THE INFLUENCE OF HABITAT AND LIFE HISTORY OF REEF-FISH ON THE EFFECTIVENESS OF A MARINE PROTECTED AREA NETWORK IN HAWAII TO REPLENISH AQUARIUM FISH

By

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THE INFLUENCE OF HABITAT AND LIFE HISTORY OF REEF-FISH ON THE EFFECTIVENESS OF A MARINE PROTECTED AREA NETWORK IN HAWAII TO REPLENISH AQUARIUM FISH

Abstract

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A network of Marine Protected Areas (MPAs) on the west coast of the island of Hawaii (West Hawaii) has been shown to vary in its effectiveness to replenish depleted aquarium fish stocks. To determine the abundance and distribution of habitats needed to better design and manage MPAs in Hawaii, underwater video transects, remote sensing data, geographic information systems (GIS) and a benthic classification scheme were combined to develop a map of reef habitats previously identified as important to the life history of aquarium fish and other reef species. Using these maps, an assessment was conducted to quantify habitat use by different life stages of targeted aquarium fish species. Results showed that deep aggregate coral-rich areas and rubble substrates adjacent to shallow turf-rich boulder habitats at various depths (i.e., 0-30m) were used by all study species. In addition, appropriate habitat type for early life history stages of fish species, large areas of these habitats on the reef, and proximity of appropriate recruit, juvenile, and adult habitats were associated with an MPA showing effective replenishment. We further use landscape metrics to explore relationships between the most heavily collected

aquarium fish species, yellow tang *Zebrasoma flavescens*, and the spatial characteristics of the reef in relation to the effectiveness of an MPA network in West Hawaii. Our results indicated that reef geomorphology, area of reef habitats, and level of habitat complexity were associated with the significant recovery of aquarium fish populations. 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. Our results demonstrate that 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. 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.

PROLOGUE

Effective management and design of MPA networks requires that we understand the combination of key spatial characteristics of MPAs that result in productive fish populations within their borders. MPAs will be more effective at protecting reef-fish species if they incorporate important habitats to targeted species. Therefore, we would expect that MPAs that incorporate the range of habitats utilized by managed species would be more effective at accomplishing their conservation goals. We investigate ontogenetic patterns of habitat use by reef-fish in relation to the effectiveness of an existing MPA network in the west coast of the island of Hawaii (West Hawaii) to replenish aquarium fish populations. We further evaluate the spatial characteristics of the reef, recruitment, and recovery time associated with effective MPAs.

Chapter 1 outlines a new method for evaluating the habitat use patterns of reef-fish among four MPAs in relation to their ability to replenish aquarium fish in West Hawaii. The new methodology combines remote sensed data and *in-situ* population sampling to describe the spatial variation of nearshore reef habitats used by yellow tang *Zebrasoma flavescens*, the most heavily exploited fish species in West Hawaii. We described the habitat use of each of the life stages of yellow tang and how environmental variables (i.e. depth, rugosity, percent cover of substrates) and abundance of reef habitats influence their abundance and distribution. We further examine the abundance and distribution of essential habitats in relation to two MPAs varying in their effectiveness to augment yellow tang populations. Recommendations on the future management and design of MPAs in Hawaii and other tropical regions are made.

Chapter 2 further demonstrates the usefulness of our approach in delineating habitats important

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to species with different life history traits. We describe the abundance and distribution of eight reef-fish species that vary in their commercial and cultural value, with four heavily targeted by the aquarium trade (yellow tang *Zebrasoma flavescens*, goldring surgeonfish *Ctenochaetus strigosus*, black surgeonfish *Ctenochaetus hawaiiensis*, brown surgeonfish *Acanthurus nigrofuscus*, multiband butterflyfish *Chaetodon multicinctus*, agile chromis *Chromis agilis*, blue-head wrasse *Thallasoma duperrey*, and arc-eye hawkfish *Paracirrhites arcatus*). We further evaluate the relationship between two effective MPAs (Anaehoomalu and Honokohau) with varying levels of replenishment and the abundance and distribution of habitats essential to fish species targeted by the aquarium trade. The development of spatial management practices are recommended for the effective replenishment of protected species in Hawaii and other regions.

Chapter 3 applies landscape metrics to investigate relationships between targeted species and the spatial characteristics of the reef in relation to the effectiveness of an MPA network in West Hawaii. Using Geographic Information Systems (GIS) and landscape metrics, we describe the geomorphology of the reef and benthic habitats for all nine MPAs in West Hawaii. We relate depth and spatial characteristics of the reef such as reef width, length, and width, number of habitat types, number of habitat patches, variability in patch size and shape, rugosity, percent cover of substrates, and abundance of habitat types with the population size of each of the life stages of yellow tang. We further investigate the spatial characteristics of the reef that are associated with the significant recovery of aquarium fish population in West Hawaii and make recommendations for the future design of MPA network in Hawaii and elsewhere in the tropical Pacific.

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Dedication

This dissertation/thesis is dedicated to my mom and dad. Thank you mom for introducing me to the beauty of the ocean and its wonders. Thank you dad, for inspiring me to become the curious scientist that I am today. To both, thank you for your love, and unconditional support on this long and challenging journey. Los quiero con todo mi corazon.

MANUSCRIPT 1:

ONTOGENETIC PATTERNS OF HABITAT USE BY REEF-FISH IN A MARINE PROTECTED AREA NETWORK: A MULTI-SCALED *IN SITU* APPROACH

ABSTRACT

A network of Marine Protected Areas (MPAs) on the west coast of the island of Hawaii (West Hawaii) has been shown to vary in its effectiveness to replenish depleted aquarium fish stocks. To determine the abundance and distribution of habitats needed to better design and manage MPAs in Hawaii, underwater video transects, remote sensing data and a benthic classification scheme were combined to develop a map of reef habitats previously identified as important to the life history of aquarium fish and other reef species. Using these maps, an assessment was conducted to quantify habitat use by different life history stages of the most commonly livecaught aquarium fish, the yellow tang Zebrasoma flavescens, in existing MPAs. Rugosity, small reef features (i.e. percent cover of dominant reef species) and the abundance and size of fish were quantified in 115 circular plots to determine the accuracy of mapping efforts and the distribution of fish life history stages across the reef in 4 MPAs. Visual classification and mapping of habitat types was 93% accurate and consistent with percent cover of substrates quantified at the quadrat level. The different life history stages of yellow tangs were distributed along distinct habitat types in all of the MPAs examined. New recruits and juveniles of the yellow tang showed similar patterns of habitat use among sites and were associating with coralrich areas and patches of the finger coral Porites compressa. In contrast, the distribution and abundance of adults varied greatly within and among sites. The development of a ground-truthed habitat map allowed a holistic examination of habitat use by yellow tang, including most life history stages, which provides key information for the design of MPAs and the advancement of ecosystem-based management.

INTRODUCTION

One important goal of reef-fish management is to identify the post-settlement processes driving the abundance and distribution of reef-fish. This is because the success of Marine Protected Areas (MPAs) in conserving reef-fish lies in knowing and conserving a range of life history stages and naturally regulating mechanisms (Hixon & Webster 2002). Understanding population dynamics requires an understanding of the habitats influencing the individual life stages of reef-fish across multiple spatial scales (Underwood et al. 2000). The patchiness typical of coral reefs creates habitats at multiple scales, each with distinctive features that may influence reef-fish at different life stages (Levin 1991, 1992). Reef-fish may associate with particular small-scale features such as percent cover of dominant species or rugosity (Tolimieri 1995, Friedlander & Parrish 1998, Aburto-Oropeza & Balaart 2001, Dahlgren & Eggleston 2001), midscale features such as large swaths of contiguous habitat type (Fowler 1990, Green 1996, Meekan & Choat 1997, Kendall et al. 2003) and large-scale features such as reef shape and morphology (Friedlander & Brown 2003) across their life span. The availability and quality of reef habitat, in turn, can affect the post-settlement demography of reef-fish directly by providing refuge from predation (Hixon & Beets 1993) or indirectly by modifying biological interactions among different species (Menge et al. 1985, Hixon & Mark 1997). Hence, the abundance and distribution of many life history stages of reef-fish can best be explained by identifying and quantifying the abundance and distribution of habitats necessary for successful recruitment, growth and reproduction (Doherty & Williams 1988, Tupper & Boutilier 1995, Friedlander & Parrish 1998).

In 1999 a network of 9 fishery replenishment areas (FRAs) was established on the west coast of the island of Hawaii (hereafter, West Hawaii) in response to declines of reef-fish taken

by aquarium collectors. FRAs are MPAs where the collecting of live fish for the aquarium trade is prohibited. Five years of monitoring in these areas has revealed significant increases in the overall abundance of aquarium fish after the closure of FRAs (Walsh et al. 2004). However, FRAs varied in their effectiveness to replenish fish populations, with only 4 of the 9 areas displaying significant increases in the most commonly collected aquarium fish, the yellow tang *Zebrasoma flavescens* (Tissot et al. 2004). Variation in the effectiveness of the FRA network in West Hawaii has been associated with several factors such as the strength of recruitment (Tissot et al. 2004) and the abundance of the finger coral *Porites compressa*, which may be important habitat for the survival and growth of juvenile yellow tang (Tissot et al. 2003, Walsh et al. 2004) and other fish (Walsh 1987). These results suggest that the abundance and distribution of habitats is an important factor influencing the effectiveness of the FRA network. Thus, in order to design and effectively manage MPAs, it is important to understand the spatial variation of habitats in relation to the distribution and abundance of the life stages of reef-fish.

Characterization and description of habitats and their associations with reef-fish have been carried out by a variety of in situ and mapping methods. Benthic sampling techniques such as quadrats and transects have been used to quantify small reef features and their associations with reef-fish (Levin 1991, Fowler et al. 1992, Gratwicke & Speight 2005). Recent mapping efforts have used aerial photography (Coyne et al. 2001), multi-beam mapping (Nasby-Lucas et al. 2002) and geographic information systems (GIS) (Stanbury & Starr 1999) to map benthic landscapes in relation to fish abundance and distribution (Kendall et al. 2003, Friedlander et al. 2007). While small-scale studies may reveal details about the underlying patterns of biological mechanisms, different generalizations are likely to emerge at larger scales (Wiens 1989). For example, remote sensing techniques used for large-scale studies may suppress considerable

ecological detail by lumping functional ecological classes into crude assemblages (Levin 1992). On the other hand, small-scale studies cannot be used to explain patterns at larger scales because different mechanisms may be acting to produce observed patterns (Levin 1992, Schneider et al. 1997). Thus, examination of fish abundance and distribution across a range of spatial scales will likely provide information pertinent to multiple ecological processes and, in turn, data useful for ecosystem-based management.

In the present study, we used a combination of the National Oceanic and Atmospheric Administration's (NOAA) hierarchical classification scheme for benthic habitats in Hawaii (Coyne et al. 2003), existing aerial photography and in situ biological and physical observations using SCUBA to develop a map of reef habitats previously identified as important to the life history of aquarium fish and other reef species. NOAA's classification scheme defined habitat types in a collapsible hierarchy ranging from broad categories of habitat structure (i.e. uncolonized volcanic rock/boulders, aggregate reef coral, rubble and others) to more detailed categories of biological substrate (i.e. emergent vegetation, algae, etc.). The present study builds on this scheme to develop a more detailed benthic habitat map that describes and georeferences reef habitats identified to be ecologically important to managed species in Hawaii. With the use of georeferenced in situ video transects, we described the physical structure and biological substrate of multiple habitat categories in relation to NOAA's aerial photography. The benthic habitat map we created describes both the distribution of large habitat features as well as small substrate features, such as solitary and reef-building coral types, rubble, boulder and sand.

