenan et al. 2015, McCoy et al 2015). To minimize interobserver variability and possible bias in fish identification and sizing, three trained observers, including one of the authors (RC Boland), conducted the mesophotic zone surveys. RC Boland conducted all TOAD surveys and participated in most SCUBA (95%) and SUB surveys (97%). On shallow reefs, CREP employed a team of divers specifically trained to conduct reef fish surveys throughout the US Pacific territorial waters. To ensure observer comparability, the divers practiced identifying and sizing fishes and were tested on silhouette models in the field (Ayotte et al. 2015).

Data Analysis Framework.—The fish surveys were conducted using four methods with different strip widths and fish size detectability and targeting different

Table 2. Summary statistics for the length of fishes in each of the seven foraging guilds, showing the results of pairwise comparisons between shallow reef and mesophotic depth zones. Numbers of fishes are noted in parentheses. $\alpha = 0.05$.

Foraging guild	Mean length (cm)		*t*-test		
	Shallow reef	Mesophotic zone	df	*t*	*P*
Herbivore	15 (1,606)	23 (161)	10	1.406	0.190
Planktivore	11 (1,113)	19 (5,377)	21	2.114	0.047
Corallivore	10 (281)	16 (41)	1	0.845	0.553
Invertivore	14 (864)	19 (1,364)	34	1.745	0.089
Cleaner	6 (23)	9 (3)	- - -	- - -	- - -
Omnivore	11 (207)	14 (91)	16	0.731	0.476
Piscivore	29 (76)	51 (60)	17	1.689	0.109

depth ranges and habitats. Because of the inherent differences in area surveyed, fish detectability, and substrate composition, all analyses used raw counts rather than density (fishes per unit area). Species-specific counts were combined to provide method-specific and depth-specific absolute and relative (proportional) estimates of fish abundance and length. These metrics were then summarized using mean, median, and range (maximum–minimum) to account for the potential lack of normality in the data distributions (Zar 1984).

Data Analysis.—These analyses considered two distinct depth zones: mesophotic (30–150 m) and shallow reef (<30 m). Fishes were grouped into seven feeding guilds based on Randall (2007): herbivore, zooplanktivore, corallivore, invertivore, cleaner, omnivore, and piscivore. Statistical comparisons required sufficiently large sample sizes, involving $n \geq 3$ fish individuals in every sample.

Because the data were not normally distributed, even after attempting several transformations, nonparametric Mann–Whitney U tests were used for analysis of individual species length comparisons. All tests were performed using SPSS software (version 13.0), except G-tests, which were calculated using custom-written software in Matlab.

Several methods are used for correcting the probability of committing a type-I error during multiple testing, which vary in how conservatively they penalize the reference alpha level used for determining statistical significance (Wright 1992). For individual species length comparisons, we opted for the most conservative approach, with the same probability of committing a type-I error across all tests, by using the Bonferroni correction, whereby $\alpha' = \alpha/\text{total number of tests} = 0.05/40 = 0.00125$. Thus, we defined statistical significance as the Bonferroni-corrected level ($\alpha = 0.00125$).

Length Comparisons.—The length of mesophotic and shallow reef fishes were compared in two ways: (1) a guild-specific comparison involving each of up to seven distinct feeding groups, and (2) a species-specific comparison involving only those species that occurred in both depth zones in sufficient numbers (sample size ≥ 3 individuals). For (1) the median length for each species was determined and used as a single observation to calculate median length for depth zones and feeding guilds. Significance was determined using a t-test.

Species Richness and Endemism.—Fish richness was quantified using two complementary metrics: species richness (number of species observed) and estimated number of species (number of species observed and unobserved) derived from the sample.

Both species richness and estimated species richness were compared across the two depths and all feeding guilds of each depth zone. Estimated species richness was computed using the Chao1 equation, which provides a median number of species and a 95% confidence interval (CI) from the abundance data (Chao 1984).

We used the overlap between the median and the 95% CI from the Chao1 estimates to assess the significance of the feeding guild species richness differences from shallow reefs vs mesophotic depths. Only those cases where there was no overlap (e.g., shallow median did not overlap with deep 95% CI, and deep median did not overlap with shallow 95% CI) were considered statistically significant.

Endemism rates were calculated using published species lists for the area (Randall 2007) to determine endemism and then dividing that number by the number of species observed (Kane et al. 2014). Estimated endemic species was accomplished using the Chao1 equation, which provides a median number of species and a 95% CI from the abundance data (Chao 1984).

