HABITAT ASSOCIATIONS OF THE SURGEONFISH, YELLOW TANG (*ZEBRASOMA FLAVESCENS*), FROM SHALLOW TO UPPER MESOPHOTIC CORAL REEFS (3- 40 M) IN WEST HAWAII

By

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ABSTRACT

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Understanding habitat utilization of coral reef fish at each life stage is critical for determining their vulnerability to changing ocean conditions and for successful reef fish management. The yellow tang (*Zebrasoma flavescens*) is a herbivorous surgeonfish and is heavily collected in the Hawaiian marine aquarium trade. Previous work suggests that recruits and juveniles utilize branching coral at mid depths (~12 m) and make an ontogenetic shift to shallow (~3 m) depths as adults. These studies, however, have not explored yellow tang abundances beyond ~18 m. Here, we analyze the distribution of yellow tang to deeper depths. Fish and benthic surveys were conducted on the west coast of the island of Hawaii (West Hawaii) along a depth gradient from shallow to upper mesophotic coral reefs (3- 40 m). The results confirmed previous research, however, adults were also found in low but consistent abundances from 21-40 m and juveniles were found to 30 m when branching coral habitat was present. Thus, the upper mesophotic zone is serving as additional juvenile and adult habitat for yellow tang in Hawaii.

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INTRODUCTION

Understanding habitat use by coral reef fish at each life stage is critical for determining their vulnerability to climate change and for successful reef fish management. Many coral reef fish species use multiple habitats throughout their lives with recruits and juveniles occupying habitats distinct from adults (Adams and Ebersole 2002; Lecchini and Galzin 2005). Small recruit and juvenile fish are prone to predation and often choose habitats that provide shelter such as lagoons, mangroves, or coral reef habitats with high structural complexity (Grol et al. 2014, Nagelkerken et al. 2000). As fish grow, their morphology and behaviors change (Lecchini and Galzin 2005). Adult fish may make an ontogenetic habitat shift to balance the increasing demands of foraging and reproduction with protection from predation (Dahlgren and Eggleston 2000; Claisse et al. 2009).

Shallow coral reefs are critical habitat for coral reef fish species as they provide substrate for recruitment, protection from predation, and foraging grounds (DeMartini and Anderson 2007; Almany 2004; Sale 1993). While essential to multiple life stages of coral reef fishes, these shallow coral reefs, ranging from 0-30m, only make up a portion of potential coral reef habitat. Deeper reefs, known as mesophotic coral ecosystems (MCEs), are extensions of shallow coral reefs that range from 30 to over 150 m and may serve as vast regions of additional fish habitat (reviewed by Hinderstein et al. 2010; Kahng et al. 2010). Due to the increasingly limited amount of time that can be spent at deeper depths with traditional SCUBA diving equipment, however, few ecological studies have been conducted below 20 m on coral reefs (Khang et al. 2014).

MCEs may provide refuge by buffering reef organisms from some natural and anthropogenic stressors (Slattery et al. 2011). For example, mesophotic reefs are largely sheltered from wave energy caused by storm activity that can cause severe damage to shallow coral reefs (Bongaerts et al. 2011). Also, deeper corals may also be protected from coral bleaching events by upwelling which brings cool water to deep corals, counteracting increased sea surface temperatures (SST) (Riel and Piller 2002). MCEs, however, may also be at a risk due to climate change as the aragonite saturation horizon becomes shallower and the upwelling of acidified water intensifies (reviewed by Slattery et al. 2011). If deep reefs are at an advantage to withstand some short-term disturbances and remain intact, shallow reef organisms that exist at deeper depths may be able to re-seed shallow populations to aid in recovery (Slattery et al. 2011).

Fish community structure has been shown to transition slowly along a depth gradient from shallow to mesophotic depths. The upper MCE (30-60 m) acts as a transition zone for fish communities by harboring both deep specialists and shallow water fish species (Van den Hoek 1978; Thresher and Colin 1986; Garcia-Sais et al. 2008; Bajarano et al. 2014; Pyle 2000; Brokovich 2008; Kane et al. in prep). Although the degree of connectivity between shallow and mesophotic depths is unclear (Lesser et al. 2009), there is evidence of shallow fish species utilizing upper mesophotic reefs (30- 60 m) by making ontogenetic shifts to deeper depths

(Nagelkerken and van der Velde 2003) and using deep reefs as spawning grounds (Nemeth 2009).

Zebrasoma flavescens, or yellow tang, is a herbivorous surgeonfish (Acanthuridae) which range expands from the western to northern Pacific, and is a species commonly found on the west coast of the island of Hawaii (hereafter West Hawaii). In Hawaii, recruit and juvenile yellow tang are known to be closely associated with the branching coral, *Porities compressa*, at mid depths (5-12 m) (DeMartini and Anderson 2007; Ortiz and Tissot 2008). This is likely due to the numerous holes and crevices provided by the branching structure of *P. compressa*, which allow small fish to seek refuge from predators (Hixon and Beets 1993; Sale 2004). Adults make an ontogenetic habitat shift to shallow (<5 m) boulder and reef flat habitats to forage when an increase in energy is needed for reproduction (Walsh 1984; Ortiz and Tissot 2008; Claisse et al. 2009).

Yellow tang are also a heavily targeted aquarium fish species collected in West Hawaii, making up about 80% of the total reported catch (Tissot et al. 2004; Williams et al. 2009). Long-term monitoring of yellow tang populations in West Hawaii has been ongoing since 1999, at 23 sites to a depth of ~14 m (Williams et al. 2009) and other scientific research on yellow tang and their habitat associations extend to ~ 20 m (Ortiz and Tissot 2008). Even though yellow tang are reported to depths of ~80 m, there have been a lack of studies on their abundances or patterns of habitat use at these deeper depths (Randall 2007).

Here, we examine deeper reef communities by studying the relationships between yellow tang and benthic habitat characteristics at shallow (3m), mid (12m and 21m) and upper mesophotic depths (30m and 40m). In particular, we focus on understanding if upper mesophotic habitats are serving as additional recruit, juvenile, or adult habitat for yellow tang. If we can extend the knowledge on the habitat associations of these ecologically and economically important species, then we can help guide management initiatives to promote the conservation of the fish species and the sustainability of the aquarium trade in Hawaii.

METHODS

Study sites

Benthic and fish surveys were conducted at 10 sites along the West Hawaii coast during 2013 and 2014. From South to North, the ten sites included: Three Caves (CAV), Kona Paradise (KPAR), Hoʻokena (HK), Sheraton (SHT), Old Airport (APT), Kaiwi Point (KPT), Pine Trees (PT), Kiholo (KIH), Puako Road (PKRD), and Puako Church (PKCH) (Figure 1). Sites were grouped for analysis into three latitudinal regions with 3 sites in the North (KIH, PKRD, PKCH), 4 sites in the central region (SHT, APT, KPT, PT), and 3 sites in South (CAV, KPAR, HK). Sites were selected based on the availability of continuous hard bottom habitat from 3 to 40m, however the specific locations of surveys within a site were chosen at random.

In 1999, due to conflicts surrounding the aquarium trade, 35% of the West Hawaii coast was designated as a network of Marine Protected Areas (MPAs) called Fishery Replenishment Areas (FRAs) (Capitini et al. 2004). Within the FRA boundaries, the commercial collection of live ornamental fish is prohibited. In areas open to collection, fishers use SCUBA to dive and collect mostly juvenile fish from branched, mounding, or stands of corals and rubble rich areas between the depths of 12.5-18 m (Stevenson et al. 2011). To look at differences in yellow tang densities inside and outside of protected areas, half of the sites chosen for this study were closed to aquarium collecting (APT, HK, PKCH, PKRD, PT) and the remaining sites were open to aquarium collecting (CAV, KIH, KPAR, KPT, and SHT) (Figure 1).

