Project Final Report

I. Effects of habitat and predation on the effectiveness of an MPA network in Hawaii to replenish the aquarium fish, yellow tang *Zebrasoma flavescens*

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II. Abstract

This proposal examined the spatial characteristics of coral reefs that are associated with the effectiveness of a Marine Protected Area (MPA) network in West Hawaii and the post-settlement processes affecting the demography of aquarium fish. Our results indicate that the geomorphology of the reef, area of reef habitats, and level of habitat complexity were associated with the significant recovery of aquarium fish populations, particularly, yellow tang *Zebrasoma flavescens*, the most heavily collected aquarium species in Hawaii. For example, locations having large areas of coral-rich and boulder-turf-rich habitats at a range of depths and retention features important for settlement, juvenile survivorship, and adult reproduction supported a higher number of each of the life stages of yellow tang. Recruit densities were higher in finger coral habitats, but not correlative relationship was detected between the abundance of recruits at both high and low levels of finger coral cover in the presence of predators. Furthermore, recruitment rate and years of closure influenced the effectiveness of the network, with more MPAs showing significant increases of yellow tang as years of protection increased and recruitment was consistent. The design of the West Hawaii MPA network was effective at replenishing aquarium fish populations by protecting both newly recruited fish to nearshore reef habitats and foraging and sheltering locations for juveniles and adult breeding populations. Our results demonstrated that guidelines for designing MPA networks should depend on the life history and spatial requirements of the species being protected. Consequently, results from this study suggest that the use of landscape metrics and new technologies, such as remote sensing and geographical information systems, coupled with *in situ* population sampling can provide managers with the information required to select and manage reef systems for maximum benefit to targeted fish populations.

III. Executive Summary

In 1999, a network of nine MPAs was established on the west coast of the Big Island of Hawaii (hereafter ‘West Hawaii). There are currently only three other networks of MPAs in the United States: the Florida Keys, the California Channel Islands, and central California. However, the West Hawaii network is the only MPA network worldwide that focuses on aquarium fisheries. These MPAs, specifically called fishery replenishment areas, were close to aquarium fish collectors at the end of 1999 as a result of the conflict between the collectors and recreational dive-tour operators over apparent declines of reef-fish. Continuous monitoring in these areas has revealed significant increases in the overall abundance of aquarium fish after the closure of the MPAs and enhancement of the most heavily-exploited ornamental species, yellow tang *Zebrasoma flavescens*, in outside areas through potential adult spillover (Walsh et al. 2004, Williams et al. 2009). However, only half of the MPAs in West Hawaii have been successful in replenishing fish populations (Walsh et al. 2004). Recent studies suggest that the spatial characteristics of the reef are likely important factors influencing the effectiveness of the MPA network to replenish aquarium fish (Walsh et al. 2004, Ortiz and Tissot 2008, Ortiz and Tissot In Review). It is therefore necessary to examine the relationship between the spatial characteristics of the reef within the entire network of MPAs in West Hawaii and their ability to augment targeted species. The purpose of this study was to apply commonly used landscape metrics to investigate relationships between yellow tang *Zebrasoma flavescens*, the most heavily collected aquarium species in Hawaii and the spatial characteristics of the reef in relation to the effectiveness of an MPA network in West Hawaii, as well as identify post-settlement processes affecting the survivorship of newly recruiting fish.

In 2005 and 2007, we developed a benthic habitat map for the near-shore waters of each of the MPAs in West Hawaii (to 25 m depth) (Fig.1). The map was developed based on aerial photographs of the island of Hawaii (Coyne et al. 2001), Light Detection and Ranging Technology (SHOALS 2002), and *in situ* biological and physical observations using SCUBA. A total of fifteen habitat types were defined using a hierarchical classification scheme using six categories of physical substratum, based on the lithology and geomorphology of the seafloor, and four categories of biological substratum (Ortiz and Tissot 2008). These types were condensed into the following reef habitats based on their physical and biological similarities: (1) deep aggregate coral-rich and sandy rubble habitats (DC), (2) mid-depth aggregate reef and boulder habitats (MB), and (3) shallow turf-rich boulder habitats (ST) (Table 1).

Reef spatial characteristics of the MPAs were calculated using ArcGIS 9.0 (ESRI 2002). These included: reef size, width and area, number of reef habitats, number of patches, variability (indicated by standard deviation) of reef habitat patch size and shape, area of reef habitats (i.e. DC, MB, ST), and area of sand.

A stratified monitoring effort was carried out to quantify abundance and size of fish at each site. Fish abundance at each location was estimated between May and August 2008 using circular plot counts. A total of 193 circular plots were surveyed within each habitat at each site. Within each plot all fish were counted and sized as recruits (< 5cm), juveniles (>5 cm and <14 cm) and adults (> 14cm). In addition, rugosity, depth and substrates types were quantified using a 10m transect. In order to evaluate the relationship among MPA effectiveness and the spatial characteristics of the reef, data from DAR's long-term monitoring study was used to calculate the absolute percent change in density of the pre-closure surveys (1999) relative to post-closure surveys (2007-2008) as a measure of effectiveness.

In order to explore relationships between targeted species and the spatial characteristics of the reef in relation to the effectiveness of an MPA network in West Hawaii, we use ArcGIS software and both univariate statistics and a multivariate canonical correlation analysis to explore the spatial characteristics that result in the effective replenishment of managed species. Analyses indicated several important conclusions. Recruit densities were associated with retention features (i.e. small bays) and optimal recruit habitat (i.e. coral-rich areas). Juvenile densities were associated with large complex areas of deep coral-rich habitats, while adult densities were associated with both deep and mid-depth coral-rich and shallow boulder turf-rich habitats. Consistent with these fish-habitat associations, sites displaying a positive increase in yellow tang densities and the highest number of recruits, juveniles, and adults had a combination of these spatial characteristics. In contrast, sites with a combination of low recruitment, habitat complexity (i.e. as measured by rugosity), and water quality displayed decreases in yellow tang densities. Recovery of yellow tang populations following closure depends on the magnitude of recruitment and years of protection, with more MPAs showing significant increases as years of protection increase and recruitment is consistent.

Deployment of an automated time-lapsing digital video camera demonstrated the utility of this approach for monitoring predator distributions in the absence of divers at two plots within the Honokohau MPA for 2 days each during July 2006. The camera recorded 2 sec every 30 sec for 0.5-6 hr per deployment, for a total of ca.13 hr of video. Results revealed predator visitation to be four times as frequent at one plot compared to the other, indicating highly variable visitation rates. To conclude a study of fish-habitat relationships during May to August 2006, 14 existing 78m^2 plots were surveyed at two FRAs, Keei and Honokohau (n= 7 plots /site). Using circular plot counts, all plots within a site were surveyed on the same day. Monitoring of the two sites occurred within a 48-hour period whenever possible. Each site was monitored seven times during the summer. Fish were identified, counted, and sized within each plot. The plots were randomly distributed along a spatial gradient of settler habitat (high and low, based on *Porites* finger-coral cover) at each site. There seemed to be a relationship between survivorship and predator density but because of low sample size we were not able to analyze it. However, at habitats with high finger coral cover, 89% of the variation was explained by the relationship between survivorship and predator density with survivorship increasing with increasing predator density.

In summary, results from this study provide strong evidence that the spatial characteristics of the reef and the frequency and intensity of recruitment can significantly influence the recovery of targeted reef-fish species within an MPA network. Therefore, the design of protected areas selected for conservation should take into account the recruitment dynamics and habitat requirements of each life stage of the targeted species on spatial scales that are appropriate to the species being protected. Although comparative studies on the efficacy of different MPA designs are challenging, the use of landscape metrics and new technologies, such as remote sensing and GIS, coupled with *in situ* population sampling can provide managers with the information required to select and manage reef systems for maximum benefit to targeted fish populations.

IV. Purpose

A. Problems or impediments: None

B. Objectives

Our study was designed to evaluate the interaction between habitat and the recruitment and survivorship of reef fish, in particular the yellow tang, in a network of MPAs in West Hawai`i. Furthermore, we examined the spatial characteristics of the MPA network that result in the effective replenishment of yellow tang in West Hawaii. The results of this project are critical to enhancing our understanding of the ecological processes governing coral reef fish assemblages. In turn, this will aid in the design and implementation of MPAs as a fisheries management tool and provide a model system that can be applied to MPA design throughout the state of Hawai`i and other tropical regions. This project also serves as a model on how to monitor and manage fishes from the aquarium trade.

The objectives of this proposal are to address the following questions:

1. How does the distribution and abundance of habitats effect MPA effectiveness to replenish depleted aquarium fishes?
2. What effects does habitat have on the recruitment of yellow tangs and other reef fishes at multiple spatial and temporal scales?
3. How does habitat availability and predation intensity influence the survivorship of newly recruited yellow tangs?

V. Approach

A. Methods

Study sites and species

We examined nine MPA in West Hawaii (Fig.1): Waiakailio Bay, Anaehoomalu, Kaupulehu, Honokohau, South Oneo Bay (S. Oneo Bay), North Keauhou (N. Keauhou), Keei, Hookena, and Milolii. This study focused on the yellow tang *Zebrasoma flavescens*, the most heavily exploited species which constitutes about 80% by number and 70% by value of aquarium landings from West Hawaii (Williams et al. 2009). Yellow tangs are one of the most abundant herbivorous surgeonfish (family Acanthuridae) (Walsh 1987, Tissot et al. 2004). They initially settle on the reef at ~ 30 mm total length during the summer and as they mature, they exhibit an ontogenetic habitat shift from deeper aggregations of coral-rich habitats as recruits and juveniles to shallow turf-rich boulder habitats as adults (Walsh 1984, Ortiz and Tissot 2008, Claisse et al. In Review).

(1)How does the distribution and abundance of habitats effect MPA effectiveness to replenish depleted aquarium fishes?

We used previously developed *in situ* groundtruthing methods to interpret and map all nine MPAs in West Hawaii (Ortiz and Tissot 2008). Using the same approach as our previously funded work, the spatial characteristics of reef habitat among all MPAs were quantified in order to examine those spatial characteristics associated with the effective replenishment of species targeted by the aquarium trade.