Again, overlap between 95% CIs was used to assess significant differences between the feeding guild endemic species from shallow reefs vs mesophotic depths.

Results

Survey Methods.—Our four surveys differed greatly in areal coverage and number of fishes sighted (Table 1). Shallow water surveys covered a total of 10,806 m^2 and yielded 4204 fishes. MCE surveys covered a total of 272,506 m^2 and yielded 7097 fishes. Proportionally, submersible surveys recorded the most fishes (85.3%), despite only surveying 17.0% of the area. TOAD surveys yielded a lower proportion of fishes (14.0%), despite covering the greatest area (82.8%). Mesophotic diver surveys surveyed the smallest area (0.2%) and yielded the lowest number of fishes (0.7%).

Guild-Specific Length Comparisons.—The median length of every fish species in the same guild was averaged into a guild mean and these were compared between the shallow reef and mesophotic zones with only mesophotic planktivores being significantly larger (t-test: df = 21, t = 2.11, α = 0.05; Table 2).

Species-Specific Length Comparisons.—The species-specific comparisons involved 24 species sighted in both mesophotic and shallow reef zones (Table 3). Nine were significantly larger in the mesophotic zone. These comprised *Acanthurus dussumieri* Valenciennes, 1835, *Centropyge potteri* (Jordan and Metz, 1912), *Chaetodon multicinctus* Garrett, 1863, *Chaetodon ornatissimus* Cuvier, 1831, *Chaetodon miliaris* Quoy and Gaimard, 1825, *Chromis verater* Jordan and Metz, 1912, *Naso brevirostris* (Cuvier, 1829) *Naso hexacanthus* (Bleeker, 1855), and *Pseudojuloides cerasinus* (Snyder, 1904).

Species Richness.—A combined total of 138 species were observed (Appendix 1). A greater number of species (99 vs 80) and estimated species richness, as evidenced by the Chao1 mean (124 vs 104), were observed in the shallow reef zone (Table 4). Differences between mesophotic and shallow reefs were also evident in the species richness of the different feeding guilds. Excluding the cleaners, with few individuals of only one species observed in both zones, the pooled shallow reef surveys yielded more observed species than the mesophotic surveys in all the feeding guilds except for planktivores, omnivores, and piscivores. The shallow reef zone had a greater Chao1 mean estimate for all feeding guilds except for invertivores and piscivores, which were greater in the mesophotic zone.

Endemism.—Species endemism was compared between depth zones and among feeding guilds (Table 5). Proportional endemism was 25% in the mesophotic zone and 20% in the shallow reef zone (Table 5). Estimated endemic species did not differ greatly between the two depths zones (Table 5). There was a significant difference in estimated endemic species between the herbivore, planktivore, and omnivore

Table 3. Species-specific comparisons of the length (cm) of major species (≥3 individuals) of mesophotic and shallow reef fishes encountered on surveys. Numbers of fishes are noted in parentheses. $\alpha = 0.00125$.

Foraging guild/species	Mean length (cm)		Mann–Whitney *U* test	
	Shallow reef	Mesophotic zone	*Z*	*P*
Herbivore				
Acanthurus dussumieri	25 (14)	42 (11)	−3.3	0.00111
Centropyge potteri	8 (18)	9 (109)	−5.2	0.00006
Chlorurus spilurus	14 (102)	8 (3)	−2.6	0.00922
Ctenochaetus strigosus	9 (257)	13 (9)	−2.6	0.00845
Zebrasoma flavescens	8 (67)	12 (5)	−1.8	0.06568
Planktivore				
Chaetodon miliaris	8 (6)	13 (118)	−5.0	0.00011
Chromis hanui	6 (31)	9 (4)	−3.1	0.00217
Chromis verater	14 (5)	18 (1286)	−11.4	0.00009
Dascyllus albisella	9 (206)	12 (5)	−2.1	0.04058
Naso brevirostris	17 (46)	37 (13)	−4.6	0.00001
Naso hexacanthus	15 (95)	42.5 (313)	−15.2	0.00001
Corallivore				
Chaetodon multicinctus	8 (29)	9 (35)	−4.1	0.00028
Chaetodon ornatissimus	13 (17)	23 (6)	−3.7	0.00002
Invertivore				
Bodianus albotaeniatus	25 (13)	27 (7)	−1.2	0.24727
Oxycheilinus bimaculatus	7 (13)	9 (86)	−2.3	0.02257
Parupeneus multifasciatus	13 (36)	12 (73)	−0.8	0.40195
Pseudocheilinus evanidus	7 (8)	6 (36)	−0.1	0.90397
Pseudojuloides cerasinus	7 (15)	9 (20)	−4.5	0.00002
Zanclus cornutus	14 (3)	17 (54)	−1.5	0.10367
Omnivore				
Canthigaster jactator	5 (94)	6 (3)	−1.5	0.10187
Chaetodon kleinii	8 (3)	12 (34)	−2.5	0.01045
Melichthys niger	20 (52)	22.5 (3)	−0.8	0.40368
Melichthys vidua	22 (16)	17.5 (9)	−2.0	0.05069