Sampling design

At each site, fish and benthic surveys were conducted along transects parallel to the shore along a depth gradient from 3 to 40 m with survey locations at 5 depths (3, 12, 21, 30, and 40 m). At one site, Puako Road, hard bottom habitat was only present to about 30 m, so 40 m transects were not conducted. To assess fish abundance, dive pairs identified, counted, and sized to total length (TL, to the nearest cm) all fish encountered along at least 3 belt transect lines at each depth, each covering an area of 25x4 m (or $100m^2$). The number of belt transect lines per depth was determined based on the amount of time divers can remain at deeper depths on SCUBA equipment using compressed air. Yellow tang count data were summed to calculate their density per transect (no. /$100m^2$).

Photoquadrat Analysis

Physical habitat characteristics were assessed using benthic photoquadrat surveys along 2 of the 3 fish survey transect lines at each site and depth. Each digital photograph (taken with a Cannon Powershot S110) captured a 0.25 m^2 area of the substrate every meter along the 25m belt transect line.

Benthic photoquadrat photos were analyzed using CoralNet, an online photoquadat analysis tool (Beijbom et al. 2012). To estimate percent cover of biota, 50 points per photograph were randomly generated and the species and substrates directly beneath the point were identified. Species were then binned into major taxonomic categories for analysis. These categories included: mounding coral, encrusting coral, branching coral, cyanobacteria, sponge, sand/sediment, turf algae, and red, green, or brown macroalgae. Mound coral species included: *Porites lobata, P. lutea,* and *P. brighami;* encrusting coral species included: *Montipora capitata, M patula, M. flabellate, Pavona varians, Leptoseris sp., Gardinoseris planulata,* and *Leptastrea sp.*; branching coral species included: *P. compressa, Pocillopora meandrina, P. damicornis,* and *P. eydouxi*; and plating coral species included *P. monticulosa.* Point data were converted to percent cover for each of the major benthic biota categories for statistical analysis.

To identify the underlying structure of the benthos, each benthic photo was assigned a primary benthic structure identification. The primary benthic structure code was determined based on the benthic structure type with a percent cover of ≥50% in the benthic photograph. All photographs had a primary benthic classification (percent cover ≥50%). The benthic structure codes used for analysis included: sand (fine grain particles), pebble/cobble (small rocks ~3- 25 cm), boulder (rocks ~25 cm or greater), bedrock (continuous lava), mound reef (reef habitat with larger hole sizes formed from mounding corals such as *P. lobata*), branching reef (complex reef matrix formed from the branching coral, *P. compressa*), and rubble (broken coral fragments). Primary benthic structure codes were then summed by transect and occurrences were averaged to generate a percentage cover of substrate for comparisons.

Data Analysis

Yellow tang are known to settle onto the reef at ~ 3 cm TL and are considered recruits until they are 5 cm TL (Walsh 1987; DeMartini and Anderson 2007) As adults, the species makes an ontogenetic shift at a median size of 13.2 cm TL (Claisse et al. 2009). Thus for this study, sizes of yellow tang were binned into the life stage classifications of recruits (≤5 cm TL), juveniles (6-12 cm TL), and adults (≥13 cm TL).

Before analyses, recruit, juvenile, and adult densities were tested for equality of sample variances. Life stage densities by latitudinal region, protection, and depth met equality of sample variance assumptions, so multifactor ANOVAs followed by Tukey's post hoc tests were used to evaluate significant factors.

Benthic structure types (sand, rubble, pebble cobble, boulder, bedrock, mound reef, and branching reef) did not meet equality of sample variance assumptions by latitudinal region, protection, or depth. Therefore, trends in benthic structure type by protection and latitudinal region were analyzed using a non-parametric Kruskal- Wallis (KW) test with a paired Steel-Dwass post hoc test. Similarity of benthic structure types between depths was determined using a Similarities Percentage Analysis (SIMPER) in the statistical program PRIMER 6 (Clarke 1993). SIMPER analysis identifies the variables most contributing to differences between groups. For this study, the SIMPER analysis identified the benthic structure types that were most common across transects at each depth to identify patterns of habitat structure along the depth gradient.

Benthic biota types did not meet the assumptions for equality of sample variances by depth. To test whether the percent cover of turf or macroalgae was significantly different between depths, nonparametric Kruskal-Wallis (KW) tests with paired Steel-Dwass post hoc analyses were performed.

Canonical Correspondence Analysis (CCA), a multivariate method, was used to describe patterns of associations between abundances and environmental variables (McGarigal et al. 2000). The resulting ordination derived from a CCA characterizes the major environmental gradient that explains patterns of fish abundances by life stage (recruits, juveniles, and adults) relative to structural, biotic, and depth associations (McGarigal et al. 2000). A Monte Carlo Randomization test was used to determine if there were significant associations between fish and benthic data by identifying axes of the CCA that were significantly contributing to variation in fish data. The significance of vectors contributing to the axes was examined with a one-way ANOVA of the Linear Combination (LC) scores with each of the benthic variables.

RESULTS

A total of 1,539 yellow tang were counted along 168 fish transect lines and 2,981 benthic photos were collected at 10 sites along the West Hawaii coast during 2013 and 2014. The species was encountered on 75% of the fish transects from 3 to 40 m. The minimum size of individuals were 3 cm recruits and the largest yellow tang observed was a 21 cm adult at 3 m. The overall density per transect was highly variable and ranged from 0 to 83 individuals/100 m^2.

Life Stages

A three-way ANOVA revealed which factors and factor interactions had a significant effect on recruits, juveniles, and adults (Table 1). Depth was a significant factor influencing each life stage, but it was confounded by a three-way interaction among latitudinal region, protection, and depth for recruits and juveniles, so further analyses of depth required additional interpretation with other factors (Table 1).

Analyses of general depths trends using multiple comparisons tests showed that overall, recruits and juveniles had higher densities at 12 and 21 m than at 3, 30, and 40 m depths (Figure 2a and 2b). Both recruit and juvenile densities at 3 m were not different to those at 30 m or 40m. While recruits were almost absent at 3, 30, and 40 m, juveniles were present at 3 m and the upper mesophotic depth of 30 m. Adult densities were greatest at 3 and 12 m and lower, but not different at 21, 30 and 40 m (Figure 2c). Adult densities at 30 m were also similar to those at 12 m. Overall, juveniles and adults were found at upper mesophotic depths, but recruits were not.

The three-factor interaction among latitudinal region, protection, and depth also significantly influenced recruits and juveniles densities, but not adult densities. In addition to Tukey's tests, interaction plots were used to assist in understanding the three factor interactions. There were three trends explaining the three-factor interaction for recruits. First, recruit densities were greatest in the north and slightly greater outside of protected areas at 21 m driven by the site Kiholo (Figure 3a, Figure 4b). Second, in the southern region, recruit densities were greatest inside of protected areas at 21 m driven by the site, Ho'okena (Figure 4b). Third, in the central region, recruits were greater inside of protected areas at 12 m, largely driven by densities at Old Kona Airport (Figure 3a, Figure 4b).

Similar to the pattern in recruits, juvenile densities were greatest in the north, outside of protected areas at 21 m and driven by densities at Kiholo (Figure 3b, Figure 5). Puako Road (a northern site, inside a protected area had similar juvenile densities to Kiholo, however, the average density inside protected areas in the north was lower due to smaller densities of juveniles at Puako Road (Figure 3b).