Geomorphology and benthic habitat mapping of reef habitats

In 2005 and 2007, we developed a benthic habitat map for the near-shore waters of each of the MPAs in West Hawaii (to 25 m depth) (Fig.1). The map was developed based on aerial photographs of the island of Hawaii (Coyne et al. 2001), Light Detection and Ranging Technology (SHOALS 2002), and *in situ* biological and physical observations using SCUBA. Reef habitats were delineated at a scale of 1:2500, with a minimum mapping unit of 1045m^2. Visual interpretation of the imagery was guided by a classification scheme that delineated reef habitat types using six categories of physical substrate (colonized volcanic rock/boulder, aggregate coral, sand, pavement, reef rubble, and unknown), based on the lithology and geomorphology of the seafloor, and five categories of biological substrate (finger coral *Porites compressa*; lobe coral *P. lobata*; cauliflower *Pocillopora meandrina;* uncolonized; mixed) (Ortiz and Tissot 2008). Reef habitat types were categorized using a three-code system where the first letter denoted the primary physical substrate (>50%) and the second and third letters denoted the primary (≥50%) and secondary (>20% and <50%) biological substrate types, respectively. For example, BEL represented at least 50% cover by boulders with at least 50% covered by cauliflower coral and at least 20% lobe coral. Using this classification scheme, a total of 15 reef habitat types were identified. However, for the habitat map and data analysis to be more applicable to managers these types were condensed into the following reef habitat categories (hereafter referred to as "reef habitats" or "habitats") based on their physical and biological similarities: (1) deep aggregate coral-rich and sandy rubble habitats (DCRH), (2) mid-depth aggregate reef and boulder habitats (MABH), and (3) shallow turf-rich boulder habitats (STBH) (Table 1).

Accuracy of the benthic habitat map was quantified using an error matrix. The matrix was made up of rows and columns that represented each reef habitat type, with each cell representing the total sites sampled for that particular reef habitat type. In 2005 and 2007, a total of 90 and 115 accuracy assessments sites were randomly sampled within mapped reef habitat types respectively. At each sampling site, a visual assessment of the reef habitat type was made. The mapped reef habitat type was then compared with that of the actual reef habitat type from field observations.

Data Analysis

Differences in reef habitat complexity were examined by comparing rugosity of each reef habitat among MPAs with a one-way analysis of variance (ANOVA). Values were log(x+1) transformed prior to statistical analysis to conform to the assumptions of parametric testing (Zar 1984). Normality was tested using a Shapiro-Wilks W test ($P < 0.05$) while a Levene's test ($P < 0.05$) was used to examine homogeneity of variance. Tukey's honestly significant difference (HSD) (Zar 1984) was used for a post hoc comparison test. Bonferroni adjustments were also conducted to account for multiple statistical testing (Holm 1979), with a P value of < 0.01 used for statistical significance.

Geomorphology of the reef within each of the study sites was described based on previous studies (Dollar 1982, Gibbs and Cochran 2009) and the use of color aerial photographs of the island of Hawaii (Coyne et al. 2001) superimposed on hillshades, derived dataset from high-resolution bathymetry (SHOALS 2002), and geo-referenced underwater video and still photography (refer to benthic habitat mapping section).

To compare the spatial characteristics of the reef among MPAs, we used the reef area, width, and length calculated with ArcGIS 9.0 (ESRI 2002). The reef area was measured as the total area from shore to a depth of 25m, the extent of the benthic habitat map. Reef width was measured as the mean distance from shore to a depth of 25m at each site, and reef length was measured as the total distance of shoreline within the MPA boundaries. The abundance of reef habitats at each site was measured as the proportion of reef area covered by each habitat. Figure 2 displays how spatial characteristics of the reef were measured.

These benthic maps served as a reference to examine spatial variation in habitat use of yellow tangs and allowed comparisons to other MPAs which have varied in their degree of effectiveness to replenish yellow tangs.

(2) What effect does habitat have on the recruitment of yellow tangs and other aquarium and reef fishes at multiple spatial and temporal scales?

Effective replenishment has been linked to the moderately high levels of newly recruiting aquarium fishes observed in 2001-2003 (Walsh et al. 2004) and the abundance and distribution of finger coral habitat. Previous work has also revealed significant ontogenetic shifts in habitat use of yellow tang in two FRA's (Ortiz and Tissot 2008). Variation in recruitment can strongly affect the distribution and abundance of reef fish species as well as the population dynamics of reef-fish. Therefore we proposed to monitor the abundance of all life stages in relation to the spatial variation of habitats and their degree of effectiveness within all MPAs. We further examined the relationship between finger coral habitat and recruitment rates and survivorship among two sites (Honokohau and Keei).

MPA Effectiveness and spatial characteristics of reef fish

Fish and Benthic Sampling

The locations of 193 sampling sites were determined using a stratified random sampling approach in which random points were assigned to each of the mapped reef habitats within each MPA (Table 2). Abundance and size of fishes were estimated between May and August 2008 using circular plot counts. A SCUBA diver recorded the number and size of fishes seen within randomly selected 5 m radius circular plots (78 m^2 plot area). Fishes were categorized as recruits, juveniles or adults based on body size and/or coloration, according to published sources (Walsh 1984, Walsh 1985, Claisse et al. 2009). Recruits were generally individuals <5 cm in total length; juveniles were 5 to 14 cm, and adults were >14 cm.

Depth, rugosity, and percent substrate cover were estimated within each circular plot using a 10 m transect line placed parallel to shore. Depth was recorded at the center and at 90° intervals around the edges of the circular plot; these 5 depth readings produced a mean depth for each circular plot. Rugosity, or the surface relief of the reef, was measured using a fiberglass tape measure extended along and following the contour of the transect. The rugosity index was calculated as the ratio of transect length to tape length. To determine percent substrate cover, an underwater digital camera was used to take 10 photoquadrats along each transect, 1 m above the substrate. Each of 1930 images was projected onto a rectangular grid using Pointcount software (Kohler and Gill 2006) and the percent cover was quantified under 20 random points on each grid. These substrate types included cauliflower, finger, and lobe coral, finger coral holes, sand, turf algae on boulders, turf algae on dead finger coral, turf algae on rubble, crustose coralline, crustose on dead finger coral, and crustose on rubble.

Data Analysis

To determine if the density of each reef-fish life stage varied significantly among reef habitats a non-parametric Kruskal-Wallis was employed with a Dunn's test for unplanned multiple comparisons (Zar 1984). Bonferroni adjustments were again conducted to account for multiple statistical testing (Holm 1979), with a P value of < 0.01 used for statistical significance. A one-way ANOVA was used to determine if the density of each life stage varied significantly among sites. Density was log(x+1) transformed prior to statistical analysis to conform to the assumptions of parametric testing (Zar 1984). Normality was tested using a Shapiro-Wilks W test ($P < 0.05$) while a Levene's test ($P < 0.05$) was used to examine homogeneity of variance.

A Spearman's rank correlation coefficient was used to determine environmental variables influencing abundance and distribution of each life stage. For all analyses, the relationship between depth, rugosity, and percent cover of substrate types with the abundance of each life stage was explored.

Population density of each life stage of yellow tang among MPAs was compared. Population densities were calculated by multiplying the mean density (# / m^2) by the total reef area (m^2) sampled (i.e., reef structure from shore to a depth of 25m) and dividing it by the reef length (km) (i.e., length of shoreline within MPA). Density calculations were done in order to account for the different shoreline lengths and reef structure from shore to depth in each site.

A Canonical Correlation Analysis (CCA) using SAS (SAS 2000) was conducted to examine multivariate associations among the spatial characteristics of the reef and abundance of each life stage of yellow tang (Table 3). CCA is a multivariate technique that extracts a series of patterns (axes) between two related data sets (Pimentel 1979). We used the variable loadings of the sites to examine how they grouped based on the unique associations between the two data sets derived from the axes. The data matrix consisted of the reef spatial characteristics of MPAs and population size of recruits, juveniles, and adults of each study species by MPA. Reef spatial characteristics of the MPAs were calculated using ArcGIS 9.0 (ESRI 2002). Because the abundance of coral-rich habitats is important to reef-fish, we separated sand from the deep aggregations of coral-rich and sandy rubble habitat category in the analysis.

In order to evaluate the relationship among MPA effectiveness and the spatial characteristics of the reef, data from DAR's long-term monitoring study was used to calculate the absolute percent change in density of the pre-closure surveys (1999) relative to post-closure surveys (2007-2008) as a measure of effectiveness. These changes were calculated with the following equation:

$$\text{Percent change in density} = \frac{(\overline{X}_{FRA-After} - \overline{X}_{FRA-Before})}{\overline{X}_{FRA-Before}} \text{ x } 100$$

Before and after differences of yellow tang densities among sites were assessed using a two-sample t-test. Thus, a statistically positive difference indicated that fish abundance within MPAs had significantly increased after closure relative to before closure. Because fish abundance varies greatly over time and space, changes in the mean density of yellow tang among the MPAs were examined from their inception to eight years after their closure.

Recruitment and habitat

We examined the effects of combinations of habitat quality (high/moderate and low, based on finger coral cover) and settler density within settler habitat at two MPAs that vary in their effectiveness to replenish aquarium fish (Honokohau and Keei). We surveyed yellow tang recruit densities daily at 14 circular plots (# / $78m^2$) ($n = 7$ /site) for 10 days. Finger coral cover and rugosity were measured using fish and benthic sampling methods outlined in the previous section. Comparisons were made between the recruitment rate (i.e. density of newly recruiting fish), survivorship of recruits and finger coral cover among two MPAs with different levels of replenishment.

(3) How does habitat availability and predation intensity influence the survivorship of newly recruited yellow tangs?

Current studies have shown a high correspondence between habitat refuge space, in the form of finger coral cover, and MPA effectiveness but a lack of correlation between recruitment intensity and MPA effectiveness (Tissot et al. 2003) suggesting that differential post-settlement mortality among sites is important. Post-settlement processes such as predation may alter the initial abundance of new settlers and substratum characteristics, particularly the complexity of coral, may offer different levels of shelter from predation to new settling fish. Therefore, we examine recruitment and juvenile survival in relation to the abundance of piscivores and the abundance of finger coral among sites.

Influence of habitat availability and predation intensity on the survivorship of newly recruited yellow tangs

Thus, to meet our third objective, patterns of abundance of common piscivores such as trumpetfish (*Aulostomus chinensis*), cornetfish (*Fistularia commersonii*), morey eels (*Gymnothorax* spp.), and groupers (*Cephalopholis argus*), we determined using both timed swim surveys and video-monitoring techniques (Hixon and Carr 1997, Webster 2003), stratified by settlement habitat and replicated at two sites (2 per site). All piscivores were identified, counted and sized during 10 min free swims passing along the center of eight 78 m^2 plots. Using remote videography, we monitored the abundance and potential impact of these piscivores in the absence of divers for one pair of plots (2 per site) in order to provide an additional assessment of predator abundance that is more likely to capture highly mobile predators (e.g., jacks). Each plot was filmed 2-4 hours using an automated digital video camera mounted on the seafloor in an underwater housing. Video cameras were placed on the reef (outside of the circular plot) focusing on the plot area. The camera recorded for 2 second every 30 seconds in each plot on *two different days*. Predatory fish passing within 9 m of the focal was counted. The proportion of time predators are present was determined based on "predator minutes" for species seen over the reef (Webster 2003). The abundance of finger coral, holes on the reef, and rugosity was calculated for each site using underwater benthic surveys as outline in the previous section.