feeding guilds (Table 5). Herbivores were the sole shallow reef guild that had greater Chao1 estimated endemic species (6-6 vs 2-2), whereas mesophotic planktivores and omnivores had greater Chao1 estimated endemic species (8-9 vs 5-5 and 3-4 vs 0).

Discussion

Mesophotic planktivores were significantly larger in size than shallow reef planktivores. Nine species of 24 examined were significantly larger in the mesophotic zone than in the shallow reef zone. This is likely the result of greater fishing pressure in the shallow reef zone, as evidenced by several prized food fish species that were either significantly smaller or completely absent in the shallow zone. Specifically *A. dussumieri*, *N. brevirostris*, and *N. hexacanthus* were significantly larger and we encountered 25 *Caranx ignobilis* (Forsskål, 1775), 4 *Caranx melampygus* Cuvier, 1833 and 10 *Seriola dumerili* (Risso, 1810) in the mesophotic zone. We infer that there is a greater amount of fishing pressure on the shallow reefs due to greater accessibility. Whereas fishers targeting shallow reef fishes with spear and hook and line gear can

Table 4. Comparison of species richness and estimated species richness (Chao1) for all fishes and for each of seven feeding guilds, from the shallow reef and mesophotic depth zones. Estimated species richness is reported as the median and the 95% CIs of the Chao1 estimate with significance reported in the Results column.

Foraging guild	Shallow reef		Mesophotic zone		Results
	Species richness	Chao1 median (95% CI)	Species richness	Chao1 median (95% CI)	
All fishes	99	124 (107–174)	80	104 (86–167)	- - -
Herbivore	23	26 (23–49)	9	10 (9–22)	Significant
Planktivore	16	22 (17–54)	19	19 (19–20)	- - -
Corallivore	6	6 (6–7)	2	2 (2–2)	Significant
Invertivore	34	45 (36–86)	26	57 (30–236)	- - -
Cleaner	1	- - -	1	- - -	- - -
Omnivore	9	10 (9–20)	10	10 (10–11)	- - -
Piscivore	10	11 (10–18)	13	18 (14–46)	- - -

either operate from the shore or from a boat, fishers must use a boat to access MCE habitats.

The differences in size for planktivores and the nine specific species seems unlikely to be driven by habitat as both depth zones had comparable reef habitat. Size differences caused by ontogenetic shifts is unlikely as adults of the large species (*A. dussumieri*, *C. ignobilis*, *C. melampygus*, *N. brevirostris*, *N. hexacanthus*, and *S. dumerili*) are observed in both protected shallow areas and mesophotic depths. Nor is it caused by a large amount of juvenile recruits in the shallows, as there were not many observed fishes smaller than 5 cm. Nevertheless, because adult sized fishes of all feeding guilds have been observed in both depth zones, these results do not suggest that size differences are caused by ontogenetic shifts, with larger fishes migrating deeper into the mesophotic zone. There is also increasing evidence that the fish structures of mesophotic and shallow reefs are unique and not connected (Fukunaga et al. 2016, Coleman et al. 2018, Rocha et al. 2018). In this study, 138 species of fishes accounted for all fishes observed in both the mesophotic and shallow reefs, but only 41 species were found at both depths, further discounting the possibility that ontogenetic shifts are responsible for the size differences observed in the present study.

Species comparisons for herbivores revealed two out of five species being significantly larger in the mesophotic zone. The size difference for *A. dussumieri* could be

Table 5. Comparison of endemism and estimated endemism richness (Chao1) for all fishes and for each of seven feeding guilds from the shallow reef and mesophotic depth zones. Estimated endemism richness is reported as the median and the 95% CIs of the Chao1 estimate with significance reported in the Results column.