Benthic Habitat

Variation in mean percent cover of benthic structure categories by latitudinal region is presented in Table 2. The same benthic structure dataset was used for the Kruskal Wallis test to analyze differences in both structure with latitude and structure with level of protection. As a result, the analyses are not independent. However, the significant p-values were less than those subjected to a Bonferroni correction for two non-independent tests.

Significant differences between latitudinal regions were found for boulder and branching reef structure (Table 2, Figure 6a and 6b). Percent cover of boulder habitat was greater in the central region (19.6%± 2.1 SE) than in the south (4.6 %±1.8 SE) and north (3.8 %±1.4 SE). The percent cover of branching reef habitat was greater in the north (23.96 % ±5.5 SE) than in the south (8.0% ± 3.4 SE) or central region (6.7% ± 2.1 SE). Differences in benthic structure by protection was only statistically significant for mound reef habitat with a greater percent cover of mound reef occurring outside (43.12% ± 4.2 SE) than inside (26.8% ± 3.8 SE) of protected areas (Table 2, Figure 6c).

Benthic structure categories varied among depths (Table 3). The percent cover of sand habitat was the greatest at 30 m (12.0%± 3.7 SE) and 40 m (21.9%± 4.5 SE); rubble habitat at 21 m (15.3%± 5.2 SE), 30 m (29.7%± 5.8 SE), and 40 m (21.6%± 4.3 SE); and pebble/cobble habitat at 3 m (14.5%± 6.4 SE). Bedrock habitat was most abundant at 3 m (42.9%±8.7 SE) and 12 m (13.3%± 3.7 SE). Mound reef habitat was most prevalent at 12 m (66.5%± 5.2 SE) and branching reef habitat was greatest at both 12 m (13.3% ± 5.2 SE) and 21 m (33.4%± 6.4 SE). Boulder habitat was the most dominant at 3 m (24.6%±7.5 SE), 30 m (3.2%± 1.6 SE), and 40 m (20.3 %± 5.0 SE). Additional boulder habitat was observed along transects at 30 m and 40 m but was not captured by photoquads (personal observations).

Similarities Percentage Analysis (SIMPER) and qualitative analysis of the benthic structure patterns by depth indicated that the shallow (3 m) depth was dominated by bedrock with some boulder habitat and a generally higher vertical relief. At mid depths, 12 m was dominated by mound reef while habitats at 21 m had a similar percent cover of mound reef and branching reef habitats. In the deeper depths, 30 m consisted of lower lying mound reef with rubble habitat and 40 m contained similar cover of mound reef, boulder, rubble, and sand habitats (Table 4, Figure 7). It was observed that branching reef habitat extended into the upper mesophotic zone (30 m) and sandy-rubble habitat increased with depth from 21 to 40 m (Figure 7).

The percent cover of turf algae was not different between survey depths and averaged about 50% cover at all depths (H= 5.22, DF=4, P=0.27, Figure 8), while the percent cover of macroalgae was low (~4%) at 3, 12, and 21 m and significantly greater (~12%) at 30 and 40 m (H= 21.04, DF=4, P=0.0003) (Figure 8).

Multivariate Analysis

The percent variation explained by the first and second axes of the CCA was 39.6% and 5.5%, respectively (Figure 9). A Monte Carlo randomization test indicated that only axis one (p=0.004) was a significant source of variation for yellow tang abundances. Of the seven habitat variables, boulder (F= 3.38, df=17, p=0.00), branching reef (F= 3.76, df=29, p=0.00), and mounding reef (F=1.75, df= 40, p=0.41) were significantly associated with axis one. Axis one describes a gradient among structural habitats whereby adults were associated with deep and shallow boulder habitats, and juveniles and recruits were associated with mid- and deeper-depth branching and mound habitats (Figure 9).

DISCUSSION

We found that the upper mesophotic zone is serving as additional habitat for yellow tang in West Hawaii as ~12% of the total and ~22% of the adults counted along transects were found at 30 and 40m. We also found that benthic structure remains an important factor influencing recruit, juvenile, and adult densities along the depth gradient from 3- 40 m.

While a majority of recruits and juveniles inhabited branching and mound reefs at mid depths, small numbers of juveniles extended to upper mesophotic depths (30 m) when branching reef was present. The three sites that had a mean percent cover of branching reef at 30m greater than 30% (Sheraton (43%), Puako Road (32%), and Kiholo (36%)), had the highest mean juvenile yellow tang densities at 30 m (Sheraton [4/100m^2], Puako Road [6/100m^2], Kiholo [4/100m^2]). Thus, when available, branching reefs that extend to deeper depths serve as additional juvenile habitat on West Hawaii reefs. Aquarium fish collectors typically collect juvenile yellow tang between the depths of 12-18m (Stevenson et al. 2011), therefore, branching reef habitats beyond 18 m may currently serve as *de facto* protected areas. There has been evidence, however, that during years of weak juvenile recruitment, fishers will dive to deeper depths to collect yellow tang (Stevenson et al. 2011). Additionally, during storm events that have the potential to destroy reef -building corals on shallow reefs (Dollar and Tribble 1993), corals on deeper reefs may be protected from wave action and serve as a refuge for fishes, such as juvenile yellow tang, dependent on the structure of branching and mound reefs (Huston et al. 1985; reviewed by Bongaerts et al. 2010).

Adult yellow tang densities were the greatest at shallow depths (3 m), where there was the highest combined percentage of bedrock and boulder habitat (69% cover) and an observed high vertical relief with ledges and fewer smaller holes. This habitat type provides refuge and increases the area accessible for algal grazing.

There were lower, but statistically similar abundances of adults from 21 m down to 40 m depths. This may be due to an increase in sandy and rubble habitat, which has an observed low vertical relief. A higher percent cover of low relief habitats at deeper depths may increase the distance between favorable adult foraging habitats such as turf-rich boulders and bedrock (Hay 1981). Even though densities of adults were lower at deeper depths, over 20% of adult abundance counted along our surveys were found at 30 and 40 m. Thus, in areas where hard bottom habitat extends to 40 m in West Hawaii, deeper depths are serving as additional habitat for adults.

It is possible that when suitable habitat is available, adults are utilizing the upper mesophotic zone as additional foraging grounds. Yellow tang primarily graze on filamentous algae, including turf algae and filamentous forms of macroalgae (Randall 2007). Claisse et al. (2009) found that sexually mature individuals make an ontogenetic shift to shallow habitats (where turf algae is abundant) when an increase in energy is needed for reproduction. This pattern suggests that shallow habitats support the most suitable algae abundances for adult yellow tang foraging; however, our results indicate that turf algae are equally abundant from 3-40 m depths and that macroalgae is more abundant at 30 and 40 m relative to shallower depths. Moreover, substantial communities of macroalgae have been previously documented by ROV surveys from 30-130 m in Hawaii with peak abundances occurring at 60-70 m (Rooney et al. 2010). Thus, because algal abundance does not decline with depth, adult yellow tang densities may be driven more by the availability of appropriate reef structure rather than the presence of algae. From personal observations, adults were found grazing near boulder habitats along fish transects at 30 and 40 m (personal observations).