B. Project Management

Aspects of the study are the result of cooperative interaction between WSU, OSU, UHH and DAR personnel. UH Scientific Divers, all UHH student divers specifically trained for the project using Quantitative Underwater Ecological Survey Techniques (QUEST), assist in field data acquisition. Equipment for the project, including Scuba equipment, transect lines, differential GPS, a research vessel, and underwater digital video cameras were available through DAR, UHH, OSU, and WSU. Data entry and verification, image analysis of habitat surveys, experimental design, field implementation and database management was developed and handled by WSU.

Original underwater data sheets and benthic habitat maps are archived in WSU facility under the supervision of Tissot and Ortiz. Data are entered into a Microsoft® Access relational database under the supervision of Ortiz. This database and benthic habitat maps are accessible through the WSU GIS database system and reports.

VI. Outcomes

A. Accomplishments and findings:

Geomorphology and benthic habitat mapping of reef habitats

Accuracy of the benthic habitat map was equivalent to the probability of correctly determining the reef habitat type present. For example, accuracy was calculated as the probability of classifying an area as uncolonized boulders in the map when it was also uncolonized boulder from field observations. The overall accuracy of the benthic habitat map ranged between 92% to 93% for MPAs mapped in 2005 (Anaehoomalu and Honokohau) (Ortiz and Tissot 2008) and 2007 (for remaining MPAs) respectively. Patchy sandy and boulder areas with low to high coral cover and aggregations of finger and lobe coral located in areas of abrupt change were less accurate (83%).

Reef geomorphology varied greatly along the West Hawaii coast (Figs. 1, 3). Reefs located in northern and central sites consisted of large (217-536 ha) wide (> 344 m) areas of sunken basalt-lava flows that formed flat to gently sloping benches between shore to a depth of 11m becoming more gentle to steep at depths down to more than 30 m. The basalt surface had large rounded boulders with scattered rock at shallow depths (0-11m), but at deeper depths (5 - 40 m) moderate to large areas of coral or accreted carbonate reef obscured the underlying volcanic surface. In contrast, central and southern sites consisted of small (89-334 ha), long (2.7 – 8.7 km), and narrow (< 344 m) reefs with sunken flat basalt-lava benches that dropped into vertical walls or steep escarpments with coral at 15 – 25 m. In summary, all northern and one central site (Waiakailio Bay, Anaehoomalu, Kaupulehu and S. Oneo Bay) had larger and wider reefs with large areas of deep coral-rich (DCRH) (> 38%) and shallow turf-rich boulder (STBH) (13- 62 %) habitats. Central and southern sites (Honokohau, N. Keauhou, Keei, Hookena, and Milolii) had smaller, and narrower reefs with smaller areas of deep coral-rich habitats (< 38%), but larger areas of shallow turf-rich boulder habitats (46-80%). Areas of mid-depth aggregate reef and boulder habitats (MABH) were present in 5 out of the nine MPAs with Anaehoomalu and Milolii having larger areas of this habitat (> 28%) relative to Honokohau, S. Oneo Bay, and Keei (< 26%).

The rugosity measurements indicated that the topographical complexity of each reef habitat varied significantly among MPAs (Fig. 4a-c). The topographical complexity of DC in Honokohau was significantly higher than Waiakailio Bay and Hookena (Fig. 5a, $F_{8,89} = 2.42$, $P < 0.05$), and the complexity of MB was significantly higher in Anaehoomalu than S. Oneo Bay (Fig. 5b, $F_{3,24} = 5.37$, $P < 0.01$). For ST, Kaupulehu had significantly lower rugosity values than Hookena and Anaehoomalu (Fig. 5c, $F_{8,74} = 3.92$, $P < 0.01$). Overall, DC and MB were most complex in Anaehoomalu and Honokohau respectively, while ST was most complex in Anaehoomalu, Hookena, and Milolii.

MPA Effectiveness and spatial characteristics of reef habitats

<u>Fish density among habitats and sites</u>

Overall, recruit and juvenile densities were higher in DCRH and MABH, while adult densities were higher in ST, but displayed broader distributions (Fig. 5). Densities of yellow tang recruits were significantly higher in DCRH compared to MABH and STBH (H=15.79, P <0.0001). Densities of juvenile yellow tang were also significantly higher in DCRH than in MABH and

STBH (H=53.95, P <0.0001) while adult yellow tang densities were higher in STBH relative to DCRH and MABH (H=6.32, P <0.05). Thus, the abundance and distribution of the early life stages of yellow tang was highest in deep coral-rich areas (i.e. DCRH), while adults yellow tang densities varied among habitats, but had highest densities in MABH and STBH.

Consistent with these fish-habitat associations, yellow tang recruit and juvenile densities were positively correlated with depth (r = 0.18 - 0.38, P < 0.01), percent cover of finger coral (r = 0.25 - 0.53, P < 0.0001), rugosity (r = 0.17- 0.26, P < 0.02), percent cover of finger coral holes (r = 0.15 - 0.47, P < 0.02) and crustose coralline (r = 0.14 - 0.33, P <0.04), but negatively correlated with the percent cover of turf algae on boulders (r = 0.16 – 0.18, P < 0.03) and percent cover of sand (r = 0.14 - 0.32, P < 0.04). Density of juvenile yellow tang was also positively correlated with the percent cover of crustose on dead finger coral (r = 0.17 - 0.32, P < 0.02), percent cover of crustose on rubble (r = 0.15 - 0.17, P < 0.04), and turf algae on dead finger coral (r = 0.24 - 0.29, P < 0.001). Density of adult yellow tang was positively correlated with depth (r = 0.16, P < 0.02), while both recruit and adult densities were positively correlated with percent cover lobe coral (r = 0.15 - 0.22, P < 0.03). Thus, finger, lobe and rubble cover substrates were found to influence the densities of newly recruited and juvenile yellow tang as they were significantly more abundant in deep coral-rich areas and/or positively correlated with the abundance of these coral types. In contrast, shallow turf-rich boulder areas and lobe coral cover substrates influenced the densities of adult yellow tang. Although statistically significant differences among sites were not detected, the abundance of recruits, juveniles, and adults was highest along central and southern sites (Honokohau, Red Hill, and Milolii), with a wide range of coral-rich and boulder turf-rich boulder habitats at a range of depths (Fig. 6).

Population density

Estimates of fish population density (# / km) were conducted for each life stage among MPAs (Fig. 7). Estimates of population density for all life stages were, overall, higher in large MPAs that contained wide reefs and large areas of recruit, juvenile, and adult habitat. Recruits were most dense in Kaupulehu and Honokohau while juvenile density was highest in Anaehoomalu, Kaupulehu, S. Oneo Bay, and N. Keauhou. Adult densities varied among sites with Anaehoomalu, Honokohau, S. Oneo Bay, and Keei having greater densities. Overall, population density of most life stages was greater in some northern and central sites (Anaehoomalu, Kaupulehu, Honokohau, and S. Oneo Bay).

Population size and MPA characteristics

The first (CC1) and second (CC2) axes of the canonical correlation analysis (CCA) provided significant ecological contrasts for yellow tangs (Figs. 8,9; Table 3). The CC1 axis provided a contrast between MPAs with large areas of MB and sand, and a large number of habitats and patches supporting a greater number of adults (S. Oneo Bay and Anaehoomalu), with MPAs showing smaller continuous areas of these habitats and fewer habitats patches supporting fewer adults (N. Keauhou, Hookena, Honokohau and Waiakailio Bay, and Kaupulehu) . Milolii and Keei, having a moderate area of MB and sand, and moderate number of habitats and habitat patches supported a moderately high number of adults. The CC2 axis provided a contrast between larger MPAs with large areas of DC, MB, and sand and numerous habitat patches supporting a large number of all life stages (S. Oneo Bay, Kaupulehu, and Anaehoomalu) and smaller MPAs with smaller areas of these habitats and fewer habitat patches supporting fewer life stages (Waiakailio Bay, N. Keauhou, Hookena, and Keei). Milolii and Honokohau supported a large to moderate number of recruit, juvenile, and adult yellow tang relative to their size, consisting of smaller narrow areas of DC, MB, and sand, and few habitat patches. On the other hand, Waiakailio Bay supported fewer numbers of each life stage relative to its large size and large area of continuous DC and sand. Overall, large MPAs, wide reefs with large areas of all reef habitats, variable size, shape, and number of these habitat patches on the reef were associated with MPAs supporting the highest number of individuals of each life stage.

<u>Changes within MPAs</u>

Density of yellow tang increased by 74% from 1999, before MPA closure, to 2008. Among the sites, seven out of the nine MPAs experienced increases: Anaehoomalu (26%), Honokohau (8%), N. Keauhou (77%), Keei (187%), Hookena (84%), and Milolii (43%); with all, but Anaehoomalu, experiencing significant increases. Waiakailio Bay (- 48%) and S. Oneo Bay (-23.2%), however, showed significant decreases in yellow tang abundance.

Density of yellow tangs varied greatly within each MPA following years of closure (Fig. 10). Yellow tangs showed steady increases in all areas beginning in 2002 with most reaching higher abundances than before closure densities. Since 2006, the MPAs have stabilized over a range of densities, with Waiakailio Bay and S. Oneo Bay showing declines below the pre-closure densities.

Recruitment and habitat

There was a significant relationship between survivorship and settler density ($p = 0.04$, $r = 0.89$). Survivorship increased as a function of settler density. Approximately 89% of the relationship was explained by this relationship at Honokohau. Low recruitment at Keei prevented us from analyzing these factors.

Influence of habitat availability and predation intensity on the survivorship of newly recruiting yellow tangs

Results revealed predator visitation to be four times as frequent at one plot compared to the other, indicating highly variable visitation rates (Table 4). There seems to be a relationship between survivorship and predator density but because of low sample size we were not able to analyze it. At high finger coral habitat, 89% of the variation was explained by the relationship between survivorship and predator density with survivorship increasing with increasing predator density.

This study used commonly used landscape metrics to explore relationships between targeted species and the spatial characteristics of the reef in relation to the effectiveness of an MPA network in West Hawaii. Our results indicate that reef geomorphology, area of reef habitats, and level of habitat complexity are associated with the significant recovery of aquarium fish populations in West Hawaii.