Foraging guild	Shallow reef		Mesophotic zone		Results
	Species richness	Chao1 median (95% CI)	Species richness	Chao1 median (95% CI)	
All fishes	20 (20%)	21 (20–28)	20 (25%)	22 (19–33)	- - -
Herbivore	5 (22%)	6 (6–6)	2 (22%)	2 (2–2)	Significant
Planktivore	5 (31%)	5 (5–5)	8 (42%)	8 (8–9)	Significant
Corallivore	1 (17%)	- - -	1 (50%)	- - -	- - -
Invertivore	6 (18%)	7 (6–20)	4 (15%)	4 (4–6)	- - -
Cleaner	1 (100%)	- - -	1 (100%)	- - -	- - -
Omnivore	1 (11%)	- - -	3 (30%)	3 (3–4)	Significant
Piscivore	1 (10%)	- - -	1 (7%)	- - -	- - -

attributed to fishing pressure on the shallow reef removing the largest individuals. *Centropyge potteri* may be larger in the mesophotic zone because it was the most common herbivore and has less competition for resources than shallow-water *C. potteri*.

Secondary consumers that were significantly larger in the mesophotic zone consisted of four planktivores, two corallivores, and a single invertivore. Both corallivore species, *C. multicinctus* and *C. ornatissimus,* were larger, possibly because these were the only two species of corallivore observed in the mesophotic zone and enough resources exist in the mesophotic zone to support these two species. Fishing pressure has been suggested as a reason planktivores *N. brevirostris* and *N. hexacanthus* were larger in the mesophotic zone, but this does not apply to *C. miliaris* or *C. verater.* Primary productivity in the mesophotic zone may not rely on benthic productivity but on planktonic productivity (Fukunaga et al. 2016) and may be the reason these two planktivores may be larger in size. The invertivore *P. cerasinus* was larger in the mesophotic zone, but for no known reason (Table 3).

The two depth zones differed in terms of species richness and proportional richness. A decrease in species richness with increasing depth has been observed by Thresher and Colin (1986), Itzkowitz et al. (1991), Fukunaga et al. (2017), and Coleman et al. (2018). The greater species richness and proportional richness of herbivores and corallivores in the shallow reef zone, and the increasing richness and proportional richness in planktivores and piscivores with depth, are in agreement with observations made by Thresher and Colin (1986), Itzkowitz et al. (1991), Feitoza et al. (2005), Weaver et al. (2006), Brokovich et al. (2010), and Bejarano et al. (2010, 2014), and likely reflect lower algal and coral primary productivity in the mesophotic zone.

The shallow reef zone had a greater estimated richness of herbivores which further supports the contention that fishes at mesophotic depths are constrained by algal resources. There were large CI intervals for the Chao1 species richness estimates for invertivores. This is due to the low reoccurrence sightings of species observed, particularly those of single individual species sightings. Chao1 estimates for a greater number of unobserved species when there are less reoccurrence and more singleton sightings. This may explain the invertivores result as these fishes are oriented to the benthos and many are cryptic.

Endemism in reef fishes increases with both latitude and depth in the Hawaiian Archipelago (DeMartini and Friedlander 2004, Randall 2007). In the NWHI, endemism is higher for mesophotic (46%–100%) vs shallow reefs (21%; DeMartini and Friedlander 2004, Kane et al. 2014, Fukunaga et al. 2017, Kosaki et al. 2017). Our surveys in the ʻAuʻau Channel observed 25% endemism in the mesophotic zone and 20% endemism in the shallow reef zone. Endemism values observed in this study are in agreement with previous estimates for the MHI. The shallow reef endemism rate (20%) is similar to the 20.9% described for shallow-water species in the MHI (DeMartini and Friedlander 2004). This, along with the higher richness and proportional richness of herbivores in the shallow reefs and planktivores in the mesophotic zone, is a possible indicator of diversification in response to areas of greatest primary productivity (Hourigan and Reese 1987, Harmelin-Vivien 2002, Lobato et. al. 2014).

The different survey techniques limited data analysis. TOAD surveys observed less fishes despite surveying the largest amount of area because large areas of TOAD surveys were sand, algal, and transitional habitats that had few fishes, while submersible surveys were in or near coral beds with large fish assemblages. Submersible and TOAD surveys in coral habitat observed similar fish assemblages. Mesophotic SCUBA surveys were the least effective due to time and depth constraints. Further research should focus on one universal technique and perhaps a limited number of habitats.