The interaction among latitudinal region, protection and depth influenced recruit and juvenile densities, but not adults in West Hawaii. However, in this study, reef structure and variation in structure by site rather than the latitudinal region, protected area status, or depth appears to have influenced recruit and juveniles densities along the reef. The three-factor interaction for recruits and juveniles was mainly driven by one site (Kiholo), which had a high percent cover of branching reef habitat. Only one site (Old Kona Airport), had a high density of recruits despite a lower percent cover of both mound and branching reef. Old Kona Airport is a Marine Life Conservation District and has been off-limits to aquarium fish collecting since 1992. It is possible that the protected area status has led to higher recruitment at this site. Long-term research in West Hawaii at 23 sites with similar habitat types has shown that FRAs have significantly higher densities of both juveniles (500% greater) at shallow (3-6 m) depths and adults (48% greater) at mid depths (8-13.6 m) inside- relative to outside-FRAs (Williams et al. 2009). Other habitat or oceanographic features at this site may also have influenced recruit densities and should be explored further in the future.

In contrast, adult densities varied only by depth. This result could be due to a lack of significant differences in bedrock habitat with latitude and protection and boulder habitat with protection. It was interesting that adult densities were not highest in the central region where the percent cover of boulder habitat was the greatest. While adults were associated with boulder and bedrock habitat as well as shallow (3 m) depths, they were found along the entire depth gradient. Adult densities were also high at 12 m, which is primarily mound reef habitat. Thus, adults may utilize multiple habitat types and may not be as closely associated with specific habitat structure as recruits and juveniles.

Further studies need to be conducted to elucidate if adult yellow tang are utilizing upper mesophotic habitats as additional foraging, breeding, and/or refuge grounds. It is possible that some yellow tangs are making ontogenetic habitat shifts from mid-depths to boulder or bedrock habitat at deeper depths as they do into shallow depths. Adults are also very mobile and make daily migrations up to 600 m and are known to make migrations to deeper coral rich habitat to spawn at dusk (Walsh 1984; Claisse et al. 2011). Consequently, it is possible that yellow tangs migrate between deep (30-40 m) and shallow (3 m) habitats throughout the day, or seasonally. However, we were unable to evaluate these hypotheses with our current study as our fish surveys were all conducted in the morning between 0900-1200. Future studies, including diel fish surveys, are necessary to investigate if yellow tang migrate between deep and shallow habitats throughout the day or if the adult yellow tang inhabiting deep habitats remain separate from shallow populations.

This study found that over 20% of adults occurred in the upper mesophotic zone; adults have also been observed as deep as 81 m in Hawaii (Randall 2007). Understanding the full extent of habitats used by fish species targeted for the marine aquarium trade and other extractive activities is important for their management and conservation. As shallow coral reefs decline, mesophotic reefs may provide refuge for target shallow-associated species from some anthropogenic and natural stressors (Khang et al. 2010). Expanding monitoring efforts to mesophotic zones will help garner more accurate population estimates for shallow-associated fish species as well as shed light on the potential for mesophotic coral reefs to re-seed depleted shallow fish populations in the future.

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Table 1: Results from a three-factor analysis of variance (ANOVA) of recruit, juvenile, and adult yellow tang abundances with depth (3,12,21,30, and 40 m), latitude (south, central, or north), and protection (inside or outside).

Factor	**Recruits**			**Juveniles**			**Adults**		
	df	*F* ratio	*P* value	*df*	*F* ratio	*P* value	*df*	*F* ratio	*P* value
Depth	4	12.40	**<0.0001**	4	26.21	**<0.0001**	4	7.87	**<0.001**
Latitude	2	0.62	0.537	2	6.76	**0.002**	2	2.57	0.080
Protection	1	0.00	0.975	1	1.46	0.228	1	1.49	0.224
Latitude * Protection	2	1.97	0.143	2	4.71	**0.011**	2	1.00	0.369
Latitude * Depth	8	1.28	0.260	8	3.25	**0.002**	8	1.47	0.171
Protection * Depth	4	0.97	0.427	4	0.39	0.812	4	0.66	0.624
Latitude * Protection * Depth	8	2.91	**0.005**	8	6.1	**<0.0001**	8	0.70	0.689

Table 2: Results from a Kruskal-Wallis test of benthic structure variables by latitude (south, central, or north), and protection (inside or outside).

Benthic structure by latitude			
Structure Type	H	*df*	*P*-value
Sand	1.41	2.00	0.50
Rubble	5.08	2.00	0.08
Pebble Cobble	1.83	2.00	0.40
Boulder	**9.41**	**2.00**	**0.01**
Bedrock	0.43	2.00	0.80
Mound Reef	1.66	2.00	0.44
Branching Reef	**12.02**	**2.00**	**0.00**

Benthic structure by protection			
Structure Type	H	*df*	*P*-value
Sand	0.69	1.00	0.41
Rubble	0.20	1.00	0.66
Pebble Cobble	0.09	1.00	0.77
Boulder	0.06	1.00	0.80
Bedrock	0.29	1.00	0.59
Mound Reef	**6.98**	**1.00**	**0.01**
Branching Reef	0.29	1.00	0.59

Table 3: Percent cover of each habitat structural category (±SE) at each depth (m). Bolded and highlighted percent cover values indicate that the structural category was significantly greater at that particular depth based on a Kruskal-Wallis test with a paired Steel-Dwass multiple comparisons test (p<0.05).

Depth	**3**		**12**		**21**		**30**		**40**	
Structure Type	% Cover	±SE	% Cover	±SE	% Cover	±SE	% Cover	±SE	% Cover	±SE
Sand	0.2	0.2	4.1	1.5	3.5	1.4	**12**	**3.7**	**21.9**	**4.5**
Rubble	10	6.1	2.3	1	**15.3**	**5.2**	**29.7**	**5.8**	**21.6**	**4.3**
Pebble Cobble	**14.5**	**6.4**	0	0	0	0	0.6	0.4	4.7	2.3
Boulder	**24.6**	**7.5**	0.6	0.4	3.1	1.9	**3.2**	**1.6**	**20.3**	**5**
Bedrock	**42.9**	**8.7**	**13.3**	**3.7**	7.2	3.8	3.5	2.4	5.3	3.2
Mound Reef	7.8	4.5	**66.5**	**5.2**	37.3	4.7	40.3	5	25.9	6.8
Branching Reef	0	0	**13.3**	**5.2**	**33.4**	**6.4**	10.7	3.7	0.2	0.2

Table 4. Results from SIMPER analysis showing which benthic structure categories were responsible for the patterns in habitat observed at each depth. A higher percent contribution (% contribution) to the similarity, indicates a greater influence on habitat patterns. The ratio of the average similarity and standard deviations (Sim/SD) is a measure of how consistently the structure contributes to similaries within groups and a good indicator structure.