Recruit densities were associated with the geomorphology of the reef, suggesting that patterns of recruitment were strongly influenced by landscape features such as the geology and size of the reef. In Hawaii, recruitment is highly variable over time and space during the summer months

(Walsh 1987, Williams et al. 2009). The current study also found recruitment to be highly variable among sites, with recruit densities ranging from high in the central and southern sites to low in the northern sites. The abundance of optimal recruit habitat (i.e. deep coral-rich areas) only partially explains the patterns of recruitment among sites, with some sites having moderate to high recruit densities despite small to moderate areas of recruit habitat (i.e. Kaupulehu, Honokohau, N. Keauhou, Hookena, and Milolii). Instead, physical characteristics affecting larval supply among sites were likely to have influenced recruitment patterns and recovery of fish within MPAs. For instance, central and southern MPAs had larger recruitment pulses than northern sites. These sites are generally small bays consisting of small and narrow reefs with sunken lava benches, high in turf algae, at shallow depths that extend up to approximately 5–11 m, with small to moderate areas of coral-rich habitats, before dropping abruptly into sandy rubble habitats reaching depths of more than 30 m. Reef geomorphology of these protected bays coupled with small to moderate areas of recruit habitat can aid in retaining larvae. Additionally, surface currents and eddies have been found to retain larvae of the family Acanthuridae in Hawaii (Sale 1970, Christie et al. In Review), and groundwater discharges, originating from far-inland, supply coastal areas of West Hawaii with larval food sources such as phytoplankton (Johnson et al. 2006). Thus, the combination of the reef geomorphology, available recruit habitat, prevailing ocean currents, and larval food supply contributes to the retention of larvae and consequently to the patterns of recruitment in West Hawaii.

The abundance and distribution of each life stage of yellow tang was influenced by mid-scale features of the reef, such as the availability of reef habitats, as they matured and migrated to adult habitats. Juveniles were associated with large complex areas of deep coral-rich habitats, while adults were associated with both deep and mid-depth coral-rich and shallow boulder turf-rich habitats. Coral-rich and boulder-turf-rich habitats at a range of depths (i.e. 0-30m) have shown to be important to a number of coral reef fishes in Hawaii (Friedlander et al. 2003), as they provide structural refuge in the form of crevices and branches (i.e. finger coral) and foraging (shallow boulder turf-rich) and shelter (coral-rich) habitats used by more mobile adults (Walsh 1984). Consistent with these fish-habitat associations, Anaehoomalu, Kaupulehu, and Milolii MPAs supported the highest number of juveniles and have an overall positive increases in yellow tang. All three sites either have moderate to large areas of complex deep coral-rich and shallow turf-rich habitats or contain all three reef habitats, suggesting that a combination of these spatial characteristics of the reef contributed to the recovery of the MPAs.

Differences in the number of reproductive adults among sites could translate into differences in a population's reproductive output and thus to the significant replenishment of fish within MPAs. The aquarium fishery targets young juvenile fish in the size range of 5-10cm (Williams et al. 2009). Consequently, lower fishing mortality in MPAs results in higher density, mean size and age, biomass, and potentially higher production of propagules of target species. In our study, the number of adults varied among our sites, with the Milolii, Keei, Honokohau, and Anaehoomalu MPAs supporting the highest number of adults and displaying a positive increase in yellow tang densities. All sites have moderate to large areas of either two or three reef habitats on both narrow and wide reefs, suggesting that the number of reef habitats, specifically complex mid-depth aggregate reef and boulder habitats, represented within each MPA contributed to supporting a greater number of reproductive adults. Only one site having fewer areas of adult habitat showed high adult abundance (i.e. Honokohau). This may be a result of migration from adjacent areas where aquarium collection is permitted and reef habitats may not offer the same food and refuge resources as inside the MPA.

Differences in reef habitat complexity, as measured by rugosity, may account for additional differences in fish recovery among sites. For example, Waiakailio Bay displays significant decreases in yellow tang compared to all other sites. This MPA is a unique site characterized by large pinnacles fragmented by large areas of sand and a narrow ledge. At large-scales, complexity at the site is high with coral-rich pinnacles extending along the water column to depths of more than 30 m. However, at smaller-scales the site's habitat complexity is the lowest surveyed and reef-fish were not seen to associate with reef features in the water column (personal observation, DOrtiz). Additionally, since 2005, Waiakailio Bay has been subjected to anthropogenic stresses from non-point pollution, such as sediment loading from coastal development (personal communication, BWalsh), and low recruitment. Thus, low recruitment and poor habitat quality may account for the significant decreases in yellow tang within the Waiakailio Bay MPA. These findings are consistent with other studies in Hawaii that have recognized the importance of reef habitat complexity in structuring reef-fish assemblage (Grigg 1994, Friedlander et al. 2003, Wedding et al. 2008). Although large-scale structures such as pinnacles might enhance species diversity, smaller–scale features may be more important for recruitment survival.

In summary, effective MPAs were associated, in part, with high numbers of juvenile and adult fish and a wide range of reef structures (i.e. reef geomorphology), that provide suitable reef habitats for all life stages. For instance, Honokohau and the southern sites (N. Keauhou, Keei, Hookena, and Milolii), which all showed the highest increases in fish relative to other sites (> 47%), were characterized by having long (2.7 – 8.7 km), narrow (< 344 m) reefs, with small to large amounts of juvenile (i.e. 6 – 37%) and adult (> 32%) habitats. In contrast, some of the larger MPAs with wide reefs (> 344 m) and large areas of both juvenile (> 38%) and adult (> 13%) habitats, display decreases (Waiakailio Bay and S. Oneo Bay), no significant increase (Anaehoomalu), and significant increases (Kaupulehu) in abundance relative to before closure estimates. However, habitat does not appear to explain all of the variability in effectiveness among MPAS. Thus, it is likely that additional factors, including such as recruitment and recovery time, are also important.

Recovery of reef-fish in MPAs can be slow and is often dependent on recruitment (Russ and Alcala 1996) and the number of years a site is protected (Russ and Alcala 2004, McClanahan et al. 2007). McClanahan et al. (2007) demonstrated that the recovery of acanthurids takes decades, with densities peaking at 7-10 years and reaching stable states after 37 years of closure. For yellow tangs, an acanthurid which can live up to 41 years and reach sexual maturity at 4 to 6 years old (JC, unpublished data) and have a high degree of inter-annual variation in recruitment (Tissot et al. 2004), recovery will likely vary significantly over time. Walsh et al. (2004) reported that yellow tang had shown significant replenishment in four of the nine MPAs, as well as in adjacent control and open areas, after five years when large recruitment of fishes began occurring. In addition, Williams et al. (2009) showed that fluctuation in the densities of juvenile and adult yellow tang within MPAs strongly tracked the intensity of recruitment. Juvenile and adult densities were highest in 2005, following three years of high recruitment (10-17/100m^2) (2003-2005), and have stabilized over the last 4 years of low recruitment events (~2/100m^2). Thus, the recovery of yellow tang depends on rates of recruitment. This may explain the recent decline in yellow tang abundance in S. Oneo Bay, a site with large areas of recruit, juvenile, and adult habitat that had experienced significant increases in 2005. Relative to the other MPAs, recruitment intensity has been consistently lower in S. Oneo Bay despite the high recruitment event in 2005. It is possible that anthropogenic impacts to reef systems combined with consistently lower recruitment in the last few years have contributed to initial declines in fish abundance at this site.

Recovery in Hawaii is likely to vary with time of closure. In 2004, five years after closure, seven out of the nine MPAs (all except Waiakailio Bay and Milolii) showed positive increases in yellow tang abundance, four of which (Anaehoomalu, Kaupulehu, N. Keauhou, and Keei) were statistically significant (Walsh et al. 2004). However, nine years after their closure, we now find six MPAs (Kaupulehu, Honokohau, N. Keauhou, Keei, Hookena, and Milolii) exhibiting statistically significant increases in yellow tang abundance. Overall, MPAs with increases in abundance continued to recover over time (i.e. Honokohau, Hookena, and Milolii). Because it is likely that only 1% of yellow tang recruits survive to adulthood when protected from fishing, we expect there to be a recovery lag as newly protected cohorts of surviving individuals slowly contribute to increases in fish populations (Claisse et al. In Review). Thus, recovery of yellow tang populations following closure depends on the magnitude of recruitment and years of protection, with more MPAs showing significant increases as years of protection increase and recruitment is consistent

VII. Evaluation

A. Attainment of project goals and objectives

Project goals and objectives have been attained.

B. Recommendations and Future Work on MPAs

The West Hawaii MPA network, combined with pre-existing MPAs, prohibits aquarium collection along 35.2% of the coastline. The network has shown to effectively replenish aquarium fish populations in West Hawaii, by enhancing fish stocks within their boundaries and outside through potential adult spillover (Tissot et al. 2004, Williams et al. 2009).

An effective MPA network has to be able to protect productive populations within their borders while also sustaining fisheries outside their borders through larval seeding and spillover (Palumbi 2003). As most reef-fish use a range of habitats throughout their life history (Dahlgren and Eggleston 2000), protection of fish populations and replenishment can only be successful if the habitats important to the life stages of targeted species and recruitment dynamics are considered (Sala et al. 2002). The West Hawaii network incorporates a minimum of 6-20% of two of the nearshore reef habitats (deep coral-rich and shallow turf-rich boulder habitats) important for recruit settlement, juvenile survival, and adult foraging and sheltering on the reef. The protected areas range in size from 89 to 513 ha among the MPAs and contain a high degree of heterogeneity (9 – 78 habitat patches per site) providing landscapes that can accomodate multiple life stages of yellow tang. As a result, most MPAs supported a moderate to large number of individuals of each life stage. It is important to note that the abundance of mid-depth aggregate reef and boulder habitats is an important nearshore habitat, as five of the nine MPAs incorporating this reef habitat supported a high number of adults. Also, the range of reef length (2.7 - 8.7 km) within MPAs was sufficient to protect adult breeding populations whose home ranges can be at least 800 meters (JT, unpublished data). As larval dispersal is highly variable, nine replicate sites spread apart (1.3-14.3 km) along the 125 km West Hawaii coastline, with available recruit habitat, ensured high larval connectivity by both protecting effective MPAs that serve as source of propagules, and providing MPA spacing within range of yellow tang dispersal distances, which can range from 15 to 184km (Christie et al. In Review).

Characteristics of the West Hawaii MPA network design, however, deviates from existing recommendations in MPA network design for benthic marine species (McLeod et al. 2009). General guidelines for MPA network design recommend MPAs to: (1) be a minimum of 10-20km in length; (2) protect three examples of at least 20-30% of each habitat type; and (3) have at least three replicates spaced a maximum distance of 15-20km apart to allow for replenishment via larval dispersal (McLeod et al. 2009). However, findings from the West Hawaii network indicates that nine closely spaced (1.3-14.3 km) MPAs of less than 10 km in length that protect less than 20% of each habitat type show recovery of the primary targeted species in the aquarium trade. Our results demonstrate, at least for yellow tangs, that to be effective the design of the MPA Networks depends on the life history and spatial requirements of the species being protected. In the case of West Hawaii, aquarium reef-fish, such as goldring surgeonfish *Ctenochaetus strigosus*, chevron tang *Ctenochaetus hawaiiensis*, and multiband butterflyfish *Chaetodon multicinctus*, to mention a few, are known to have similar life history traits such as high-site fidelity, ontogenetic shifts in habitat use, and recruitment patterns (Walsh 1987, Parrish and Claisse 2006, Eble et al. 2009, Ortiz and Tissot In Review). As a result, the design of the West Hawaii MPA network is effective at replenishing reef-fish among sites by protecting both newly recruiting fish to nearshore reef habitats and foraging and sheltering locations for juvenile and adult breeding populations; thus, protection of yellow tang is likely to benefit most species targeted by the aquarium trade.