This study suggests that mesophotic and shallow reef fish assemblages in the ʻAuʻau Channel differ in several ways, with important ecological and management implications. The mesophotic depths of the ʻAuʻau channel are refuge for some, but not all commercially harvested fish species. Mesophotic planktivores and some specific herbivore species are larger and herbivores and corallivores in the shallow depths have a higher estimated species richness. These ecological differences are likely influenced both by bottom-up control (e.g., magnitude and fate of primary production) and by top-down control (e.g., fishing pressure).

Because the fish assemblages of both depth zones can be considered unique, with little exchange of individuals through diel foraging movements or ontogenetic habitat shifts, protecting one would minimally benefit the other (Tenggardjaja et al. 2014, Lindfield et al. 2016, Pyle et al. 2016, Coleman et al. 2018). Thus, management actions targeting fish populations will have to address these depth zones separately and consider the habitat heterogeneity associated with shallow shelves and deeper mesophotic reefs.

Acknowledgments

Thanks to C Kelley for translating the submersible tracks and plots. Thanks to C Bradley for her advice and for being my sub diving buddy. Funding and support provided through NOAA NCCOS Deep-CRES Program and the NOAA Advanced Studies Program.

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Appendix 1. All fish species observed with feeding guilds and depth zone in which they were observed.

Species	Feeding guild	Shallow reef zone	Mesophotic zone
Abudefduf abdominalis	Planktivore	X	
Abudefduf vaigiensis	Planktivore	X	
Acanthurus blochii	Herbivore	X	
Acanthurus dussumieri	Herbivore	X	X
Acanthurus leucopareius	Herbivore	X	
Acanthurus nigrofuscus	Herbivore	X	
Acanthurus nigroris	Herbivore	X	
Acanthurus olivaceus	Herbivore	X	X
Acanthurus thompsoni	Planktivore	X	X
Acanthurus triostegus	Herbivore	X	
Acanthurus xanthopterus	Herbivore	X	
Aphareus furca	Piscivore		X
Aphareus rutilans	Planktivore		X
Apolemichthys arcuatus	Omnivore		X
Aprion virescens	Piscivore	X	
Arothoron hispidus	Omnivore		X
Aulostomus chinensis	Piscivore		X
Bodianus albotaeniatus	Invertivore	X	X
Calotomus carolinus	Herbivore	X	
Cantherhines dumerilii	Omnivore	X	
Cantherhines sandwichiensis	Herbivore	X	
Cantherhines verucundus	Omnivore		X
Canthigaster amboinensis	Omnivore	X	
Canthigaster coronata	Omnivore		X
Canthigaster epilampra	Omnivore		X
Canthigaster jactator	Omnivore	X	X
Carangoides orthogrammus	Invertivore	X	X
Caranx ignobilis	Piscivore		X
Caranx melampygus	Piscivore		X
Carcharhinus plumbeus	Piscivore		X
Centropyge fisherii	Herbivore	X	X
Centropyge potteri	Herbivore	X	X
Cephalopholis argus	Piscivore	X	
Chaetodon frembli	Invertivore		X
Chaetodon kleinii	Invertivore	X	X
Chaetodon lunula	Omnivore	X	
Chaetodon lunulatus	Corallivore	X	
Chaetodon miliaris	Planktivore	X	X
Chaetodon multicinctus	Corallivore	X	X
Chaetodon ornatissimus	Corallivore	X	X
Chaetodon quadrimaculatus	Invertivore	X	
Chaetodon unimaculatus	Corallivore	X	
Cheilio inermis	Invertivore		X
Chlorurus perspicillatus	Herbivore	X	
Chlorurus spilurus	Herbivore	X	X
Chromis agilis	Planktivore	X	

Appendix 1. *Continued*.