Depth: 3 m *(Average similarity: 73.53)*				
Structure Type	Av. Similarity	Sim/SD	% Contribution	%Cummulative
Bedrock	34.72	1.02	47.22	47.22
Boulder	16.98	0.55	23.09	70.31
Pebble Cobble	12.38	0.54	16.84	87.15
Rubble	5.93	0.27	8.07	95.22
Depth: 12 m *(Average similarity: 72.45)*				
Structure Type	Av. Similarity	Sim/SD	% Contribution	%Cummulative
Mound reef	48.25	3.08	66.6	66.6
Branching reef	9.86	1.03	13.6	80.21
Bedrock	7.94	0.76	10.95	91.16
Depth: 21 m *(Average similarity: 74.72)*				
Structure Type	Av. Similarity	Sim/SD	% Contribution	%Cummulative
Mound reef	29.26	2.38	39.16	39.16
Branching reef	23.82	1.27	31.88	71.04
Rubble	8.62	0.62	11.53	82.57
Sand	7.81	0.88	10.46	93.03
Depth: 30 m *(Average similarity: 77.59)*				
Structure Type	Av. Similarity	Sim/SD	% Contribution	%Cummulative
Mound reef	33.16	2.1	42.74	42.74
Rubble	26.74	1.62	34.46	77.2
Sand	7.98	0.67	10.29	87.49
Branching reef	6.48	0.48	8.35	95.84
Depth: 40 m *(Average similarity: 71.34)*				
Structure Type	Av. Similarity	Sim/SD	% Contribution	%Cummulative
Mound reef	19.43	1.13	27.23	27.23
Rubble	17.41	1.34	24.4	51.64
Sand	15.79	1.7	22.13	73.77
Boulder	13.63	0.97	19.1	92.87

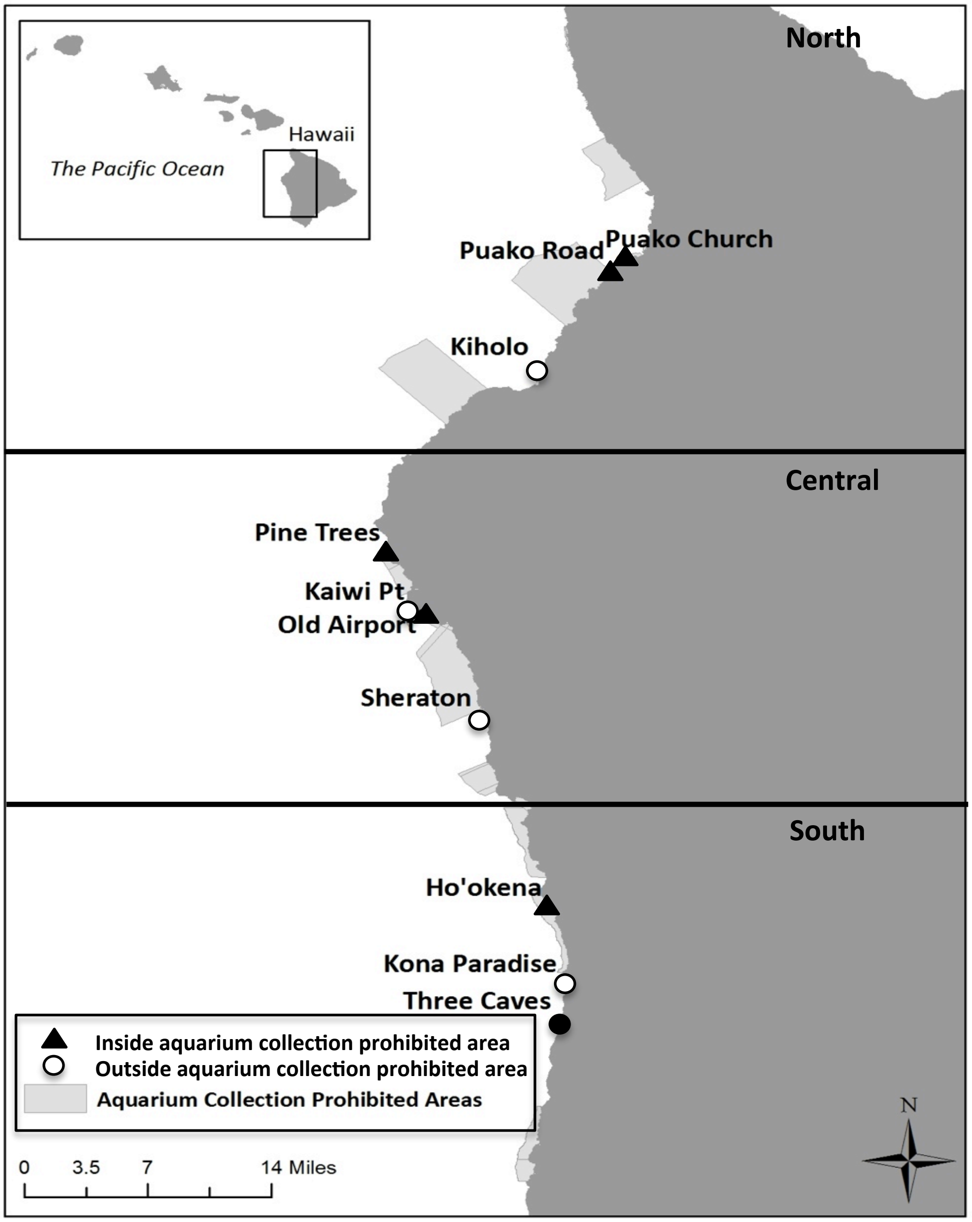

Figure 1: Map depicts sampling fish and benthic survey sites relative to Fishery Replenishment Areas (FRAs) and other sites where aquarium fishing is prohibited in West Hawaii. The sites are also displayed by latitudinal region (north, central, or south).

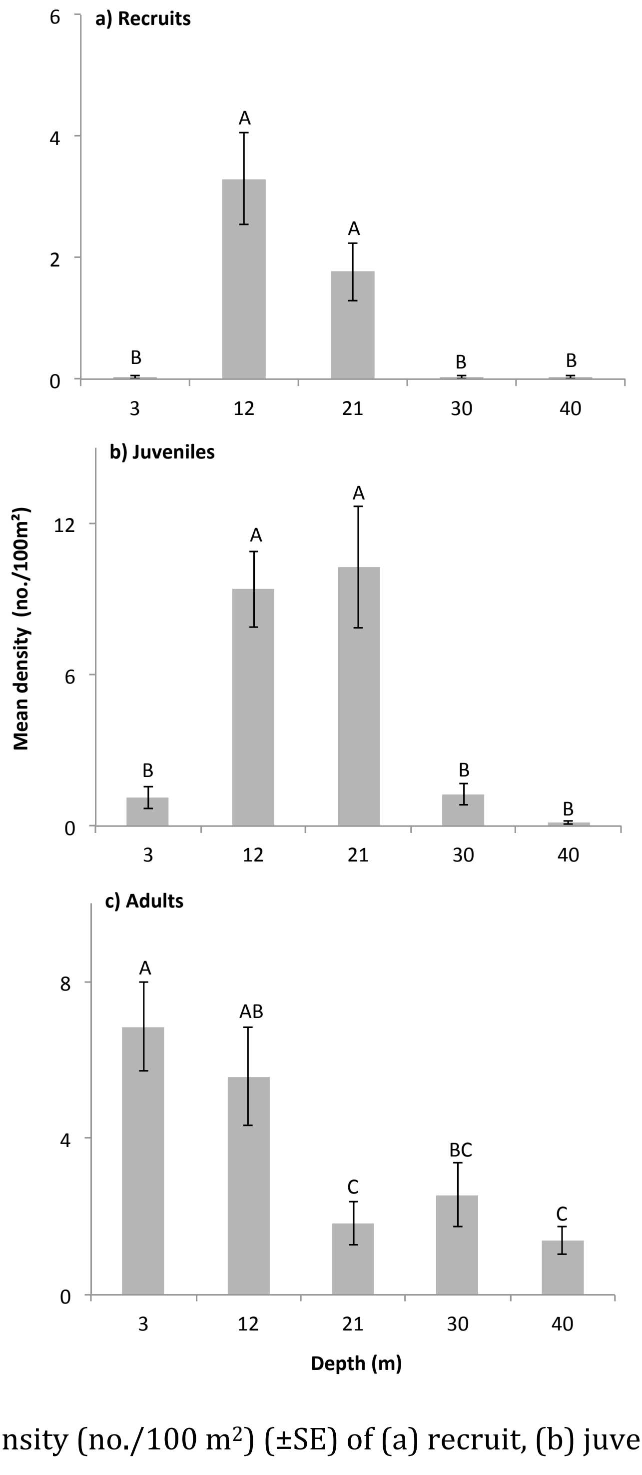

Figure 2: Mean density (no./100 m^2) (±SE) of (a) recruit, (b) juvenile, and (c) adult yellow tang abundances with depth (3- 40 m). Letters are non-significant groupings determined by the Steel-Dwass multiple comparisons test (all KW; $p<0.0001$).