The results of this study have applications for the future design of MPA networks in Hawaii and elsewhere in the tropical Pacific, if the species being protected have life history traits similar to yellow tang. First, MPAs should be placed in areas where larval retention can be substantial due to current patterns and retention features, such as bays with large areas of recruit habitat (i.e. coral-rich habitats). Second, MPAs should protect multiple examples of 10-20% of complex coral-rich and boulder turf-rich habitats, specifically mid-depth aggregate reef and boulder habitats, at a range of depths (i.e. 0-30 m) in both protected and adjacent open areas. These measures will afford protection of targeted species within and along the boundaries of the MPAs. Third, MPA size should account for the home range of reef-fish species. Because most adult species can move hundreds of meters, using a 2:1 protection to movement ratio will protect adult breeding populations by accounting for their daily movements. In this way the center of the MPA can ensure the protection of adults while minimizing negative effects at the edges of the MPA boundaries where extensive fish mortality can occur due to fishing and lower quality habitats (Carr et al. 2003). Fourth, MPAs should be places at a much wider range of distances (i.e. 15-30 km) to allow for replenishment via larval dispersal. Fifth, closure of MPA networks should span decades in order to account for the slow recovery from fishing pressure and ensure full recovery of depleted populations, although recovery of common species may occur in the first five years. Sixth, the feasibility of enforcement and ecological monitoring of the MPAs should be considered when deciding the shape, size, and number of sites. Lastly, MPAs should not be established in areas of low water quality in order to achieve conservation goals.

B. Dissemination of Findings

Scientific publications

Ortiz DM and BN Tissot. 2008. Ontogenetic patterns of habitat use by reef-fish in a Marine Protected Area network: a multi-scaled remote sensing and *in-situ* approach. Marine Ecology Progress Series 365: 217-232.

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VIII. Signature Investigator must sign and date Project Final Report

Dr. Brian N. Tissot (P.I.)

Table 1. Description of pooled reef habitat types using the classification scheme in Ortiz and Tissot 2008 study: A = aggregate reef; M = mixed; B = boulders; P = pavement; E = cauliflower coral (*Pocillopora. meandrina*); L = lobe coral (*Porites lobata*); C = finger coral (*P. compressa*); u = uncolonized; T = scattered coral rock; R = reef rubble; S = sand.

Reef Habitat	**Code**	**Habitat types included**	**Reef Zone**	**Depth Range (m)**
Deep aggregate coral-rich and sandy rubble habitats	DCRH	ACL, ALC, AM, BM, Ru, S	Reef slope	5-40
Mid-depth aggregate reef and boulder habitats	MABH	ALE, AEL, BLL, BLE	Reef slope and Boulder	5-25
Shallow turf-rich boulder habitats	STBH	BEL, PEL, Bu, Pu, Tu	Boulder and Reef flat	0-11

Table 2. Sampling allocation by reef habitat at each site. Values indicate the number of circular plot counts conducted in each habitat and site. Empty cells represent habitats that were not present in the study area. Reef habitats are deep coral-rich and sandy rubble habitats (DCRH), mid-depth aggregate reef and boulder habitats (MABH), and shallow turf-rich boulder habitats (STBH).

Site	DCRH	MABH	STBH	Total
Waiakailio Bay	16	-	7	23
Anaehoomalu	13	5	5	23
Kaupulehu	6	-	15	21
Honokohau	6	5	7	18
S. Oneo Bay	11	2	12	25
N. Keauhou	6	-	9	15
Keei	13	10	3	26
Hookena	6	-	11	17
Milolii	15	4	6	25
Total	92	26	75	193

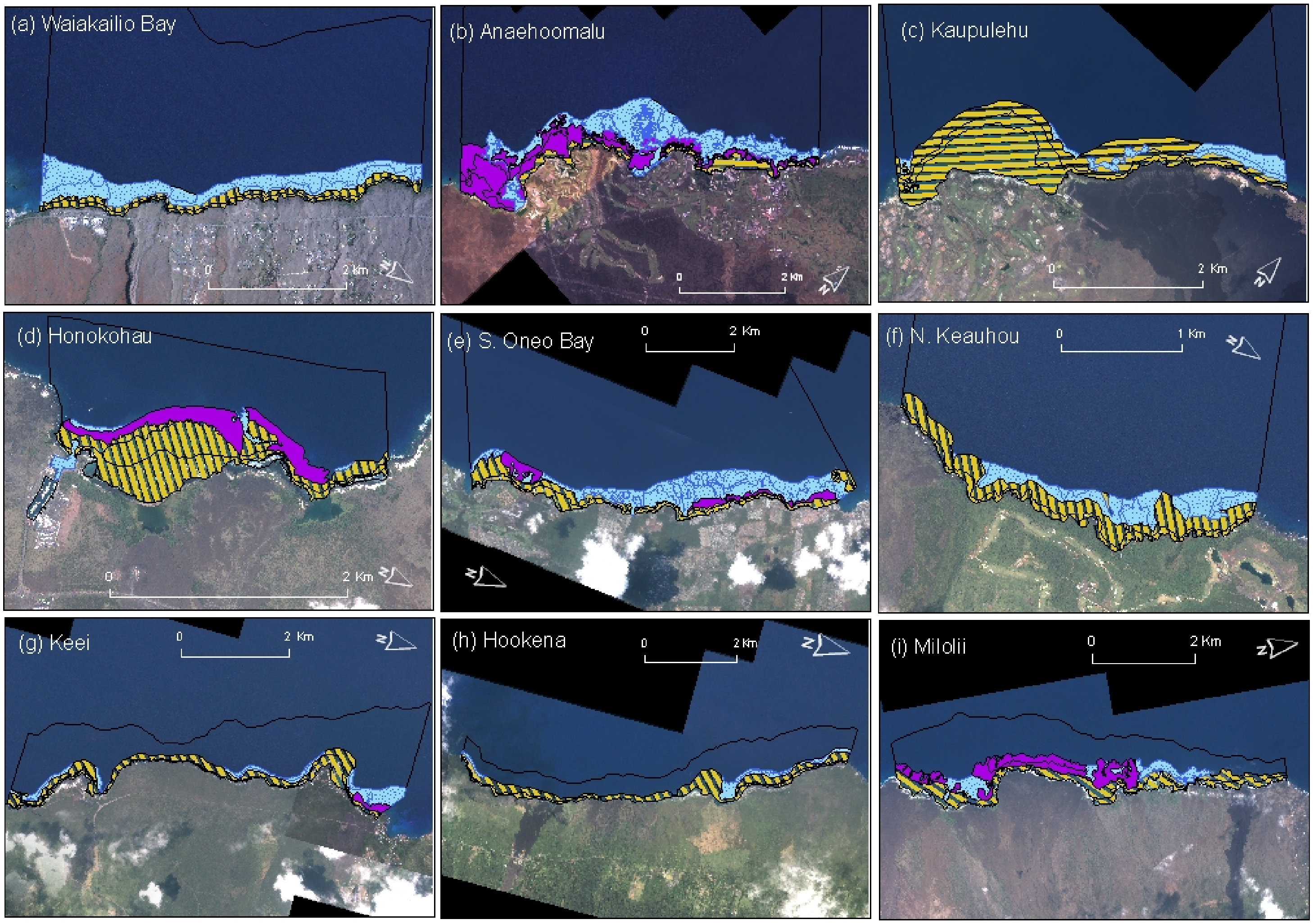
Table 3. Reef spatial characteristics of MPAs and population size of each of the life stages of yellow tang. Reef spatial characteristics are the following: total area (ta), mean reef width (rw), reef length (rl), standard deviation of patch shape (psh), standard deviation of patch size (ps), number of habitat categories (hc), number of habitat patches (hp), areas of sand (S), areas of deep aggregations of coral-rich habitats (DCRH), areas of mid-depth aggregate reef and boulder habitats (MABH), and areas of shallow turf-rich boulder habitats (STBH). Population size of recruits, juveniles, and adult of yellow tang are described by the first letters of the common name, and the third letter denoting the life stage. For instance YTR stands for the total number of yellow tang recruits within an MPA.

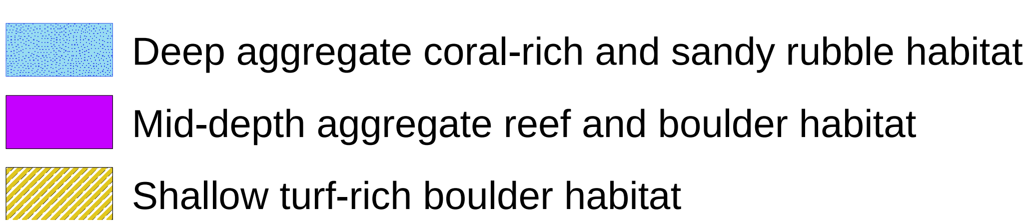
MPA	ta (ha)	rw (m)	rl (km)	psh (ha)	ps (ha)	hc (#)	hp (#)	S (ha)	DCRH (w/out sand) (ha)	MABH (ha)	STBH (ha)
Waiakailio Bay	1,758	353	5.5	0.41	17	2	12	68	81	0	68
Anaehoomalu	3,341	742	6.8	0.40	14	3	78	158	87	212	66
Kaupulehu	4,009	529	5.1	0.54	38	2	11	28	81	0	180
Honokohau	320	344	2.7	0.15	7	3	14	2	5	28	76
S. Oneo Bay	3,101	621	8.7	0.65	30	3	27	152	178	35	171
N. Keauhou	742	253	3.3	0.30	10	2	14	10	23	0	56
Keei	816	172	7.4	0.53	21	3	16	15	45	7	126
Hookena	619	183	8.7	0.59	27	2	9	21	18	0	165
Milolii	806	358	7.6	0.57	27	3	21	42	50	88	156

MPA (Cont)	YTR	YTJ	YTA
Waiakailio Bay	2,402	27,684	32,054
Anaehoomalu	5,458	146,095	159,106
Kaupulehu	11,805	122,777	33,344
Honokohau	7,767	11,194	72,521
S. Oneo Bay	7,692	187,752	132,874
N. Keauhou	1,410	89,900	47,920
Keei	597	37,964	80,765
Hookena	856	39,395	20,087
Milolii	9072	93136	82,651

Table 4. Descriptive statistics of automated video census of piscivorous reef fishes. Data are mean (SE).