Species	Feeding guild	Shallow reef zone	Mesophotic zone
Chromis hanui	Planktivore	X	X
Chromis leucura	Planktivore		X
Chromis ovalis	Planktivore		X
Chromis struhsakeri	Planktivore		X
Chromis vanderbilti	Planktivore	X	
Chromis verater	Planktivore	X	X
Cirrhilabrus jordani	Planktivore		X
Cirripectes vanderbilti	Herbivore	X	
Coris gaimard	Invertivore	X	
Coris venusta	Invertivore	X	
Ctenochaetus strigosus	Herbivore	X	X
Dactyloptena orientalis	Invertivore		X
Dascyllus albisella	Planktivore	X	X
Decapterus macarellus	Planktivore	X	
Diodon hystrix	Invertivore		X
Exallias brevis	Corallivore	X	
Fistularia commersonii	Piscivore	X	X
Forcipiger flavissimus	Invertivore	X	
Gomphosus varius	Invertivore	X	
Gymnothorax flavimarginatus	Piscivore	X	X
Gymnothorax melatremus	Piscivore		X
Gymnothorax meleagris	Piscivore	X	
Gymnothorax nuttingi	Piscivore		X
Halichoeres ornatissimus	Invertivore	X	
Heiniochus diphreutes	Planktivore		X
Iniistius pavo	Invertivore	X	
Iracundus signifer	Piscivore		X
Labroides phthirophagus	Cleaner	X	X
Lactoria diaphana	Invertivore		X
Liporpoma aurora	Piscivore		X
Lutjanus fulvus	Invertivore	X	
Lutjanus kasmira	Invertivore	X	X
Luzonichthys earlei	Planktivore		X
Macropharyngodon geoffroy	Invertivore	X	
Malacanthus brevirostris	Planktivore		X
Melichthys niger	Omnivore	X	X
Melichthys vidua	Omnivore	X	X
Monotaxis grandoculis	Invertivore	X	
Mulloidichthys flavolineatus	Invertivore	X	X
Mulloidichthys vanicolensis	Invertivore		X
Myripristis berndti	Planktivore	X	
Myripristis kuntee	Planktivore	X	
Naso annulatus	Planktivore	X	
Naso brevirostris	Planktivore	X	X
Naso hexacanthus	Planktivore	X	X
Naso lituratus	Herbivore	X	X

Appendix 1. *Continued*.

Species	Feeding guild	Shallow reef zone	Mesophotic zone
Naso unicornis	Herbivore	X	X
Odontathias fuscipinnis	Planktivore		X
Ostracion meleagris	Invertivore	X	X
Oxycheilinus bimaculatus	Invertivore	X	X
Oxycheilinus unifasciatus	Piscivore	X	
Oxycirrhites typus	Invertivore		X
Paracirrhites arcatus	Invertivore	X	
Paracirrhites forsteri	Piscivore	X	
Parapercis schauinslandi	Invertivore		X
Parupeneus chrysonemus	Invertivore		X
Parupeneus cyclostomus	Piscivore	X	X
Parupeneus insularis	Invertivore	X	X
Parupeneus multifasciatus	Invertivore	X	X
Parupeneus pleurostigma	Invertivore	X	X
Parupeneus porphyreus	Invertivore		X
Pervagor aspricaudus	Omnivore	X	
Plagiotremus goslinei	Piscivore	X	
Plectroglyphidodon imparipennis	Omnivore	X	
Plectroglyphidodon johnstonianus	Corallivore	X	
Pristiapogon kallopterus	Invertivore	X	
Pseudanthias hawaiiensis	Planktivore		X
Pseudanthias thompsoni	Planktivore		X
Pseudocheilinus evanidus	Invertivore	X	X
Pseudocheilinus octotaenia	Invertivore	X	X
Pseudocheilinus tetrataenia	Invertivore	X	
Pseudojuloides cerasinus	Invertivore	X	X
Ptereleotris heteroptera	Planktivore	X	
Rhinecanthus rectangulus	Invertivore	X	
Sargocentron tiere	Invertivore	X	
Sargocentron xantherythrum	Invertivore	X	
Scarus dubius	Herbivore	X	
Scarus psittacus	Herbivore	X	
Scarus rubroviolaceus	Herbivore	X	
Scorpaenopsis diabolus	Piscivore	X	
Seriola dumerili	Piscivore		X
Stegastes marginatus	Herbivore	X	
Stethojulis balteata	Invertivore	X	
Sufflamen bursa	Omnivore	X	X
Sufflamen fraenatum	Invertivore		X
Thalassoma ballieui	Invertivore	X	
Thalassoma duperrey	Invertivore	X	X
Thalassoma quinquevittatum	Invertivore	X	
Torquigener florealis	Omnivore		X
Xanthichthys auromarginatus	Planktivore		X
Zanclus cornutus	Invertivore	X	X
Zebrasoma flavescens	Herbivore	X	X