Our overall objective is to develop a new method to examine the ontogenetic patterns of habitat use by reef-fish and provide information whereby the effectiveness of a well-studied MPA network can be evaluated relative to the distribution and abundance of habitat types at

multiple spatial scales. In the present study we describe the development of the method and illustrate its usefulness using data on the yellow tang, a species which comprises the majority of the catch for the aquarium trade in West Hawaii (Walsh et al. 2003). However, the method is also of broad use to a variety of reef species, which we will present elsewhere. In the present study, we specifically (1) develop a georeferenced habitat map which describes the abundance and distribution of habitats within 4 sites, (2) evaluate spatial patterns of abundance and distribution of individual life stages of yellow tangs in these sites, (3) evaluate the relationship between FRA effectiveness and the abundance and distribution of habitats and describe how our method can be used to design MPA networks and promote ecosystem-based management.

MATERIALS AND METHODS

Study sites

We examined 4 different MPAs (Fig. 1). Two of these sites were FRAs, Honokohau (19° 40.26' N, 156° 01.82' W) and Anaehoomalu Bay (19° 57.17' N, 155° 51.97' W), that have varied in their effectiveness to replenish aquarium reef-fish (Walsh et al. 2004b). FRA effectiveness (R) represents the change in density of targeted fish in FRAs relative to adjacent reference control sites. The 2 reference control sites, Wawaloli (19° 42.00' N, 156° 02.99' W) and Puako (19° 58.19' N, 155° 50.93' W), are MPAs where the collection of aquarium fish has been prohibited for more than 10 yr (Department of Land and Natural Resources, 1996). These sites were the control sites used in the effectiveness measurement by Walsh et al. (2004b), but for the purpose of the present study are only used to illustrate the usefulness of our method in evaluating the spatial patterns of abundance and distribution of individual life stages of yellow tangs. R

density between each FRA and control site during baseline to post-baseline surveys (Walsh et al. 2004). Although R measures the changes within the FRA as a percent of the baseline abundance relative to control sites, another measure of change in the FRAs is the absolute percent change in density of the post-closure surveys relative to the baseline surveys (Walsh et al. 2004). Thus, both of these measures serve to determine how functional the FRAs are in replenishing targeted aquarium fish. The Honokohau FRA showed a 40% percent change in yellow tang density, but relative to its control site (Wawaloli) it showed an 18% decrease in yellow tang. Both of these results were not statistically significant. On the other hand, Anaehoomalu has shown a statistically significant 79% change in yellow tang density and a 54% increase in yellow tang relative to its control site (Walsh et al. 2004b).

Habitat map development

The development of a multi-scale benthic habitat map was based on aerial photographs of the island of Hawaii (Coyne et al. 2001), Light Detection and Ranging Technology (LIDAR) data (SHOALS LIDAR Bathymetry 2002) and in situ geographically referenced underwater video (UV) surveys (Fig. 2a,b). NOAA's benthic habitat maps of the Main Hawaiian Islands define habitat types based on insular-shelf zones and structure of benthic communities greater than 1 acre (0.4 ha) in size (Coyne et al. 2003). The characterization of habitat types in the present study adds to the classification scheme developed by NOAA.

UV surveys

In situ benthic habitat data were obtained by conducting georeferenced UV surveys. The start positions of the transects were randomly generated along the delineated 25 m boundary of NOAA's maps using the random point generator extension in ArcView (Jenness 2005). An underwater scooter, mounted with an underwater video camera, compass and dive computer, was

used to run transects perpendicular to shore while recording the bottom with the camera. A total of 41 transects (Puako = 8, Anaehoomalu = 11, Honokohau = 10 and Wawaloli = 12) were run from a depth of 2 to 25 m. The range of transect lengths and dive times was ca. 50 to 900 m, and 15 to 35 min, respectively. Geographic coordinates for all transects were obtained by placing a global positioning device (GPS) in a dry bag, connected via a float and dive flag to the diver's buoyancy compensation device (BCD) using a 100 m transect line. The diver was ca. 2 m off the bottom while recording the substrate, followed by the GPS at the surface. The GPS device was kept directly above the diver by adjusting the transect line attached to the diver's BCD. Before every dive, the GPS device was set to track the location of the diver. The time on the video camera was synchronized with the time on the GPS device before every dive, so that benthic data was linked to the geographic position. The geographic coordinates matching the time on the camera were used to determine the location and extent of changes in habitat type.

Video analysis and habitat mapping

A single observer (Ortiz) viewed the 5 h of video generated from the underwater transects. The videos were analyzed and transects subdivided into contiguous segments of unique habitat types. We defined habitat types based on 7 categories of physical substrate, based on the lithology and geomorphology of the seafloor, and 5 categories of biological substrate. Physical substrate categories were based on NOAA's benthic habitat classification and comprised B (colonized volcanic rock/boulder), A (aggregate reef), S (sand), P (pavement), T (scattered coral rock), U (unknown), and R (rubble) (Coyne et al. 2001). Biological substrate were based on previous UV surveys in West Hawaii (Tissot & Hallacher 2003) and comprised C for the finger coral *Porites compressa*, L for the lobe coral *Porites lobata*, E for the cauliflower coral *Pocillopora meandrina*, M for mixed coral (denotes areas where the dominance of cauliflower,

finger and lobe coral varied), and u for uncolonized. Habitat types were categorized using a 3code 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 (e.g. BEL represented at least 50% cover by boulders with at least 50% covered by cauliflower coral and at least 20% lobe coral).

Benthic habitat maps were then created using NOAA's habitat digitizing extension in ArcView 3.3 (Kendall et al. 2001) and ArcGIS 8.3 software. Using the location and classification of each video-transect within a site, bathymetric data and aerial photographs, borders were drawn around areas representing similar habitats. Thus, the benthic habitat map displays homogeneous areas of habitat types derived from the video-transect data. From here on, habitat type refers to those areas on the benthic habitat maps and not the video-transect data, unless specified. an andA minimum mapping unit (MMU) of 1 045 m2 and a restricted mapping scale of 1:2 500 was used. These settings allowed for mapping of features larger than the MMU selected and for digitization to occur at the same level of detail. Both the area of habitat types and percent area of the physical substrate categories at each site was determined using ArcGIS Xtools extension (ESRI 2002).

Accuracy of the benthic habitat map was quantified using an error matrix. The matrix is made up of rows and columns that represent each habitat type, with each cell representing the total sites sampled for that particular habitat type. A total of 90 sites were randomly sampled within mapped habitat types. At each sampling site, a visual assessment of the habitat type was made. The mapped habitat type was then compared with that of the actual habitat type from field observations. Accuracy of the benthic habitat map is equivalent to the probability of correctly determining the 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.

Bathymetry

Airborne Bathymetric Lidar surveys of Hawaii were conducted in 2000 using LIDAR by the Airborne Lidar Bathymetry Technical Center of Expertise (SHOALS LIDAR Bathymetry 2002). These surveys allowed rapid and accurate measurements of high-resolution bathymetric data. Depth data for our study sites was downloaded and displayed as 5 m grids using ArcGIS 8.3 (ESRI 2002) and used to describe depth ranges for habitat types in the present study (Table 1).

Fish and benthic surveys

Fish abundance at each location was assessed between May and July 2005 using circular plot counts. Surveys were done within each habitat type at each site. A SCUBA diver recorded the abundance and length of fish seen within 115 randomly selected 5.0 m radius circular plots (78 m2 plot area). The circular plot method was chosen because it easily randomized sample locations within a given depth strata, increased the potential replication in a given survey period due to its quick deployment and thus allowed a short period of time in a survey area, thereby decreasing bias estimates due to net movement of reef-fish (Watson et al. 1995). In order to avoid bias and prevent over- and under-counting of individuals, fish that were unlikely to remain in the area (i.e. mobile fishes) were tabulated first and then ignored. The diver periodically calibrated estimates of the sample radius with a 10 m transect line marking the circumference of the circle. One complete rotation was made for each plot, and size estimates of fish were verified using a cm-scaled underwater slate. Fish were categorized as recruits, juveniles or adults based on body size and/or coloration. For the purpose of analysis, recruits were generally individuals

<5 cm in size. Juveniles refer to individuals of 5 to 14 cm, and adults refer to individuals >14 cm in length.

Depth, rugosity and percent substrate cover were estimated within each plot using a 10 m transect line positioned parallel to shore. Depth was recorded at the center, and at 90° intervals around the edges of the circular plot. The 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. A ratio of the length of the tape compared to the length of the transect was used as an index of rugosity. An underwater digital camera was used to take 10 photoquadrats along each transect, 1 m above the substrate. Each of 1 150 images was projected onto a rectangular grid using Photogrid software (Bird 2003). Percent cover for substrate types was quantified under 20 random points on each grid. These substrate types included finger coral, lobe coral, cauliflower coral, finger coral holes/crevices, coralline crustose, sand, turf algae, turf algae on boulders and turf algae on rubble. Percentage cover of substrates at each site was calculated as the percentage of the points on each transect occupied by the same substrate type within each site.

Data analysis

Detrended Correspondence Analysis (DCA) was used to describe associations between habitat circular plot data from the benthic habitat map and quadrats along transects . A matrix of plot samples classified by habitat type (115 plots) and quantified by percent cover of substrate (1 150 quadrats) was used in the analysis. DCA produces a graphical ordination that shows the similarity between observations (habitat types) and variables (substrates) derived from a frequency table (SAS Institute 2000). Observations that correspond in sampling space are close

together in ordination, while the strength of the relationship between observations and variables is indicated by the direction of the points from the plot's origin (Pimentel 1979). Percent area of physical substrate (aggregate reef, rock/boulder, pavement, rubble and sand) from the benthic habitat map and percent cover of substrate (finger coral, lobe coral, cauliflower coral, finger coral holes/crevices, coralline crustose, sand, turf algae, turf algae on boulders and turf algae on rubble) from the quadrat data were used to describe dominant substrata among sites. Percent area of physical substrate was calculated using ArcGIS Xtools extension (ESRI 2002), while the percent cover of substrates was calculated as the percentage of the points on each transect occupied by the same substrate type within each site.

A Canonical Correspondence Analysis (CCA) was carried out to describe patterns in the distribution of yellow tang life stages among habitat types and how they relate to a set of environmental variables. A matrix of circular plot samples classified by habitat type and abundance of yellow tangs (density of recruit, juvenile and adult within each plot) and environmental variables (depth, rugosity, percent cover of finger, cauliflower and lobe coral and turf algae within each plot) was used in the analysis. CCA produces a graphical ordination that detects the patterns of variation in life history stages that can best be explained by environmental variables (Ter Braak 1986). Thus, the location of individual circular plots (habitat type scores) in the multivariate space indicate how the abundance of yellow tang life stages at each habitat type varied in relation to the combination of environmental variables, while the location of yellow tang life stages (life stages scores) indicate the mean values of the response curves (abundance variations) of yellow tangs on the CCA axes (Ter Braak 1986). In order to better interpret the results of the CCA, the 14 individual habitat types were condensed into 3 broad but distinct habitat categories based on their physical and biological similarities: deep aggregate coral-rich

and sandy rubble habitats (ACL, ALC, AM, Ru and S), mid-depth aggregate reef and boulder habitats (ALE, AEL, BLL and BLE) and shallow turf-rich boulder habitats (BEL, PEL, Bu, Pu and Tu).