	Site-H21	Site-H22
Number of video days:	2	2
Video duration (hr / day):	2.290 (2.410)	4.000 (0.219)
Visits per video-hour:		
Caranx melampygus	0.031 (.0430)	0.032 (0.045)
Cephalopholis argus	0.0274 (0.033)	0.270 (0.150)
Fistularia commersoni	0.028 (0.039)	0.000
Aulostomus chinensis	0.000	0.002 (0.003)
All predators	2.500 (0.707)	10.000 (5.650





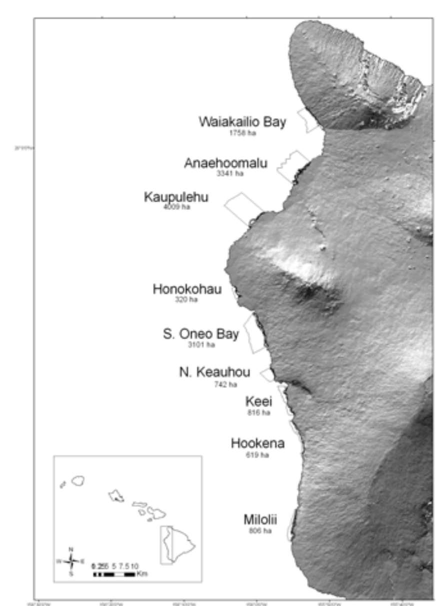


Figure 1. Benthic habitat maps of MPAs in West Hawaii.

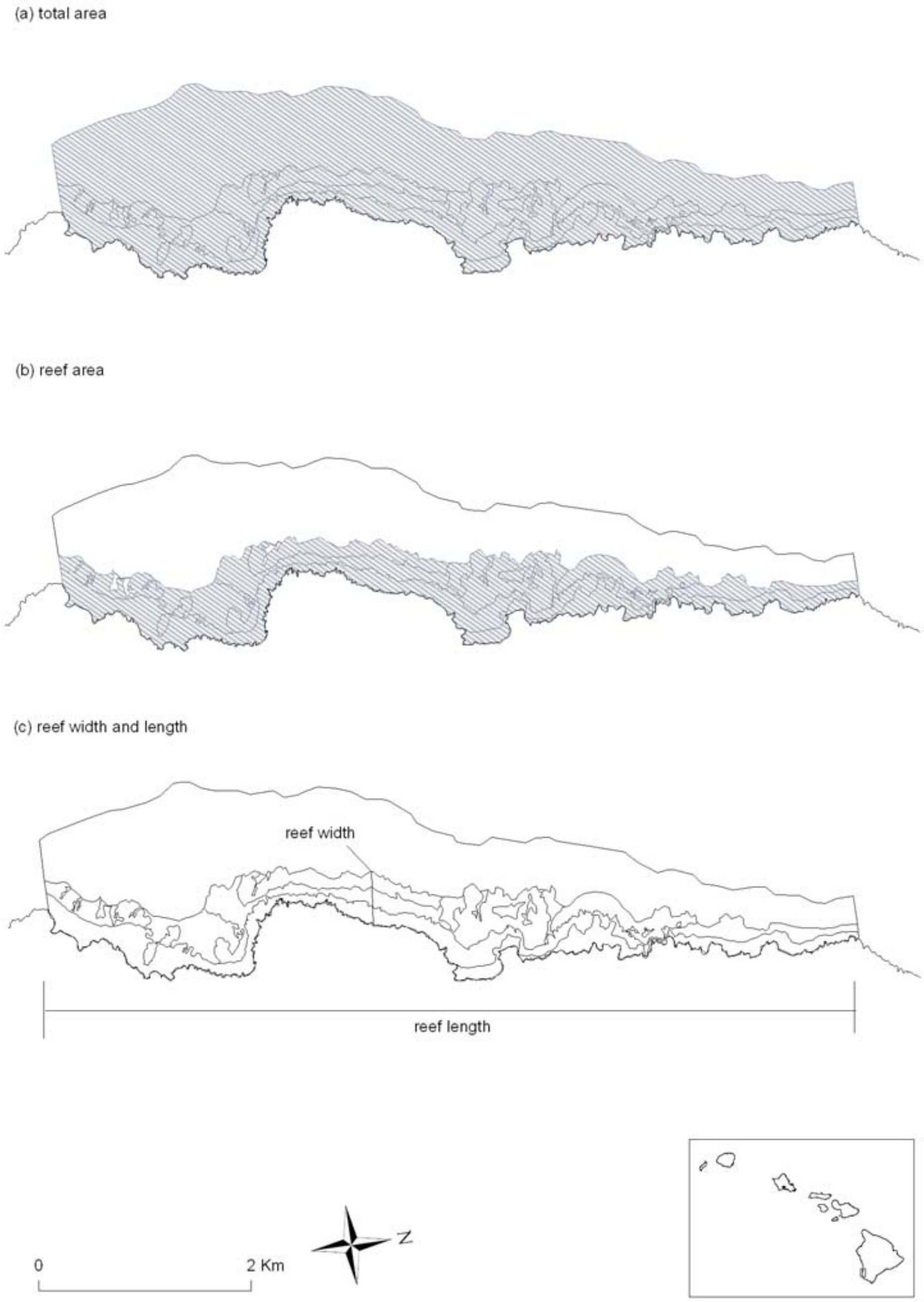


Figure 2. Example of spatial and reef measurements at the Milolii MPA. Measurements included (a) total area, (b) reef area, and (c) reef width and length. Total area represents the area extending from shore to a depth of 600ft. Reef area represent the area extending from shore to a depth of 25m. Reef width was measured as the average distance from

shore to a depth of 25m. Reef length was measured as the total distance of shoreline within the boundaries of the MPA

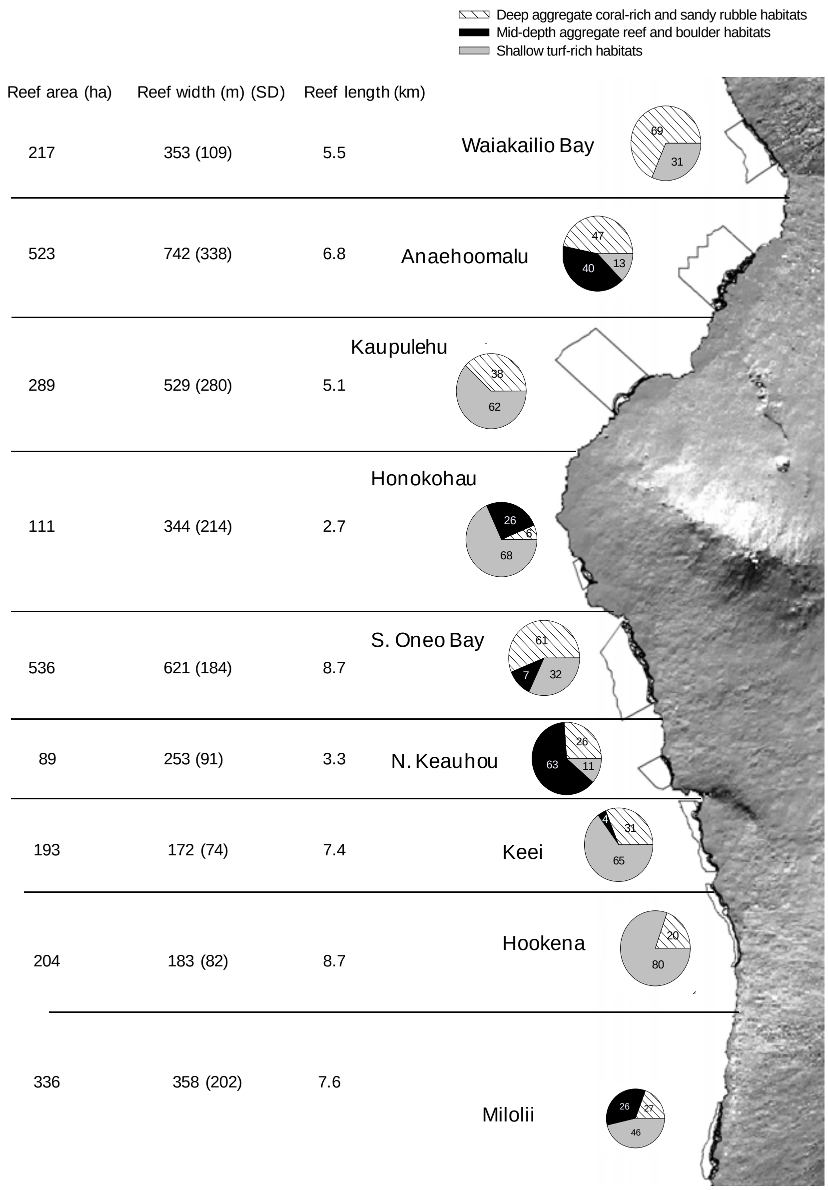


Figure 3.Reef characteristics of each of the nine fishery replenishment areas along West Hawaii including reef area, width, and length, and percent area of each reef habitat (indicated in pie charts). Reef area represents the total area of reef habitats mapped (shore to a depth of 25m). Reef width is the mean distance from shore to the reef slope (approximately at a depth of 25m). Reef length is the total distance of the shoreline within each MPA. The percent area of each reef habitat represents the proportion of the reef area covered by each reef habitat.