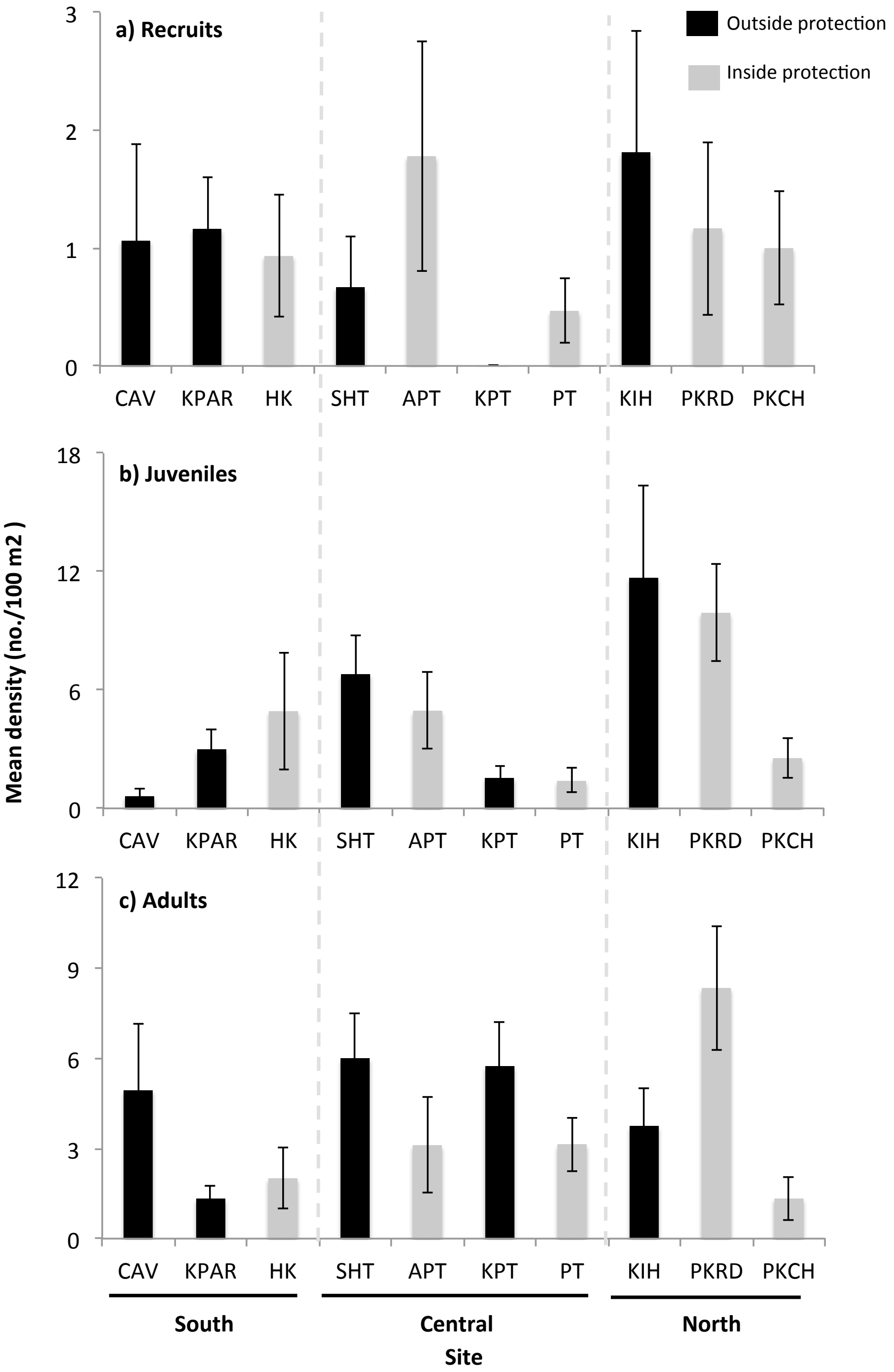

Figure 3: Mean density (no. / 100m^2) (±SE) of recruits, juveniles, and adults across latitudinal region (south, central, and north) and protection (outside or inside).

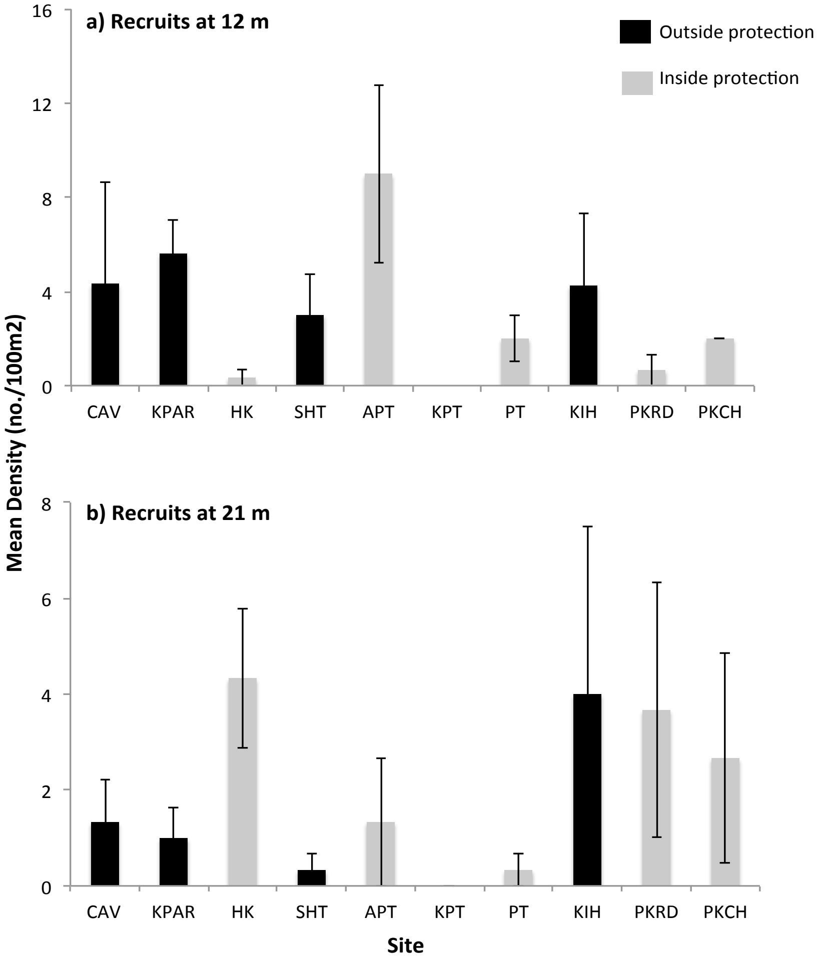

Figure 4. Mean density (no./100m^2) (±SE) of recruits by site (arranged from south to north) and protection (outside or inside) at (a) 12 and (b) 21 m.