Differences in the density of each life stage among habitat categories and sites were compared using a Kruskal-Wallis test or an ANOVA with Dunn's test for unplanned multiple comparisons depending on whether they met the assumptions for ANOVA (Zar 1984). Bonferroni adjustments were conducted to ameliorate concerns over multiple statistical testing (Holm 1979).

In order to evaluate the relationship between FRA effectiveness and the abundance and distribution of habitats, we compared population size estimates of recruit, juvenile and adult yellow tangs relative to percent area of habitat categories at 1 FRA showing significant increases and 1 FRA showing a decrease in yellow tang densities. Population size estimates were calculated by multiplying the mean density of each life stage by the reef area derived from the habitat map (i.e. reef structure from shore to a depth of 25 m) and dividing it by the reef length (i.e. length of shoreline) at each site (Table 2). This adjustment was done to account for the different shoreline lengths and reef structure from shore to depth. The percent area of habitat categories represents the total percent area of habitat types belonging to each category. Both the reef area and length were calculated using ArcGIS 8.3 (ESRI 2002). Habitats with low coverage area and exceeding 25 m depths were not sampled and excluded from the analysis owing to fewer sightings of yellow tang and extent of habitat map, respectively. Although some habitats were not sampled, we were able to account for more than 70% of the reef area at each site.

RESULTS

Habitat classification

Using an error matrix the overall accuracy of the benthic habitat map was 93%. Patchy 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%), in part due to the patchy nature of these habitats.

The DCA revealed strong correlations between the visual assessment of habitat types and the percent cover of substrates among all sites (Fig. 3). The percent variation explained by the canonical dimensions was 36 and 23% for the first and second axes, respectively. Aggregations of finger and lobe coral habitats (AM and ACL) were associated with high cover of lobe and finger coral and finger coral holes/crevices substrate. Aggregate and colonized boulder with high to low cauliflower and lobe coral cover habitats (ALE, AEL, BLL, BLE, BEL, PEL and Bu) were associated with turf algae on boulders, coralline crustose, cauliflower coral and lobe coral substrates. Sand and rubble habitats (S and Ru) were associated with sand and turf algae on rubble substrates. These associations demonstrate that the benthic habitat map was largely consistent with percent cover data measured using quadrats.

Description of reef habitats

A total of 14 habitat types occurred among all study sites (Table 1). The abundance and distribution of habitat types, depths and rugosity varied among sites (Table 2, Fig. 4). At Honokohau, uncolonized boulder (Bu) and pavement (PEL and Pu) habitats were dominant in shallow depths while colonized boulder with lobe and cauliflower coral cover habitats (BLL and BEL) dominated deeper depths. Wawaloli was dominated by colonized boulder and pavement with cauliflower and lobe coral cover habitats (BEL and PEL) at both shallow and deeper depths. Puako was dominated by uncolonized boulders (Bu) and boulder with cauliflower and lobe coral

cover habitats (BEL) at shallow depths, while aggregate reef with finger and lobe coral habitats (ACL) were dominant at deeper depths. Anaehoomalu was dominated by uncolonized boulder habitats (Bu) and colonized boulder with lobe and cauliflower coral cover habitats (BLE) at shallow depths followed by aggregate reef with finger, lobe and cauliflower coral (ACL and ALE) at deeper depths. The central reef area of Anaehoomalu was heavily fragmented and isolated by sand (S). Uncolonized rubble (Ru) habitats were generally found at deeper depths at most sites. Rubble habitats in Wawaloli had the lowest rugosity (1.14), while boulder habitats in Honokohau and Anaehoomalu had the highest rugosity (>1.62) among all sites. Rugosity of aggregate reef habitats varied greatly among sites (1.18 to 1.37) (Table 2).

Percent cover of substrata varied among sites (Fig. 5). Overall, of the 4 sites mapped, Honokohau and Wawaloli were predominantly composed of pavement and boulder substrate, while Puako and Anaehoomalu were predominantly boulder and aggregate reef, and some had a mixture of sand and rubble substrates (Fig. 5). Puako was dominated mostly by finger coral (27%), turf algae (14%) and lobe coral (11%), while finger coral (27%), turf algae (15%) and sand (13%) were the dominant substrata in Anaehoomalu. Honokohau and Wawaloli were dominated by turf algae (24 and 38%, respectively), finger coral (20 and 11%, respectively) and coralline crustose (15 and 11%, respectively). Although finger coral was abundant in Honokohau and Wawaloli, distribution of this substrate was largely fragmented and distributed along patches of reef overlaying boulder and pavement substrata (Ortiz pers. obs.).

Habitat use

A total of 115 circular plots (Honokohau = 34, Puako = 27, Wawaloli = 24 and Anaehoomalu = 30) were surveyed for fish (Fig. 4). Overall, new recruits and juvenile yellow tangs were most abundant on both deep aggregate coral-rich and sandy rubble and mid-depth

aggregate reef and boulder habitats (AM, ACL, ALC, ALE, AEL, BLL, BLE, Ru and S), while adults were most abundant at the shallow turf-rich boulder habitats on the reef flat (BEL, PEL, Bu, Pu and Tu) (Figs. 6 & 7).

CCA revealed significant associations among the sizes of tang, habitat types and environmental variables at each site (Fig. 6) (Chi-square; all axes p < 0.001). The percent variation explained by the canonical dimensions was 96 and 4% for the first and second axes, respectively. The abundance of recruits and juveniles was highest within deep aggregate coral-rich and sandy rubble and mid-depth reef and boulder habitats. Adult abundance was higher within the shallow turf-rich boulder habitat (Figs. 6 & 7).

However, these patterns varied among sites. At Honokohau and Wawaloli recruits and juveniles were distributed along mid-depth aggregate reef and boulder and shallow turf-rich boulder habitats having patchy areas of finger and cauliflower coral substrate (Figs. 6 & 7c–d), while Puako and Anaehoomalu sites had recruit and juveniles associating with deep aggregate coral-rich and sandy rubble and mid-depth aggregate reef and boulder habitats (Fig. 7a–b). Adults were strongly associated with the shallow turf-rich boulder habitat, but were also found across all habitats to some extent (Figs. 6 & 7).

Environmental variables influencing abundance and distribution of yellow tang

Depth, rugosity and percent cover of turf algae and finger, lobe and cauliflower coral explained the major variation among yellow tang recruits, juveniles and adults (Fig. 6). Depth, accounting for 49% of the variance, decreased along the first axis. Percent cover of turf algae, accounting for 86% of the variance, increased along the second axis. Percent cover of finger, cauliflower and lobe coral and rugosity, accounting for 86, 40, 67 and 60% of the variance,

respectively, increased along the second axis. Thus, recruits and juveniles were mainly found in deep habitats with the highest percentage of finger, cauliflower and lobe coral cover, with recruits also found in deeper sandy rubble habitats, while adults occurred in shallow complex habitats with the highest percentage of turf algae.

Fish density among habitats and sites

The density of each life stage was significantly different among habitat categories. Recruits were significantly different among habitats (H = 20.9, p < 0.001), being significantly higher in deep aggregate coral-rich and sandy rubble habitat averaging 5.7 (\pm 7.7 SD) recruits per circular plot (78m2), compared to shallow turf-rich and boulder habitat which averaged only 1.2 (\pm 3.9 SD) recruits. Significant differences among habitats were detected for juveniles (H = 30.7, p < 0.001). Juvenile densities were significantly higher in deep aggregate coral-rich and sandy rubble habitat, averaging 7.7 (\pm 7.6 SD) juveniles, compared to both mid-depth aggregate reef and boulder and shallow turf-rich boulder habitats averaging 3.2 (\pm 5.5 SD) and 0.5 (\pm 1.4 SD) juveniles, respectively. Adults differed significantly among habitats (H = 28.2, p < 0.000). Adults were significantly higher in shallow turf-rich boulder habitats, averaging 13.4 (\pm 18.6 SD) adults. Variation in the mean density of recruit, juvenile and adult yellow tang among sites was not significantly different.

Population size, habitat and FRA effectiveness

The estimated population size of yellow tangs in each size-class varied among sites (Table 3). Overall, recruits, juveniles and adults were more abundant in Anaehoomalu and less abundant in Wawaloli. The Anaehoomalu FRA, with significant increases in yellow tang densities and the greatest abundance of deep aggregate coral-rich and sandy rubble and mid-

depth aggregate reef and boulder habitats had the highest number of recruits and juveniles, while the Honokohau FRA, with a decrease in yellow tang densities and lower abundance of these habitats, had lower numbers of recruit and juveniles (Table 3). In addition, Honokohau, with a higher abundance of the shallow turf-rich boulder habitat, had a lower density of adults compared to Anaehoomalu. Adults were more abundant on those sites with lower shallow turfrich boulder habitat (Puako and Anaehoomalu) compared to those that had more than 68% of these habitats (Honokohau and Wawaloli). Juvenile numbers were highest on those sites dominated by the deep aggregate coral-rich and sandy rubble habitat (Puako and Anaehoomalu). Recruits were more abundant in Anaehoomalu, with more than 52% of the deep aggregate coralrich and sandy rubble habitat, followed by Honokohau, with less than 6% of this habitat. However, recruit numbers were 3 times higher in Honokohau than in Puako, which has 23% deep aggregate coral-rich and yrubble habitat (Table 3).

Reef area and the number of yellow tang in each size-class varied among sites (Fig. 8). Anaehoomalu had the largest reef area and the greatest number of recruits, juveniles and adults. Wawaloli had the smallest reef area and fewest numbers of recruits, juveniles and adults. Honokohau, with the second largest reef, had a greater number of recruits than Puako, while Puako, with the third largest reef area, had a greater number of juveniles and adults than Honokohau.

DISCUSSION

Habitat mapping

A combination of remotely sensed data and in situ benthic sampling has provided numerous advantages in examining fish-habitat associations (Christensen et al. 2003, Friedlander et al. 2003, Friedlander et al. 2007), detecting habitat changes (Parsons et al. 2004) and assessing fish stocks (Nasby-Lucas et al. 2002). This integration of methods provided a useful quantitative approach for the description of coral reef habitats and the examination of ontogenetic patterns of habitat use by a reef-fish, the yellow tang. Our findings showed a strong correlation between the benthic habitat maps and substrate cover, and ground-truthing confirms that the maps produced from this method can provide an accurate representation of the spatial variation of reef habitats and fish distributions.