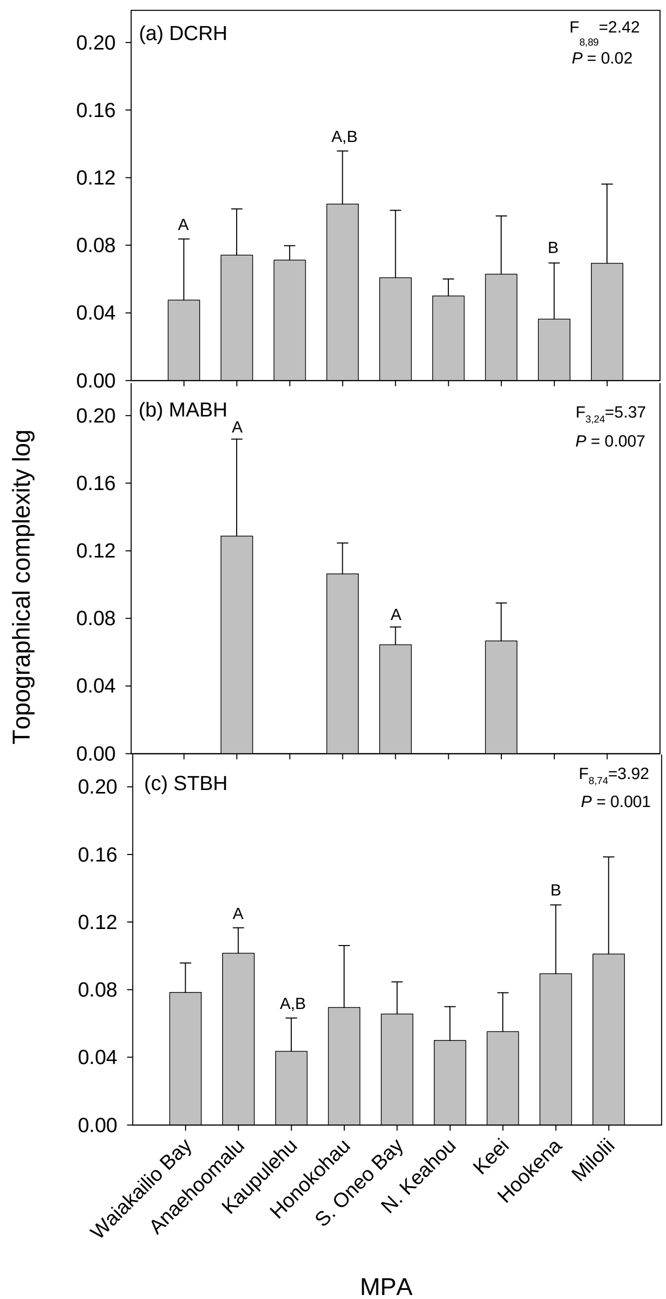


Figure 4. One-way ANOVA test comparisons of topographical complexity within (a) deep-coral rich and sandy rubble habitats, (b) mid-depth aggregate reef and boulder habitats, and (c) shallow turf-rich boulder habitats between MPAs. Common letters denote significant differences of $P < 0.05$. Values are log-scaled for better interpretation

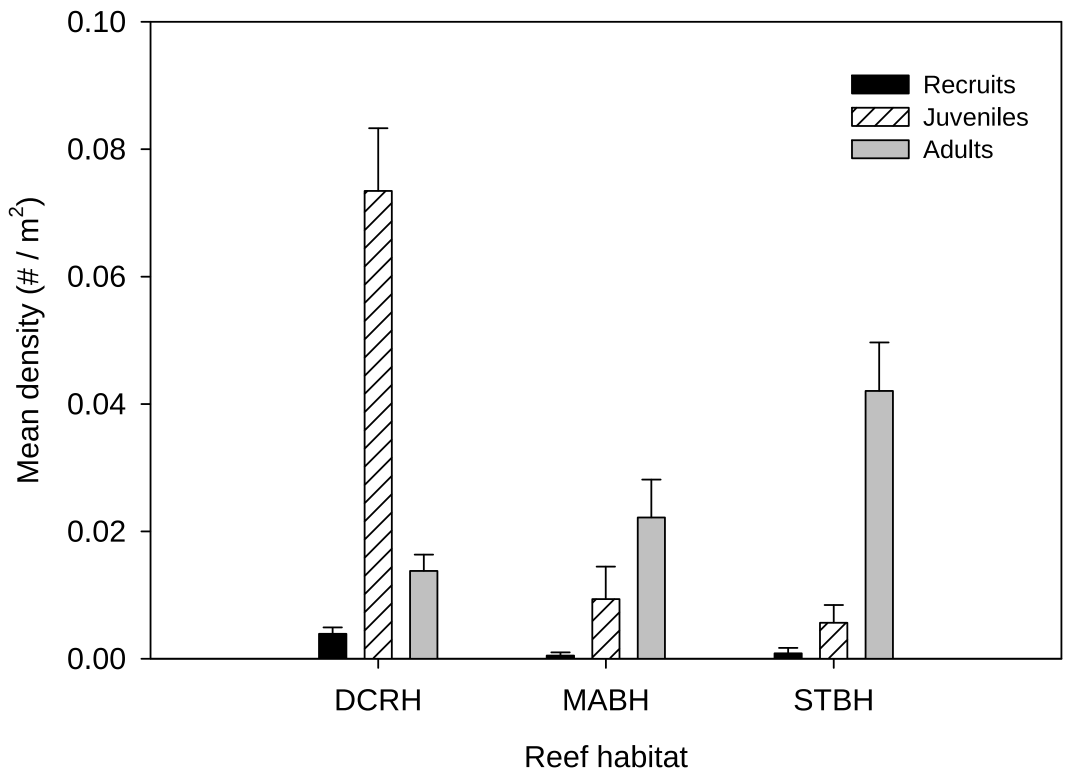


Figure 5. Density (# / m^2, mean + standard error) of recruit, juvenile, and adult yellow tang among reef habitats for all sites. Reef habitats include deep aggregate coral-rich and sandy rubble habitats (DCRH), mid-depth aggregate reef and boulder habitats (MABH), and shallow turf-rich boulder habitats (STBH).

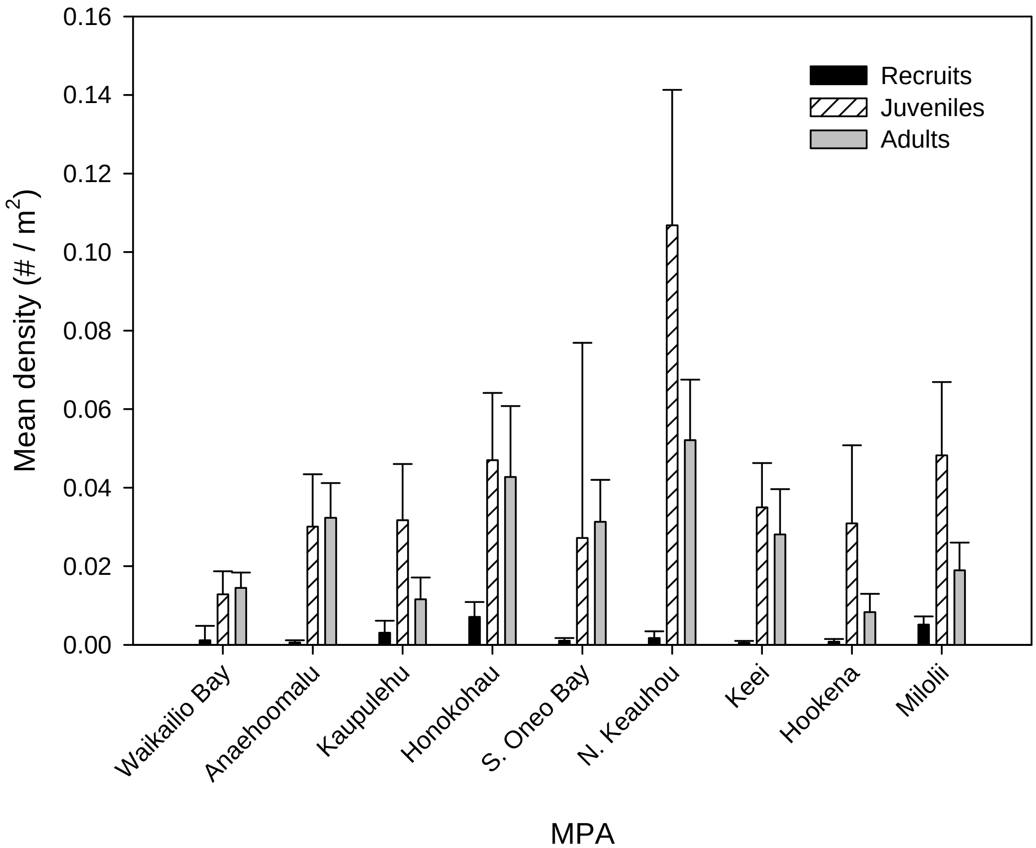


Figure 6. Density (# / m^2, mean + SE) of recruit, juvenile, and adult yellow tang among study sites

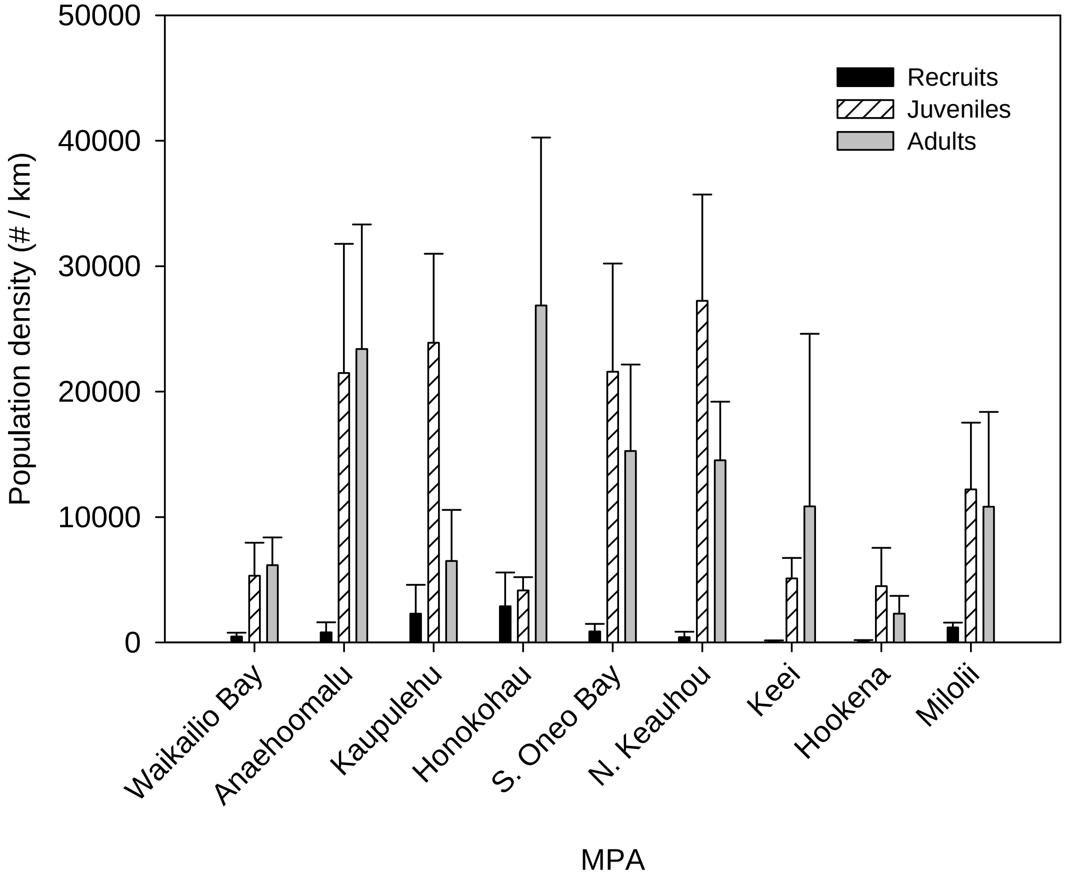


Figure 7. Population density (# / km, mean + SE) of recruit, juvenile, and adult yellow tang at each study site.