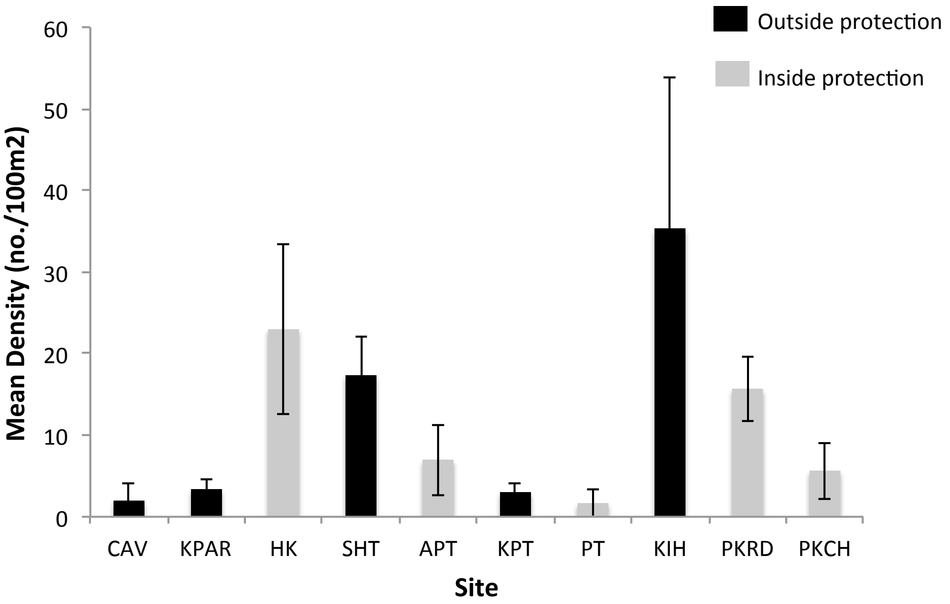

Figure 5. Mean density (no./100m^2) (±SE) of juveniles at 21 m by site (arranged from south to north) and protection (outside or inside).

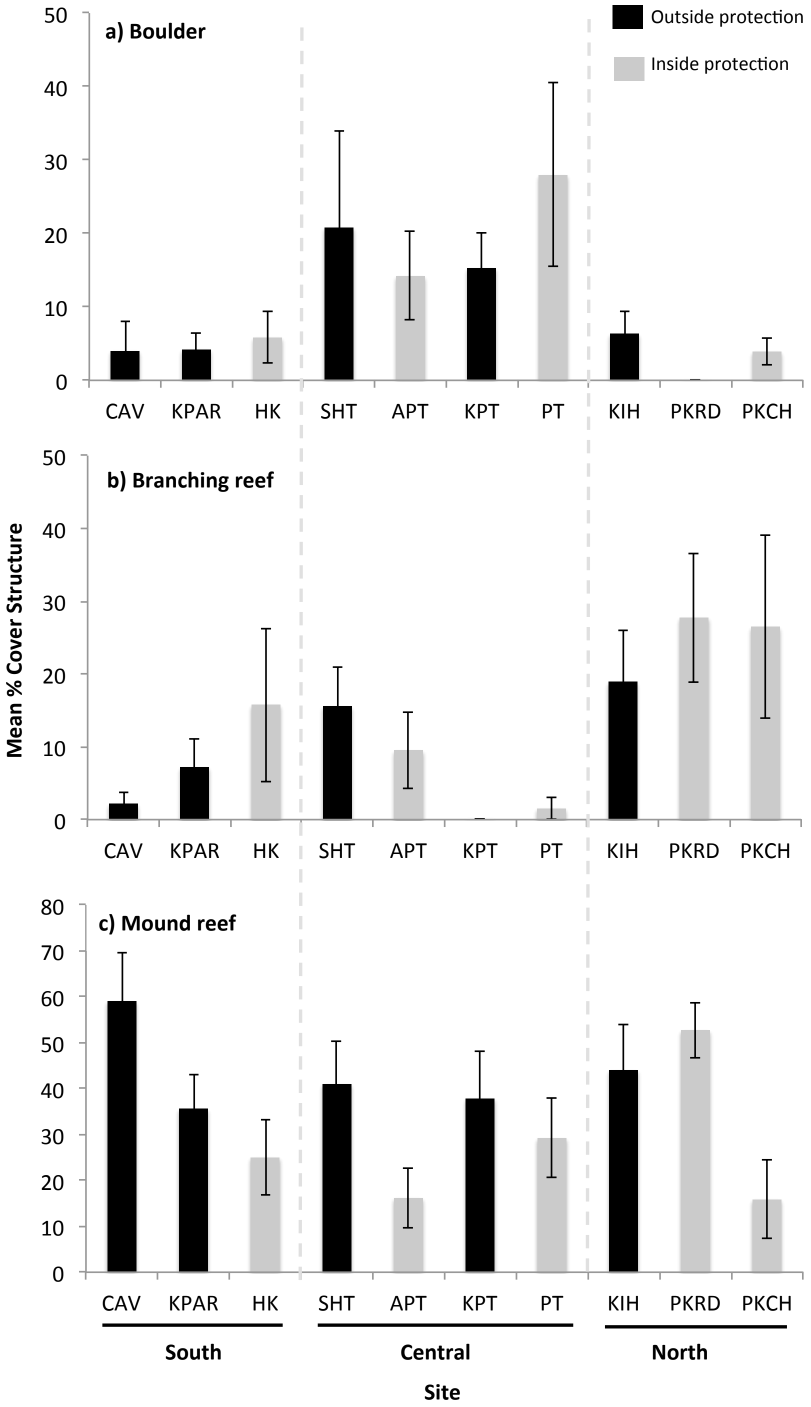

Figure 6. Mean percent cover (±SE) of the benthic structure categories significantly different between latitudinal region ((a) boulder and (b) branching reef) or protection ((c) mound reef) based on Kruskal-Wallis tests.

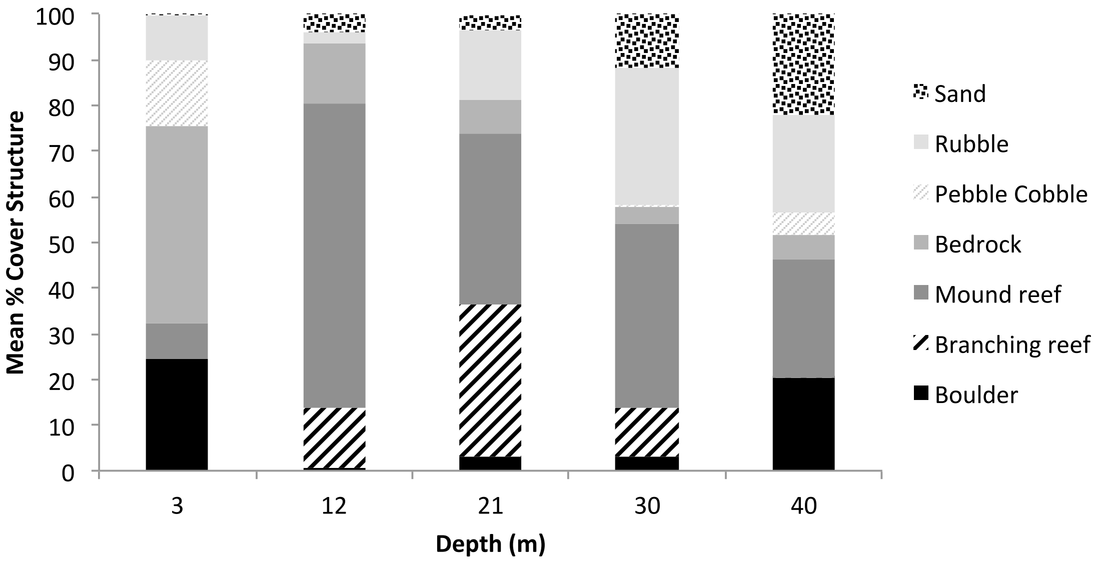

Figure 7: Mean percent cover of each primary habitat structural categories (sand, rubble, pebble/ cobble, bed rock, mound reef, branching reef, and boulder) with depth (3- 40 m).