Most studies examining fish-habitat associations have relied on transects and quadrats placed along reef zones or many benthic classifications such as sandy bottom, rubble or rocky/boulder habitat (Fowler et al. 1992, Green 1996, Aburto-Oropeza & Balaart 2001, Nanami & Nishihira 2002) and patch reefs (Depcznski & Bellwood 2004). More recent methods have used aerial photography (Coyne et al. 2001), acoustic devices (Armstrong et al. 2006) and GIS (Stanbury & Starr 1999) to map benthic landscapes. Fish-habitat association studied at the quadrat level, although informative, can fail to detect habitat use patterns at the landscape level by not including the mosaic and spatial arrangement of reef habitats important to reef-fish. For example, Parsons et al. (2004) found that without benthic habitat mapping, significant changes in benthic community structure would have not been detected with the use of traditional sampling methods (i.e. quadrats and transects). Nevertheless, the use of transects and quadrats is still an efficient way to carry out long-term studies and test specific hypotheses without requiring expensive technology and/or training.

Mapping efforts can be time consuming and costly, often requiring the use of expensive equipment and intensive sampling to validate the mapping effort. Our approach presents several advantages. First, our methods are relatively simple and present an inexpensive way to map and

examine benthic landscapes in relation to reef- fish abundance, providing, of course, that aerial photographs are available. Second, the method does not require extensive training and equipment. Third, it can describe the spatial arrangement, distribution and abundance of reef habitats at multiple spatial scales. Fourth, population and community ecology data from a wide range of habitat types can be studied and applied to future management efforts. Fifth, the methodology here can be adapted for other regions and used to design and designate future MPA sites.

Ontogenetic habitat shifts

In the present study, the development of a habitat map allowed an examination of ontogenetic patterns of habitat use by a reef-fish. Reef-fish often settle in nursery areas (i.e. seagrass) or specific coral habitats (i.e. Porites sp.) and subsequently migrate to on-reef adult habitats in order to meet their changing needs (i.e. predator avoidance, reproduction and growth) as they mature (Beets & Hixon 1994, Green 1996, Dahlgren & Eggleston 2000). For example, within the vicinity of Lee Stocking Island, Bahamas, early juvenile Nassau grouper exhibit an ontogenetic movement from macroalgal clumps to patch reef habitats after settlement (Eggleston 1995). The present findings indicate that yellow tang exhibit an ontogenetic habitat shift from deeper aggregations of coral-rich habitats as recruits and juveniles to shallow turf-rich boulder habitats as they mature, a pattern previously described by Walsh (1985). Recruits (£5 cm) and juveniles (>5 and <14.0 cm) showed strong patterns of habitat selection among sites. The abundance of these early life stages is known to have a strong correlation with finger coral substrate (Walsh et al. 2004, Fig. 6). Therefore, the distribution of yellow tang is strongly influenced by the distribution of finger coral habitats because of ontogenetic shifts in habitat use by recruits and juveniles (Figs. 6 & 7).

Recruit density was high in Honokohau even though this area has a lower abundance of finger coral substrate and aggregate finger and lobe coral-rich areas compared to Puako and Anaehoomalu (Fig. 5, Table 3). Recruitment variation among sites may be the result of several factors such as spatial variation in recruitment, movement and/or differential post-settlement mortality due to differential shelter from predation (Hixon & Beets 1993, Carr & Hixon 1995, Sale 2004). Alternatively, variation in recruitment among sites may result from area effects such that sites with smaller finger coral areas could have the same recruitment as sites with larger finger coral area, but end up with substantially high densities due to its smaller total area. Some of these sources of variation could be addressed by looking at recent studies. First, long-term data shows that the recruitment patterns among sites has been similar among years. From 1999 to 2004, there has been consistently higher recruitment at Honokohau relative to Anaehoomalu and Puako (Tissot & Walsh unpubl. data). Second, the early juvenile stages of yellow tang have small ranges and rarely move from the settlement habitat (Parrish & Claisse 2006). Third, density calculations were made to include discrepancies in the reef area and length among sites in order to account for possible area effects in the present study. Thus, the present study suggests that while differences in habitat (i.e. finger coral) may play a role in determining the abundance and distribution of recruits, these effects are influenced by other sources of variation that are not discernable among sites. Recruitment variation may be driven by a multiplicity of factors that will determine larval supply, active habitat selection and differential post-settlement mortality, which in turn depends on the availability of habitat, food and predators (Sale 2004). However, a more detailed study is required to test these hypotheses before any conclusions can be made as to why the spatial distribution of recruits is different among sites.

The distribution of juveniles varied greatly among habitats and sites. The wide range of habitat utilization by juveniles may reflect size-dependent processes weakening habitat selection as the species grows (Dahlgren & Eggleston 2001) or the continued effects of variation in predation intensity. Conversely, shifts in habitat use may not have been as distinct in some sites where aggregations of coral-rich habitats were abundant. The abundance of adults (³14.0 cm) was greater in shallow turf-rich boulder habitats, although their distribution varied greatly among and within sites (Figs. 6 & 7). The wide distribution of adults within shallow boulder areas along the reef flat and deep aggregation of coral-rich areas along the reef slope and cliff edge may reflect the availability and proximity of shelter and foraging habitats necessary for growth and reproduction. These results also follow observations made on adult movement where adults have been observed moving between foraging (shallow turf-rich boulder) and refuge (deep aggregate coral-rich) habitats (Walsh 1984).

Applications to MPA design and management

Empirical studies have shown that MPA size and the abundance and distribution of habitats are important to managed species and can influence the effectiveness of MPAs to protect targeted fish species (Sala et al. 2002, Friedlander et al. 2003, Gladstone 2006, Friedlander et al. 2007). Our findings that appropriate habitat type for early life history stages, large areas of these habitats on the reef and proximity of appropriate recruit, juvenile and adult habitats were associated with an FRA showing effective replenishment (i.e. significant increases in yellow tang) are consistent with these general conclusions. Even though the FRAs in the present study were not replicated, replicate plots within each site revealed that differences between the 2 FRAs were robust. For example, Anaehoomalu (significant replenishment), with the largest reef area and abundance of recruit, juvenile and adult habitats, had the greatest number of yellow tang in
each life stage, while Honokohau (no significant replenishment) had the fewest. In addition, overall recruit abundance was lower in the Honokohau FRA, with less than 6% aggregate finger and lobe coral-rich habitats, compared to the Anaehoomalu FRA where recruit habitat is more than 52% (Table 3). However, recruit densities in Honokohau were high relative to Puako and Wawaloli. One explanation for high recruit density and no significant replenishment in Honokohau may be differences in the availability of habitats. For instance, the availability of reef habitats can affect the post-settlement demography of reef-fish directly by providing refuge from predation (Hixon & Beets 1993). For example, the Honokohau site may have high recruitment, but few individuals survive to adulthood due to a lack of available habitat suitable for recruits. Thus, the effectiveness of the Anaehoomalu and Honokohau FRAs to replenish aquarium fish population may be driven by the reef size, abundance and distribution of essential fish habitats. Efforts are under way to examine habitat use pattern of other targeted fish species for all 9 FRAs in West Hawaii and how it relates to the effectiveness of the West Hawaii FRA system in replenishing aquarium fish populations.

Based on these results, it would be prudent to incorporate habitat essential to targeted species in future MPA design. For example, the present study suggests that for effective management of populations of yellow tang, sites should contain high abundance of aggregations of finger and lobe coral distributed at various depths (i.e. 7 to 25 m) adjacent to colonized boulders with low to high turf algae (10 to 80%) and high coral cover (50 to 80%) at a range of depths (i.e. 0 to 30 m).

CONCLUSIONS

Even though the FRAs were established in 1999, no comprehensive evaluation of the effectiveness of FRAs in relation to the abundance and distribution of habitats had been conducted until now. Findings from the present study suggest that habitat characteristics may largely contribute to the effectiveness of MPAs to replenish the targeted reef-fish, although there are certainly other important factors as well. Current efforts in Hawaii, focused on improving management of the fishery, should therefore incorporate habitats identified in the present study to the design and management of MPAs. MPAs will be more effective at protecting reef-fish species, life stages and the mechanisms that regulate them if they include habitats important to managed species (Sala et al. 2002). This information will help improve management of MPAs, enhance marine ecosystem conservation by identifying locations for future MPAs and provide valuable information to develop cogent resource management practices in Hawaii and other tropical regions.

Table 1. Habitat types and classification scheme based on the present 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

			Depth
Habitat code	Reef zone	Description	(m)
			0-3
Bu	Reaf flat	uncolonized houlders	
Du			0-3
Pu	Reefflat	uncolonized pavement	0-3
PEL	Reef flat	colonized pavement with cauliflower and lobe coral cover	2-8
Tu	Reef flat	scattered coral rock	4-5
BEL	Boulder	colonized boulders with cauliflower and lobe coral cover	3-11
BLL	Boulder	colonized boulders with lobe coral cover	5-20
BLE	Boulder	colonized boulders with lobe and cauliflower coral cover	5-25
AEL	Reef slope	aggregate reef with cauliflower and lobe coral cover	5-10
ALC	Reef slope	aggregate reef with lobe and finger coral cover	7-10
ALE	Reef slope	aggregate reef with lobe and cauliflower coral cover	5-24
AM	Reef slope	aggregate reef with mixed cover	8-30
ACL	Reef slope	aggregate reef with finger and lobe coral cover	8-30
Ru	Rubble	uncolonized rubble	20-40
S	All zones	Sand	0-40

Table 2. Area coverage, reef length, sampling allocation, depth and rugosity for habitat types at each study site. SE is standard error, N is the total number of surveys, and MR is the mean rugosity per habitat at each site. Habitat types are ordered from deep to shallow depths at each site

Site	Habita	Area	Reef	Ν		Mean de	pth (m)
	t	coverage	length		x _	Depth	SE
	code	(ha) [%	(km)		Σ		
		area]					
Puako	S	0.99 [<1]		-	-	-	-
	Ru	2.10 [2]		-	-	-	-
	ACL	21.9 [21]		12	1.37	8.96	2.05
	AEL	9.06 [9]		3	1.22	8.73	0.77
	BEL	16.3 [16]		8	1.22	3.60	1.52
	Tu	2.73 [3]		-	-	-	-
	PEL	2.67 [3]		-	-	-	-
	Bu	48.5 [46]		4	1.25	1.88	0.39
Total		104	3.30	27			
Anaehoomal	S			2	1.16	11.40	2.60
u		157 [30]					
	ACL	63.4 [12]		9	1.24	9.89	2.19
	AM	23.6 [5]		8	1.18	8.68	2.20
	ALE	86.7 [17]		5	1.31	8.53	2.45
	ALC	0.8[<2]		-	-	-	-
	AEL	42.9 [8]		-	-	-	-
	BLE	83.2 [15]		-	-	-	-
	BEL	2.8 [<1]		6	1.62	3.62	1.03
	Bu	63.3 [12]		-	-	-	-
Total		524	6.80	30			
Wawaloli	Ru			2	1.14	15.63	1.05
		2.22 [6]					
	AM	0.46 [1]		3	1.24	14.39	1.47
	BEL	17.7 [49]		10	1.20	11.96	3.02
	BLE	2.58 [7]		3	1.15	10.73	1.47
	PEL	10.1 [28]		5	1.16	4.23	1.57

Table 2. (Continue

	Pu	3.13 [9]		-	-	-	-
Total		36.2	2.00	23			
Honokohau	S	2.12 [2]		-	-	-	-
	Ru	2.84 [2]		-	-	-	-
	AM	2.09 [2]		8	1.31	12.19	1.25
	BLL	28.9 [26]		11	1.62	8.76	1.30
	BEL	12.0 [11]		8	1.82	6.71	1.27
	PEL	32.3 [29]		8	1.51	5.02	1.21
	Pu	31.8 [28]		-	-	-	-
	Bu	0.55 [<1]		-	-	-	-
Total		112	2.70	35			