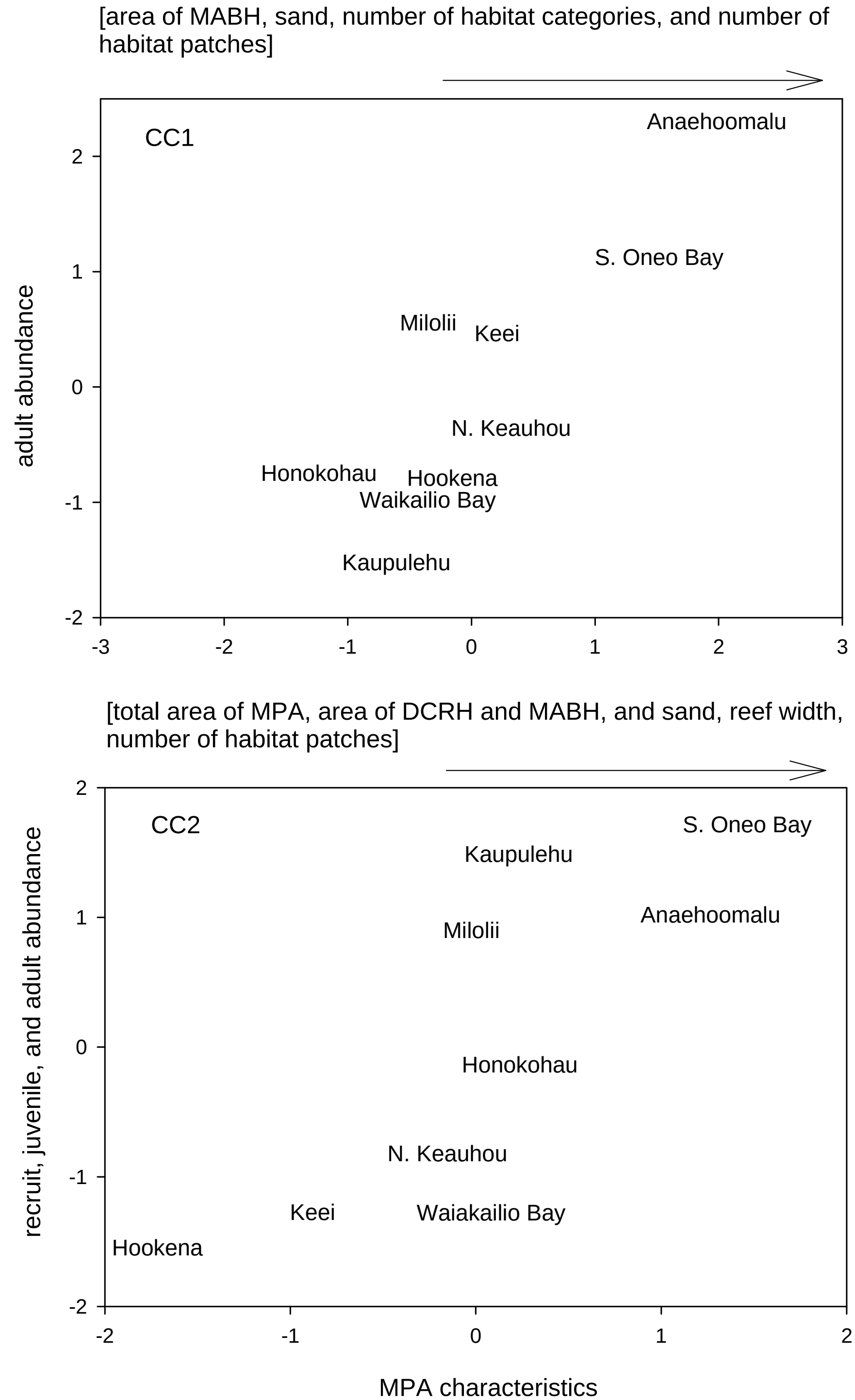


Figure 8. Canonical scores of MPAs on the two axes of the canonical correlation analyses. The canonical correlation coefficient (r = 0.33 for axis 1, r = 0.33 for axis 2) measures the overall association between the reef spatial characteristics of MPAs and abundance of recruit, juvenile, and adult yellow tang (see Table 3). High positive loadings on axis 1 define large MPAs with large areas of MABH and sand, and a large number of reef habitats and habitat patches supporting a greater number of adult tang. Large negative loadings on axis 1 define small MPAs with smaller and narrower reefs having continuous areas of MABH and sand, and fewer reef habitats and habitat patches supporting fewer adult yellow tang.

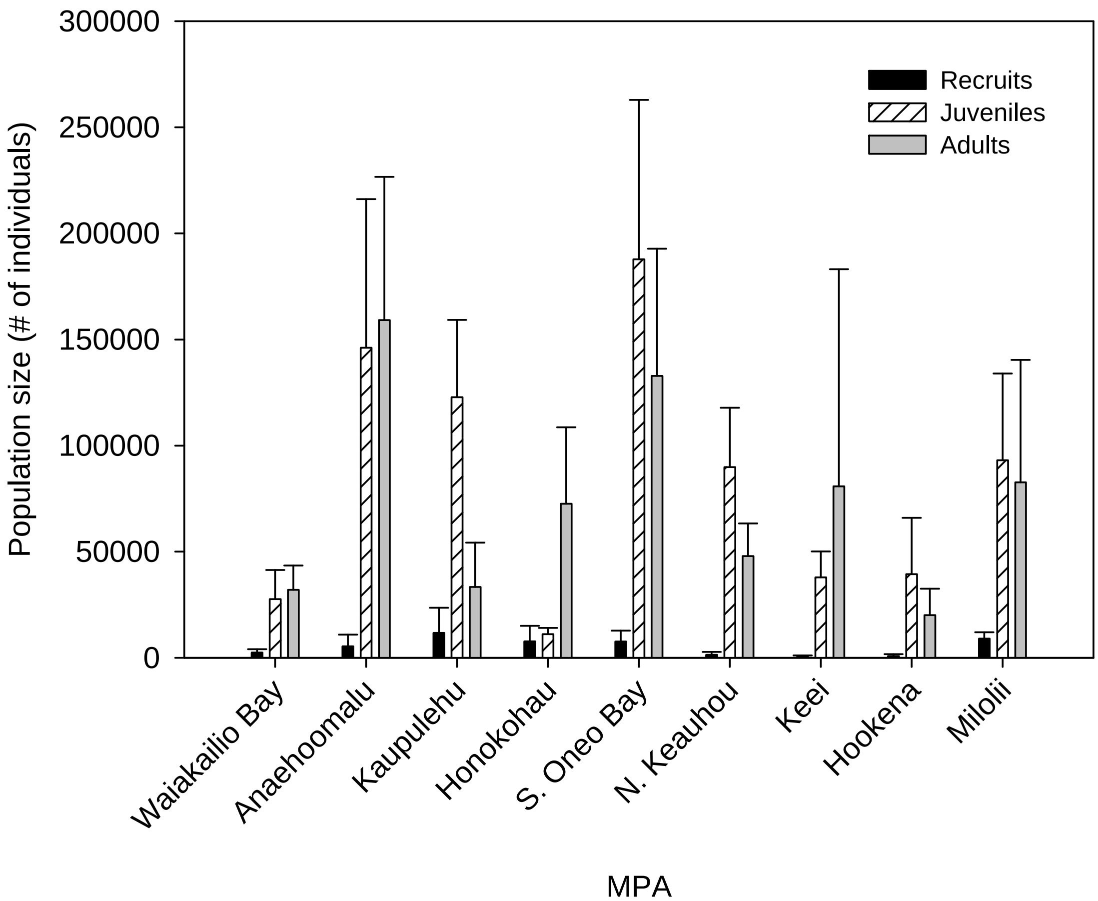


Figure 9. Population size (# of individuals) of recruit, juvenile, and adult yellow tang at each study site.

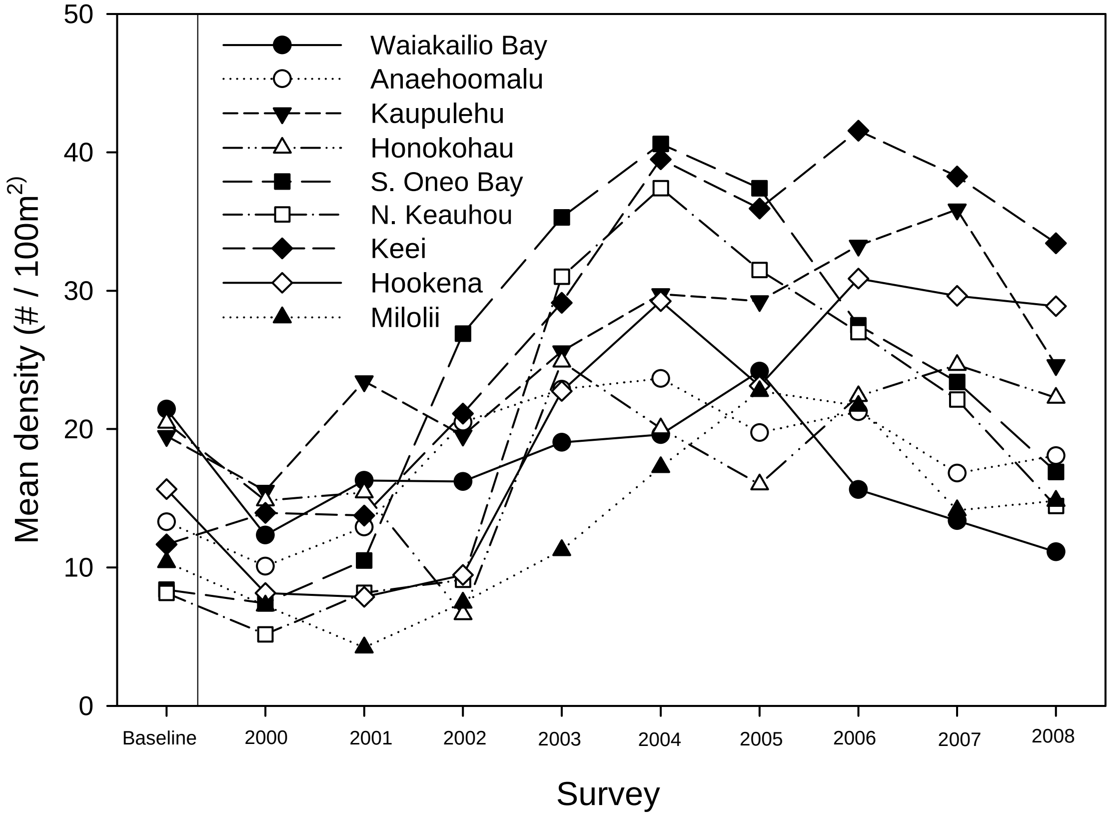


Figure 10. Changes in yellow tang abundance in MPAs from 1999-2008.