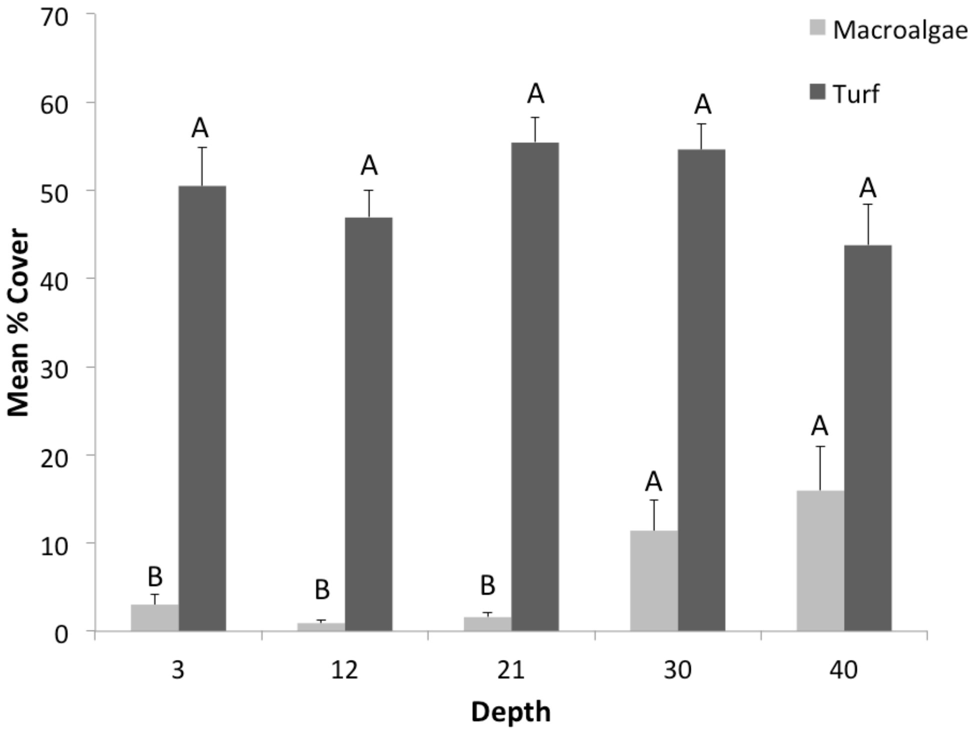

Figure 8: Mean percent cover (±SE) of turf algae and macroalgae across depth (3-40 m). Letters represent non-significant groupings determined by two separate Steel-Dwass multiple comparisons test for turf algae and macroalgae. Turf algae was not significantly different across depth (KW; $p>0.05$). Macroalgae was significantly different across depth with a greater percent cover at 30 and 40 m (KW; $p<0.05$).

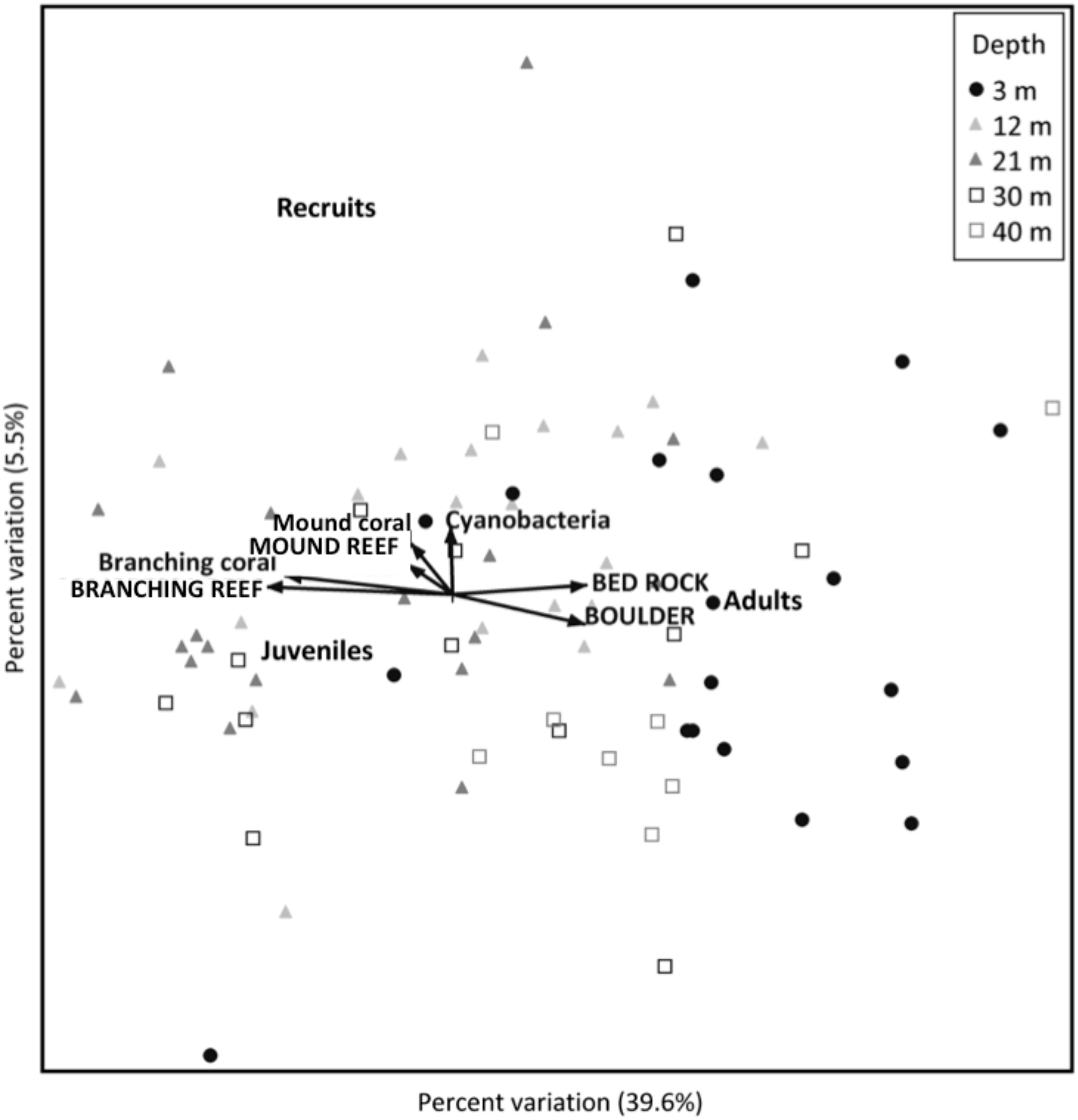

Figure 9: CCA analysis of the habitat associations of yellow tang recruits, juveniles, and adults with biotic (lower case letters) and structural (upper case letters) habitat characteristics. Each transect depth is depicted by a different symbol (see legend). The percent variation explained by axis one is 39.6% and the percent variation explained by axis two is 5.5%.