Table 3. Comparison of management regime, percent area of habitat categories among sites and population size (no. of ind. km^{-1} rounded to the nearest 1 000) of recruits, juvenile and adult yellow tang at each study site. Habitat categories are coded as followed: (C1) deep aggregate coral-rich and sandy rubble habitat (ACL, ALC, AM, Ru and S), (C2) mid-depth aggregate reef and boulder habitat (ALE, AEL, BLL and BLE) and (C3) shallow turf-rich boulder habitat (BEL, PEL, Bu, Pu and Tu). Numbers in bold indicate highest percent area of habitat category and greater density of yellow tangs among sites. Numbers in parentheses indicate SE. Population size estimates were calculated by first multiplying the average density (no. m⁻²) of recruits, juveniles and adults per habitat type at each site by the area of the corresponding habitat type (in m²). Overall recruit, juvenile and adult estimates per habitat type per site were summed to obtain the total number of individuals of each life stage per site. Finally, the total number of individuals per life stage per site was divided by the length of the reef (in km) at each site to obtain the population size estimates (no. km⁻¹) listed

Habitat				
categories	Puako	Anaehoomalu	Wawaloli	Honokohau
Management	MPA	FRA	MPA	FRA
C1	23	52	7	6
C2	9	35	7	26
C3	68	13	86	68
Recruits	3 000 (1000)	9 000 (3 000)	2 000 (2 000)	9 000 (7 000)
Juveniles	13 000 (5 000)	27 000 (17 000)	2 000 (1000)	5 000 (2 000)
Adults	73 000 (53 000)	15 000 (4 000)	14 000 (4 000)	22 000 (7 000)

FIGURE CAPTIONS

Fig. 1. Study areas in the Island of Hawaii showing the location of 4 study sites

Fig. 2. Benthic habitat maps developed for Honokohau, Hawaii. Mapping was completed using NOAA's (a) aerial photographs and (b) underwater video (UV) survey transects, bathymetry and randomly assigned habitat assessments (red circles)

Fig. 3. Detrended Correspondence Analysis (DCA) of the associations between habitat types derived from benthic habitat maps and substrate cover derived from quadrat data among 4 study sites. Sampling locations (circular plots) were classified by habitat type. Quadrat data included percent cover of substrates (finger coral, lobe coral, finger coral holes/crevices, cauliflower coral, coralline crustose, turf algae and sand) within circular plots

Fig. 4. Habitat maps of study sites (a) Puako, (b) Anaehoomalu, (c) Wawaloli and (d) Honokaohau in Hawaii created using aerial photography and *in situ* video transects. Yellow circles indicate location of circular plots

Fig. 5. (a) Percent area of physical substrate for each site derived from benthic habitat maps. (b) Percent cover of the 7 most abundant substrates derived from quadrat data at each site: C (finger coral), L (lobe coral), PH (finger coral holes/crevices), E (cauliflower coral), Cr (coralline crustose), TU (turf algae) and S (sand)

Fig. 6. Canonical Correspondence Analysis (CCA) of the associations of yellow tang recruits, juveniles and adults to habitat types and environmental variables at all study sites. Sampling locations (circular plots) were classified by habitat type from benthic habitat maps. Quadrat data included yellow tang abundance (recruit, juvenile and adult densities) and environmental variables (depth, rugosity, percent cover of finger, cauliflower and lobe coral and turf algae

cover) within circular plots. Habitat types were grouped into 3 distinct habitat categories in order to aid in the interpretation of the data (see text). Habitat types and life stages are represented by points and environmental variables by arrows, whereby the length of the arrow is a measure of how much the distribution of each life stage differs along environmental variables (Ter Braak 1986).

Fig. 7. Mean density (±1 SE) of recruits, juveniles and adults of yellow tangs along habitats at each study site: (a) Puako, (b) Anaehoomalu, (c) Wawaloli and (d) Honokohau. Sites are ordered from north to south (top to bottom). Habitats are ordered from deep to shallow depths (left to right)

Fig. 8. (a) Estimated population sizes of yellow tang life stages and (b) reef area at each study site





Fig. 1



Fig. 2



Habitat Classification

- Aggregate Reef/Mixed
 Aggregate Reef/Finger-Lobe coral
 Aggregate Reef/Lobe-Finger coral
 Aggregate Reef/Lobe-Cauliflower coral
 Aggregate Reef/Cauliflower-Lobe coral
 Colonized Boulder/Lobe-Lobe coral
 Colonized Boulder/Lobe-Cauliflower coral
 Plots
 - Fig. 3



- ACL / AMALE / AEL
- BLL / BLE
- BEL
- 🗆 Bu
- ♦ PEL
- △ Ru / S



Fig. 4



Fig. 5



Fig. 6



Fig. 7



REFERENCES

- Armstrong RA, H Singh, J Torres, RS Nemeth, A Can, C Roman, R Eustice, L Riggs, G Garcia-Moliner (2006) Characterizing the deep insular shelf coral reef habitat of the Hind Bank marine conservation district (US Virgin Islands) using the Seabed autonomous underwater vehicle. Continental Shelf Research 26:194-205
- Beets JP, MA Hixon (1994) Distribution, persistence and growth of groupers (Pisces:Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bulletin of Marine Science 55: 470-483
- Bird C (2003) Ecological Analysis of Digital Photographs. Honololulu, HI
- Carr MH, MA Hixon (1995) Predation on early post-settlement survivorship of coral reef fishes. Marine Ecology Progress Series 124: 31-42
- Christensen JD, CFG Jeffrey, C Caldow, ME Monaco, MS Kendall, RS Appledorn (2003) Crossshelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf and Caribbean Research 14 (2): 9-27.
- Coyne MS, ME Monaco, M Anderson, W Smith, P Jokiel (2001) Classification scheme for benthic habitats: main eight Hawaiian Islands Biogeography program. US Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Silver Spring Maryland, 16 pp
- Coyne MS, TA Battista, et al. (2003) Benthic habitats of the main Hawaiian islands. NOAA technical Memorandum NOS NCCOS CCMA 152: 1-48,
- Dahlgren CP, DB Eggleston (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81(8): 2227-2240
- Dahlgren CP, DB Eggleston (2001) Spatio-temporal variability in abundance, size and microhabitat associations of early juvenile Nassau grouper *Epinephelus striatus* in an off-reef nursery system. Marine Ecology Progress Series 217: 145-156
- Department of Land and Natural Resources (DLNR) 1996 Hawaii fishing regulations Division of Aquatic Resources, DLNR, Honolulu
- Depczynski M, DR Bellwood (2004) Microhabitat utilization patterns in cryptobenthic coral reef fish communities. Marine Biology 145: 455-463.
- Doherty JB, DM Williams (1988) The replenishment of coral reef fish populations. Oceanography and Marine Biology Annual Review 26: 487-551
- Eggleston DB (1995) Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Marine Ecology Progress Series 124: 9-22

- ESRI (2002) Environmental Science Research Institute: ET Spatial Techniques: ET GeoWizards for ArcGIS, Pretoria, South Africa
- Fowler AJ (1990) Spatial and temporal patterns of distribution and abundance of chaetodontid fishes at One Tree Reef, southern GBR. Marine Ecology Progress Series 64: 39-53
- Fowler AJ, PJ Doherty, DMcB Williams (1992) Multi-scale analysis of recruitment of a coral reef fish on the Great Barrier Reef. Marine Ecology Progress Series 131: 131-142
- Friedlander AM, JD Parrish (1998) Habitat characteristics affecting fish assemblages on a Hawaiian Reef. Journal of Experimental Marine Biology and Ecology 224: 1-30
- Friedlander AM, EK Brown, PL Jokiel, WR Smith, KS Rodgers (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22: 291-305
- Friedlander AM, E Brown (2003) Fish Habitat Utilization Patterns and Evaluation of the Efficacy of Marine Protected Areas in Hawaii: Integration and Evaluation of NOS Digital Benthic Habitats Maps and Reef Fish Monitoring Studies. Final Report to NOAA National Ocean Service Biogeography Program: 1-78
- Friedlander AM, E Brown, ME Monaco (2007) Coupling Ecology and GIS to Evaluate Efficacy of Marine Protected Areas in Hawaii. Ecological Applications 17(3): 715-730
- Gladstone W (2006) Requirements for marine protected areas to conserve the biodiversity of rocky reef fishes. Aquatic Conservation: Marine and Freshwater Ecosystems 17: 71-87
- Gratwicke B, MR Speight (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66: 650-667
- Green AL (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). Marine Ecology Progress Series 133: 1-11
- Hixon MA, JP Beets (1993) Predation, prey refuges, and the structure of coral reef fish assemblages. Ecological Monographs 63: 77-101
- Hixon MA, HC Mark (1997) Synergistic Predation, Density Dependence, and PopulationRegulation in Marine Fish. Science 277: 946-949
- Hixon MA, MS Webster (2002) Density Dependence in Reef Fish Populations In: Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem, ed. Sale, PF (Academic, San Diego), pp 303-325

Holm S (1979) A simple sequentially rejective multiple test procedure. Scan J Stat 6: 65-70

Jenness J (2005) Random Point Generator 1.3v, Jenness Enterprises Flagstaff, AZ

- Kendall MS, CR Kruer, KR Buja, JD Christensen, M Finkbeiner, ME
 Monaco (2001) Methods used to map the benthic habitats of Puerto Rico and the US Virgin Islands. National Ocean Service, Center for Coastal Monitoring and Assessment, Biogeography Program, Silver Spring, MD 45 pp
- Kendall MS, JD Christensen, Z Hillis-Starr (2003) Multi-scale data used to analyze the spatial distribution of French grunts, *Haemulon flavolineatum*, relative to hard and soft bottom in a benthic landscape. Environmental Biology of Fishes 66: 19-26
- Levin PS (1991) Effects of microhabitat on recruitment variation in a Gulf of Maine reef fish. Marine Ecology Progress Series 75: 183-189
- Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73: 1943-67
- Meekan MG, JH Choat (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical fishes. Marine Biology 128: 373-383
- Menge BA, J Lubchenco, LR Ashkenas (1985) Diversity, heterogeneity and consumer pressure in a tropical rocky intertidal community. Oecologia (Berl) 65: 394-405
- Nanami A, M Nishihira (2002) The Structure and Dynamics of Fish Communities in an Okinawan Coral Reef: Effects of Coral-based Habitat Structures at Sites with Rocky and Sandy Sea Bottoms. Environmental Biology of Fishes 63(4): 353-372
- Nasby-Lucas NM, BE Embley, MA Hixon, SG Merle, BN Tissot, DJ Wright (2002) Integration of submersible transect data and high-resolution multibeam sonar imagery for a habitat-based groundfish assessment of Heceta Bank, Oregon. Fishery Bulletin 100: 739-751
- Oropeza O, EF Balaart (2001) Community structure of reef fish in several habitats of a rocky reef in the Gulf of California. Marine Ecology 22 (4): 283-305
- Parrish JD, JT Claisse (2006) Post-settlement life history of key coral reef fishes in a Hawaiian marine protected area network. NOAA Final Project Report 1-42
- Parsons DM, NT Shears, RC Babcock, TT Haggit (2004) Fine-scale habitat change in a marine reserve, mapped using radio-acoustically positioned video transects. Marine and Freshwater Research 55: 257-265
- Pimentel RA 1979 Morphometrics, the multivariate analysis of biological data. Kendall-Hunt, Dubuque, 276 p
- Sala E, O Aburto-Oropeza, G Paredes, I Parra, JC Barrera, PK Dayton (2002) A general model for designing networks of marine reserves. Science 298: 1991-1993

- Sale PF (2004) Connectivity, Recruitment Variation, and Structure of Reef-Fish Communities. Integrative and Comparative Biology 44: 390-399
- SAS Institute (2000) JMP Statistics and Graphics Guide. Version 4.00 SAS Institute Inc, Cary, NC, USA
- Schneider DC, R Walters, S Thrush, P Dayton (1997) Scale-up of ecological experiments: Density variation in the mobile bivalve *Macomona liliana*. Journal of Experimental Marine Biology and Ecology 216: 129:152
- SHOALS LIDAR Bathymetry (2002), viewed March 2005, <<u>http://shoals.sam.usace.army.mil/hawaii/pages/Hawaii_Data.htm</u>>
- Stanbury K, RM Starr (1999) Applications of Geographic Information Systems (GIS) to habitat assessment and marine resource management. Oceanologica Acta 22 (6): 699-703
- Ter Braak CJF (1986) Canonical Correspondence Analysis: A New Eigenvector Technique for Multivariate Direct Gradient Analysis. Ecology 67 (5): 1167-1179
- Tissot BN, LE Hallacher (2003) The effects of aquarium collectors on coral reef fishes in Hawaii. Conservation Biology 17(6): 1759-1768
- Tissot BN, WJ Walsh, LE Hallacher (2003) Evaluating the effectiveness of a marine reserve in West Hawaii to improve management of the aquarium fishery. NOAA Technical Report 1-20
- Tissot BN, WJ Walsh, LE Hallacher (2004) Evaluating the effectiveness of a marine reserve network in Hawaii to increase the productivity of an aquarium fishery. Pacific Science 58(2): 175-188
- Tolimieri N (1995) Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia 102: 52-63
- Tupper M, RG Boutilier (1995) Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Aquatic Science 52: 1834-1841
- Underwood AJ, MG Chapman, SD Connell (2000) Observation in ecology: you can't make progress on processes without understanding the patterns. Journal of Experimental Marine Biology and Ecology 250: 97-115
- Walsh WJ (1984) Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. PhD Dissertation, University of Hawaii, p 118
- Walsh WJ (1985) Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. Bulletin of Marine Science 36: 357-376
- Walsh WJ (1987) Patterns of recruitment and spawning in Hawaiian reef fishes. Environmental Biology of Fishes 18(4): 257-276

- Walsh WJ, BN Tissot, L Hallacher (2004) A Report on the Finding and Recommendations of Effectiveness of the West Hawaii Regional Fishery Management Area. Department of Land and Natural Resources, Honolulu, HI
- Watson RA, GM Carlos, MA Samoilys (1995) Bias introduction by the non random movement of fish in visual transect surveys. Ecological Modeling 77: 205-214
- Wiens JA (1989) Spatial Scaling in Ecology. Functional Ecology 3 (4): 385-3

Zar JH (1984) Biostatistical analysis. Prentice Hall, NJ

MANUSCRIPT 2:

EVALUATING HABITAT STRUCTURE IN RELATION TO THE EFFECTIVENESS OF AN MPA NETWORK TO REPLENISH CORAL REEF FISH IN WEST HAWAII

ABSTRACT

Identifying habitats important to vulnerable life stages of reef-fish is an important goal for the effective design and management of Marine Protected Areas (MPAs). However, data on habitat requirements for most fish species are very limited. Using a benthic habitat map that characterized reef habitats on the island of Hawaii, we examined ontogenetic patterns of habitat use by each of the life stages of endemic and non-targeted fish species (i.e., brown surgeonfish, Acanthurus nigrofuscus; agile chromis, Chromis agilis; saddle wrasse, Thallasoma duperrey; arc-eye hawkfish, *Paracirrhites arcatus*), and commercially important aquarium fish species (i.e., yellow tang, Zebrasoma flavescens; goldring surgeonfish, Ctenochaetus strigosus; black surgeonfish, Ctenochaetus hawaiiensis; multiband butterflyfish, Chaetodon multicinctus) in relation to the effectiveness of existing MPAs to replenish depleted fishes. Deep aggregate coralrich areas and rubble substrates adjacent to shallow turf-rich boulder habitats at various depths (i.e., 0-30m) were used by all study species, highlighting areas that are essential both to protected and endemic fish species in Hawaii. Appropriate habitat type for early life history stages of fish species, large areas of these habitats on the reef, and proximity of appropriate recruit, juvenile, and adult habitats were associated with an MPA showing effective replenishment. Four species (goldring surgeonfish, brown surgeonfish, multiband butterflyfish, and yellow tang) showed similar ontogenetic shifts in habitat use by using deep aggregate coral-rich areas as recruits and juveniles and shallow turf-rich boulder habitats as adults. The saddle wrasse exhibited opposite shifts in habitat use by using shallow turf-rich boulder habitats as juveniles and deep aggregate coral-rich areas as adults. Three species (agile chromis, black surgeonfish, and arc-eye hawkfish) used similar habitats in both juvenile and adult life stages by remaining in mid-depth aggregate reef and boulder habitats. Overall, our study shows that habitat characteristics largely

influenced the effectiveness of MPAs in replenishing targeted species. It is therefore necessary to incorporate habitats important to the life history of protected species if MPAs are to meet their conservation goals.

INTRODUCTION

The ongoing decline of coral reef fisheries, habitat loss, and the failure of conventional management practices has led to the increasing widespread use of marine protected areas (MPAs) as an important fishery management tool for conserving biodiversity and resources in coral reef systems (Roberts 1995, Murray et al. 1999, Hastings and Botsford, 1999). Studies have suggested that in order to be effective, MPAs must incorporate habitats important to vulnerable life stages of reef fish, where the fish will benefit the most from habitat protection during vulnerable times (Roberts et al. 2003). Studies have also shown that in the absence of detailed information, habitats are a good surrogate for biodiversity (Ward et al. 1999, Sala et al. 2002; Gladstone 2007). Therefore, by incorporating habitats important to reef-fish populations at various life stages, MPAs will be more effective at protecting reef-fish species and the ecological processes regulating these populations (Sala et al. 2002; Sale et al. 2005). In addition, investigating the habitat-use patterns of reef-fish can provide valuable insight into potential locations for future MPAs, fish habitat affinities, and evaluation of MPA effectiveness. However, data on habitat requirements for most fish species are very limited, and often MPAs are designed without prior knowledge of habitats important to fish populations (Sala et al. 2002; Botsford et al. 2003).

In Hawaii, where ornamental fish species are among the most commercially valuable and targeted reef-fish, designation of MPAs to replenish aquarium fish populations was based

primarily on those areas of high conflict among aquarium fish collectors and dive tour operators and not on habitat-based criteria (Wood 1985; Tissot and Hallacher 2003; Tissot et al. 2003; Capitini et al. 2004; Walsh et al. 2004). In 1999, a network of nine fishery replenishment areas was established on the west coast of the island of Hawaii (hereafter "West Hawaii") in response to declines of reef fishes taken by aquarium collectors. fishery replenishment areas are MPAs in which the collecting of live fish for the aquarium trade is prohibited. These areas were closed to aquarium collectors at the end of 1999 and have been rigorously monitored up to the present. Studies reveal significant increases in the overall abundance of aquarium fish in four of the nine fishery replenishment areas (Walsh et al. 2004). Because only half of the MPAs have been productive, these studies suggest that the abundance and distribution of habitats are likely to be important factors influencing the effectiveness of the MPA network to replenish aquarium fish (Walsh 1987; Tissot et al. 2003; Tissot et al. 2004; Walsh et al 2004; Ortiz and Tissot 2008). It is, therefore, necessary to evaluate the effectiveness of MPAs relative to the abundance and distribution of habitats important to targeted fish species.

Identifying habitats important to reef-fish is problematic because of ontogenetic shifts in habitat use which requires the study of habitat utilization patterns at multiple spatial scales for a variety of species (Syms 1995; Eggleston 1995; Dahlgren and Eggleston 2000; Lechini 2006; Ortiz and Tissot 2008). However, recent studies have mapped features of reef habitats at multiple scales. These maps have been used to quantify large swatch of contiguous reef habitats and their associations with reef-fish (Christensen et al. 2003; Friedlander et al. 2007).

Using a combined remote sensing and in situ mapping approach, we outlined a new method for evaluating the habitat use patterns of reef fish among MPAs in relation to their ability to replenish aquarium fish (Ortiz & Tissot 2008).. This approach has shown that the distribution

of habitats is an important factor influencing the replenishment of aquarium fish populations in West Hawaii in MPAs.

Here, we examine ontogenetic patterns of habitat use by eight reef fish species to evaluate how habitat distributions influence the effectiveness of existing MPAs in Hawaii. Although our study focuses on species targeted by the aquarium trade, we also examine non-targeted species to demonstrate the usefulness of our methods in delineating habitat important to species with different life history traits. In this paper we: (1) describe the habitat use of the life stages of targeted and non-targeted reef-fish species at four MPA sites; (2) evaluate the relationship between MPAs with varying levels of replenishment and the abundance and distribution of habitats; (3) discuss implications for the design of effective MPAs; and (4) make recommendations regarding the conservation of targeted reef-fish populations in Hawaii and other regions.

MATERIAL AND METHODS

Study Area and Species

We examined four MPAs (Fig. 1). Two were fishery replenishment areas, Honokohau (19° 40.26'N, 156° 01.82'W) and Anaehoomalu Bay (from here on "Anaehoomalu") (19° 57.17'N, 155° 51.97'W) that have varied in their effectiveness to replenish aquarium reef-fish (Walsh et al. 2004) and two sites were reference control sites, Wawaloli (19° 42.00'N, 156° 02.99'W) and Puako (19°58.19'N, 155° 50.93'W), that were the closed-control sites used for measurements of effectiveness by Walsh et al. (2004)..

"MPA effectiveness" represents the change in density of targeted fish in fishery replenishment areas relative to an adjacent reference closed-control site, which is an MPA that also prohibits aquarium collecting but has been in effect for longer than 20 years. Effectiveness was measured as the change in the difference in fish density between each fishery replenishment area and closed-control site during before closure and after closure surveys (Walsh et al. 2004). For instance, a statistically significant before versus after effect indicates a change in fish abundance within the MPA after closure relative to before closure. Although effectiveness measures the changes within the MPA as a percent of the before closure abundance relative to control sites, another measure of change in the MPA is the absolute percent change in density of the before closure surveys relative to the after closure surveys (Walsh et al. 2004). Both of these measures reflect the functionality of the MPAs in replenishing targeted aquarium fish. For example, the Honokohau MPA showed an 8% percent change in aquarium species density between 1999-2004, but relative to its control site (Wawaloli) it showed a 1 % decrease in aquarium fish species, although neither change was statistically significant. In contrast, Anaehoomalu has shown a statistically significant 20 % increase in aquarium fish relative to its closed-control site and an 11 % percent change in aquarium fish density between 1999 and 2004 (Walsh et al. 2004).

The study focused on eight reef-fish species with different life-history characteristics (Table 1): yellow tang (*Zebrasoma flavescens*), goldring surgeonfish (*Ctenochaetus strigosus*), black surgeonfish (*Ctenochaetus hawaiiensis*), brown surgeonfish (*Acanthurus nigrofuscus*), multiband butterflyfish (*Chaetodon multicinctus*), agile chromis (*Chromis agilis*), blue-head wrasse (*Thallasoma duperrey*), and arc-eye hawkfish (*Paracirrhites arcatus*). Study species vary in their commercial value with four of the eight species heavily collected by aquarium collectors. Yellow tangs comprise the majority of the commercial aquarium fish harvest in West Hawaii (Williams et al. 2009).

Benthic habitat mapping

In 2005, we used the National Oceanic and Atmospheric Administration's (NOAA) hierarchical classification scheme for benthic habitats in Hawaii (Coyne et al. 2003), existing aerial photography, and *in situ* biological and physical observations using SCUBA to develop a map of reef habitats within our study sites. Visual interpretation of the habitat types was guided by a classification scheme using six categories of physical substrate, based on the lithology and geomorphology of the seafloor, and five categories of biological substrate (Ortiz and Tissot, 2008). Physical substrate categories were based on NOAA's benthic habitat map classification and included: U (unknown), B (colonized volcanic rock/boulder), A (aggregated coral), S (sand), P (pavement), T (scattered coral rock), and R (reef rubble) (Coyne et al. 2001). Biological substrates were based on previous underwater video surveys in West Hawaii (Tissot and Hallacher, 2003) and included: C finger coral (*Porites compressa*), L lobe coral (*P. lobata*), E cauliflower coral (*Pocillopora meandrina*), M mixed coral (denotes areas where the dominance of cauliflower, finger, and lobe coral varied), and u uncolonized.

Habitats 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 (\geq 50%) and secondary (>20% and <50%) biological substrate types, respectively (e.g., BEL represented at least 50% cover by boulders with at least 50% covered by cauliflower coral and at least 20% lobe coral). The major product of this effort is a digital benthic habitat map consisting of 14 habitat types and characterized by a 93% spatial and thematic accuracy (Ortiz and Tissot 2008). These habitat types were condensed into 3 distinct habitat categories based on their physical and biological similarities, so results would be more applicable to resource managers (Table 2).

Field Sampling design

The habitat map was used to assist in the development of a habitat-stratified fish sampling design. The location of sampling locations was determined using a stratified random sampling approach where random points were assigned to each of the mapped habitat categories.

The abundance and size of fishes were estimated between May and July, 2005 using circular plot counts. A SCUBA diver recorded the number and size of fishes seen within randomly selected 5 m radius circular plots (78 m² plot area). Fishes were categorized as recruits, juveniles or adults based on body size (TL) and/or coloration according to published sources (Walsh 1984, 1985; Randall 2007; Fish Base, <u>www.fishbase.org</u>) (Table 1). The circular plot method was chosen to easily randomize sample locations within a given depth strata, increase the replication in a given survey period due to quick deployment, and to spend a short period of time in a survey area, thereby decreasing bias estimates due to net movement of reef fish (Watson et al. 1995).

Depth, rugosity, and percent substrate cover were estimated within circular each plot using a 10 m transect line placed parallel to shore. Depth was recorded at the center, and at four 90° intervals around the edges of the circular plot. The 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. A ratio of length of tape divided by length of transect was used as an index of rugosity. An underwater digital camera was used to take 10 photoquadrats along each transect, 1 m above the substrate. Each of 1150 images was projected onto a rectangular grid using Photogrid software (Bird 2003) and percent cover for substrate types was quantified under 20 random points on each grid and included finger coral, lobe coral, cauliflower coral, sand, turf algae, turf algae on boulders, and turf algae on rubble.

We used Detrended Correspondence Analysis (DCA) to describe associations between the habitat category classifications (115 plots) and abundance of species (density of each life stage per plot). DCA produces a graphical ordination that shows the similarity between observations (habitat map types) and variables (fish life stage) derived from a frequency table (SAS Institute 2000). Observations that correspond in sampling space are close together in the ordination while the strength of the relationship between observations and variables is indicated by the direction of the points from the plot's origin (Pimentel 1979). Data for the DCA were derived by tabulating the abundance of recruits, juveniles, and adults within each circular plot at each site.

A series of ANOVAs and pair-wise comparisons were used to determine if the density of each life stage varied among habitat categories and sites. All data were checked for normality and equal variances and were transformed where appropriate. If the assumptions of normality and equal variances were not met, a non-parametric Kruskal-Wallis was employed with a Dunn's test for unplanned multiple comparisons (Zar 1984).. If the assumptions were met, a two-way ANOVA with Tukey's honestly significant difference (HSD, Zar 1984) for post hoc comparison test was used. Bonferroni adjustments were conducted to account for multiple statistical testing (Holm 1979), with a p-value of < 0.01 used for statistical significance.

To determine environmental variables influencing abundance and distribution of life stages we used Spearman's rank correlation coefficient. For all analyses, the relationship between the percent cover of all substrate types with the abundance of life stages for all species was explored.

To evaluate the relationship between MPA effectiveness and the abundance and distribution of habitats, we compared population density estimates of three species (goldring surgeonfish, black surgeonfish, and multiband butterflyfish) to percent area of habitat categories, reef area and length, between the Anaehoomalu and Honokohau MPAs. Population density estimates 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 this manner in order to account for the different shoreline lengths and reef structure from shore to depth in each site. The percent area of habitat categories represents the total percent area of habitat types belonging to each category. Both the reef area and length were calculated using ArcGIS 9.0 (ESRI 2002). In addition, we compared fish population size of the three managed species among sites. Population size estimates were calculated by multiplying the mean density ($\#/m^2$) of recruits, juveniles, and adults by the total reef area (m^2) sampled at each site.

RESULTS

A total of 115 sampling locations (Honokohau = 34, Puako = 27, Wawaloli = 24, and Anaehoomalu = 30) were surveyed along each habitat type (Table 3). Habitats with low coverage area and those exceeding 25 m depths were not sampled. We sampled within 70% of the reef area at each site. The Puako habitat map is given as an example to show sampling locations by habitat type (Fig. 2).

Ontogenetic habitat use of reef fish

A total of 786 recruits belonging to 4 species and 1,867 juveniles and 1,872 adults belonging to all 8 study species were observed at all study sites combined. All life stages were observed for four species and only juvenile and adult stages for the remaining species (Table 1).

DCA revealed significant associations among each of the life stages of fish species and habitat categories at each site (Fig. 3) (Chi square, all axes p < 0.01). The percent variation explained for the canonical dimensions was 22% and 11% for the first and second axes,

respectively. The first axis contrasted predominately deep coral rich areas with mid-depth aggregate reef and shallow, boulder and turf habitats; while the second axis was confounded by differences in the abundance of habitat categories among sites. Five species showed significant ontogenetic shifts in habitat use among life stages (Fig. 3). For yellow tang, goldring surgeonfish, brown surgeonfish, and multiband butterflyfish, recruits and juveniles were most abundant in deep aggregate coral-rich and sandy rubble habitats while adults were more abundant on shallow turf-rich boulder habitats along the reef flat. However, abundance of brown surgeonfish recruits did not overlap with the habitat used by the other three species; brown surgeonfish recruits were more abundant in the deeper rubble habitat along the reef slope. In addition, saddle wrasse juvenile abundance was highest on shallow turf-rich boulder habitats while adult abundance was highest on deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate reef and boulder habitats. Agile chromis, black surgeonfish, and arc-eye hawkfish displayed similar habitat use patterns at both juvenile and adult stages. The abundance of juvenile and adult agile chromis was highest at both deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate reef and boulder habitats along the reef slope. For black surgeonfish, juvenile and adult abundance was highest at deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate reef and boulder habitats along the reef slope. The abundance of juvenile and adult arc-eye hawkfish was highest in mid-depth aggregate reef and boulder habitats. Overall, most recruits and juveniles were associated with deep aggregate coralrich and sandy rubble habitats and mid-depth aggregate and boulder habitats while adults were associated with shallow turf-rich boulder habitats except for agile chromis and black surgeonfish. Among-habitat and site variation in the abundance of individual life stages by species Goldring and black surgeonfish

Densities of recruit and juvenile goldring surgeonfish were different among habitats (H = 23.4, p < 0.0001 for recruits; H = 4.98, p < 0.0001 for juveniles), but not among sites (Table 4). Post hoc comparisons indicated that densities of recruits and juveniles were both higher in deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate reef and boulder habitats, averaging $3.5 (\pm 5.0 \text{ SD})$ recruits and $7.8 (\pm 8.6 \text{ SD})$ juveniles and $2.8 (\pm 4.7 \text{ SD})$ recruits and $4.7 (\pm 6.6 \text{ SD})$ juveniles respectively, compared to shallow turf-rich boulder habitats, averaging $0.7 (\pm 2.7 \text{ SD})$ recruits and $0.5 (\pm 1.6 \text{ SD})$ juveniles. With adults, there was no interaction ($F_{6, 102} = 0.80$, p = 0.58) as densities were relatively low at all sites. Densities of juvenile and adult black surgeonfish were similar among habitats or sites (Table 4).

Brown surgeonfish

Densities of recruit brown surgeonfish were similar among habitat and sites (Table 4). However, there was an interaction as density of recruits was highest in deep aggregate coral-rich and sandy rubble habitats at Wawaloli ($F_{6, 102} = 3.02$, p < 0.01), but lower elsewhere. Post hoc comparison tests indicated that recruit density was higher (p < 0.05) at Wawaloli than at all other sites. Juvenile densities were similar among habitats or sites (Table 4) while adult densities were different among habitats (H = 11.1, p < 0.01), but not among sites (Table 4). Adult densities were higher at shallow turf-rich boulder habitats, averaging 4.5 (\pm 7.3 SD) adults, compared to deep aggregate coral-rich and sandy rubble habitats, averaging 1.0 (\pm 3.8 SD) adults, but not mid-depth aggregate reef and boulder habitats, which were similar to either deep aggregate coralrich areas and sandy rubble habitats or shallow turf-rich boulder habitats.

Multiband butterflyfish

Densities of recruit multiband butterflyfish were similar among habitats or sites (Table 4) while the density of juveniles was different among habitats (H = 11.0, p < 0.01), but not sites.

Post hoc comparisons indicated that juveniles were higher in deep aggregate coral-rich and sandy rubble habitats, averaging $0.79 (\pm 1.5 \text{ SD})$ juveniles, compared to shallow turf-rich boulder habitats, averaging $0.1 (\pm 0.4 \text{ SD})$ juveniles, while mid-depth aggregate reef and boulder habitats did not differ from deep aggregate coral-rich and sandy rubble habitats and shallow turf-rich boulder habitats (Table 4). Analyses on adult multiband butterflyfish was not possible due to low sample size.

Agile chromis

Juvenile densities of agile chromis were similar among sites while those of the adults were similar among sites and habitats (Table 4). Juvenile densities were different among habitats (H = 19.1, p < 0.01). However, post hoc comparisons did not detect any differences in juvenile densities among habitats due to the fact that juveniles were not found on shallow turf-rich boulder habitats while 2.0 (\pm 5.1 SD) and 0.1 (\pm 0.6 SD) juveniles were found on deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate reef and boulder habitats respectively.

Saddle wrasse and arc-eye hawkfish

Densities of juvenile and adult saddle wrasse were different among habitats (H = 15.3, p < 0.0001 for juveniles; $F_{2, 102} = 5.46$, p < 0.01 for adults), but not sites (Table 4). Post hoc comparisons indicated that juveniles were higher in shallow turf-rich boulder habitats, averaging 1.8 (± 2.6 SD) juveniles, compared to deep aggregate coral-rich and sandy rubble habitats, averaging 0.2 (± 0.4 SD) juveniles, but not mid-depth aggregate reef and boulder habitat, which were similar to deep aggregate coral-rich and sandy rubble habitats. Post hoc comparisons indicate that adults were higher at shallow turf-rich boulder habitats, averaging 5.1 (± 3.9 SD) adults, compared to deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate

reef and boulder habitats, averaging 3.4 (\pm 3.5 SD) and 2.5 (\pm 1.7 SD) adults respectively, but no differences between deep aggregate coral-rich and sandy rubble habitats and mid-depth aggregate reef and boulder habitats were detected. Densities of juvenile and adult arc-eyed hawkfish were similar among habitats or sites (Table 4).

Environmental variables influencing abundance and distribution of life stages

The abundance of juvenile goldring surgeonfish and agile chromis and adult chevron tang were positively correlated with percent cover of finger coral (r = 0.24 - 0.43, p < 0.01) while juvenile and adult brown surgeonfish, adult agile chromis, and juvenile saddle wrasse were negatively correlated with percent cover of finger coral (r = 0.23 - 0.27, p < 0.02). Recruit goldring surgeonfish, juvenile brown surgeonfish, and adult saddle wrasse were positively correlated with lobe coral (r = 0.19 - 0.23, p < 0.04). The abundance of juvenile agile chromis was positively correlated with cauliflower coral (r = 0.30, p < 0.01). Juvenile brown surgeonfish, saddle wrasse, and arc-eye hawkfish and adult brown surgeonfish and arc-eye hawkfish were negatively correlated with cauliflower coral (r = 0.19 - 0.25, p < 0.04). Adult arc-eye hawkfish was positively correlated with sand (r = 0.20, p < 0.02). Juvenile saddle wrasse and adult brown surgeonfish and saddle wrasse were positively correlated with turf on boulders (r = 0.19 - 0.34, p < 0.03). Recruit goldring surgeonfish and multiband butterflyfish and juvenile goldring surgeonfish were negatively correlated with turf on boulders (r = 0.21 - 0.21) 0.41, p < 0.02). Recruit brown surgeonfish, juvenile arc-eye hawkfish, and adult saddle wrasse and arc-eye hawkfish were positively correlated with turf on rubble (r = 0.23 - 0.40, p < 0.01).

Comparisons of MPA characteristics and population density of managed species

The population density of recruit, juvenile, and adult goldring surgeonfish, black surgeonfish, and multiband butterflyfish varied among MPAs (Fig. 4). Overall, sites having deeo-coral rich

and sandy rubble habitats, mid-depth aggregate reef and boulder habitats, and shallow turf-rich boulder habitats (habitat used by recruit, juvenile, and adult reef-fish) and large areas of these habitats had the highest densities of recruits, juveniles, and adults. For instance, Anaehoomalu, with the largest area of habitats used by recruits, juveniles, and adults on the reef, had the highest density of recruit, juvenile, and adult goldring surgeonfish and juveniles of multiband butterflyfish and black surgeonfish while Puako, Wawaloli, and Honokohau, with smaller areas of these habitats, had the lowest density of juvenile multiband butterflyfish, adult black surgeonfish, and all life stages of goldring surgeonfish, and recruit and adult multiband butterflyfish and juvenile black surgeonfish respectively. In other words, sites with greater abundance of recruit, juvenile, and adult habitats and large areas of these habitats on the reef had the highest densities of individuals using these habitats. For example, the highest recruit, juvenile, and adult density of most species was found in Anaehoomalu and Puako. In Anaehoomalu, 87% of the total reef area consisted of recruit and juvenile habitat, and 13% of the total reef area of adult habitat while 32% and 68% of the total reef area of Puako consisted of recruit and juvenile, and adult habitats respectively (Fig. 4). On the other hand, Honokohau and Wawaloli, with smaller reefs and less than 32% of the total reef area consisting of recruit and juvenile habitat had the lowest density of recruit and juvenile life stages of most species.

Reef-fish habitat and MPA effectiveness

Sites with large areas of recruit, juvenile, and adult habitat, supported a larger number of recruits, juveniles, and adults for goldring surgeonfish, black surgeonfish, and multiband butterflyfish. For example, Anaehoomalu and Puako, with the largest area of appropriate recruit, juvenile, and adult habitat, supported a larger population of life stages for most species (Fig. 5). On the other hand, Honokohau and Wawaloli, with smaller areas of recruit, juvenile, and adult
habitats on the reef, supported the lowest number of multiband butterflyfish and black surgeonfish recruits and recruit, juvenile, and adult goldring surgeonfish and adult black surgeonfish, respectively.

Differences in the reef area and length and abundance of appropriate habitats used by recruit, juvenile, and adult reef-fish were found between two MPAs that show different levels of replenishment (Fig. 4, 5). The effective Anaehoomalu MPA was associated with large and wide reefs with 87% of the total reef area consisting of recruit and juvenile habitat and 13% adult habitat. In addition, the MPA supported the greatest number of recruits, juveniles, and adults for black surgeonfish, multiband butterflyfish, and goldring surgeonfish, except for adult multiband butterflyfish and black surgeonfish (Fig. 5). In contrast, the ineffective Honokohau MPA, with 6%, 26%, and 68% of the total reef area consisting of recruit, juvenile, and adult habitat respectively, had a lower number of recruits, juveniles, and adults for all three species.

DISCUSSION

Effectiveness of MPAs

Overall, comparisons of habitat utilization patterns for all species illustrates habitats important to the individual life stages of reef-fish species based on the physical structure (e.g., boulder, aggregate, rubble), biological substratum (e.g., finger coral) and depth (e.g., shallow) they afforded. For example, deep aggregate coral-rich areas and rubble substrates adjacent to shallow turf-rich boulder habitats at various depths (i.e., 0-30m) were used by all our study species, highlighting areas that are essential to protected and endemic fish species in Hawaii. Identification and delineation of habitats is necessary for the designation of conservation areas and MPAs are more effective at protecting reef-fish species if they incorporate important habitats (Sala et al. 2002). Therefore, we would expect that MPAs that incorporate the range of habitats utilized by managed species would be more effective at accomplishing their conservation goals. Our findings in West Hawaii, show that appropriate habitat type for early life history stages of fish species, large areas of these habitats on the reef, and proximity of appropriate recruit, juvenile, and adult habitats were associated with an effective MPA. The Anaehoomalu MPA with the largest reef area and high abundance of recruit, juvenile, and adult habitats, supported larger populations of life stages (multiband butterflyfish, black surgeonfish, and goldring surgeonfish) while the ineffective Honokohau MPA had a smaller area of habitats used by all life stages and proportionally smaller areas for juveniles and adults. This discrepancy between the abundance of important habitat and early life stages of reef-fish among sites was also reported for yellow tang (Ortiz and Tissot 2008).

Part of the differences in abundance among sites is related to variability in recruitment. Recruitment variability among sites could be the result of several factors such as, differential larval-supply due to currents, movement, inter-specific competition, and differential postsettlement mortality due to predation (Jones 1991, Hixon 1991). Although recruitment varied spatially, previous studies have shown that these species have similar recruitment patterns (Walsh 1987), and that these patterns have been consistent among sites from year to year (Tissot, B.N, and Walsh, W.J., unpublished data). A more detailed study is required to test these hypotheses, before any conclusion on the variability in recruitment can be made.

Ontogenetic habitat shifts

Reef fishes often shift habitats in ways that meet the demands of foraging, avoiding predators, or reproducing (Dahlgren and Eggleston 2000). Our findings reveal distinct patterns of ontogenetic habitat use among reef fishes in West Hawaii. First, four species (yellow tang,

goldring surgeonfish, brown surgeonfish, and multiband buttlerflyfish) showed similar ontogenetic shifts in habitat use by using deep aggregate coral-rich areas as recruits and juveniles and shallow turf-rich boulder habitats as adults. Second, three species (agile chromis, black surgeonfish, and arc-eye hawkfish) used similar habitats among both juvenile and adult life stages by remaining in mid-depth aggregate reef and boulder habitats. For example, in Moorea, 12 of the 20 most abundant species settled in specific areas and later migrated to different habitats as adults while some used the same habitats during the juvenile and adult stages (Lechini and Galzin 2005). Third, the saddle wrasse exhibited contrasting shifts in habitat use by using shallow turf-rich boulder habitats as juveniles and deep aggregate coral-rich areas as adults. In Palau, this pattern has also been demonstrated in the humphead wrasse (*Cheilinus undulates*), a major component of the life fish trade, where juveniles who had originally settled in shallow habitats had shifted unto deeper patch reefs as they mature (Tupper 2007).

Live finger, cauliflower, and lobe coral substrates were found to be essential to newly recruited and juvenile yellow tang, goldring surgeonfish, and multiband butterflyfish, adult black surgeonfish, and juvenile agile chromis as they were significantly more abundant in deep coral-rich areas and/or positively correlated with the abundance of these coral types (Tissot et al. 2003; Ortiz and Tissot 2008). In Hawaii, the structural complexity of reefs made of finger, cauliflower, and lobe coral has been found to support a high species richness and fish abundance by providing a variety of rich microhabitats important to fish (Friedlander and Parrish 1998; Friedlander et al. 2003). Similar findings have been found in lagoons at Moorea where structurally complex patch reefs composed of *Porites* coral were found to support a high diversity and abundance of fish by providing surface branches and crevices for a variety of fish to occupy (Brook et al. 2007). Recruits of the brown surgeonfish, however, displayed strong

preferences for coral rubble, as they were significantly more abundant at sites with a higher aerial cover of deep, reef slope rubble habitats and abundance of rubble overgrown with turf substrate. The importance of coral rubble habitat has been demonstrated for other managed species where rubble areas have been used as nursery habitats for commercially valuable reef fishes in Palau (Tupper 2007). We expected brown surgeonfish, with similar life history traits as other surgeonfish species, to occupy areas similar to yellow tang and brown surgeonfish, but, in fact, the opposite was true. Brown surgeonfish have been found to be higher in those areas of lower yellow tang and goldring surgeonfish abundance and in lower abundance where these surgeonfish species were abundant. Thus, other possible reasons why brown surgeonfish, with similar life history traits as other surgeonfish, settle in rubble habitat might be due to interspecific competition, resulting in the displacement of brown surgeonfish to areas with a lower abundance of recruit and juvenile yellow tang and/or goldring surgeonfish.

Shallow areas with boulders overgrown with turf substrate were found to be important habitat for juvenile and adult saddle wrasse and adult brown surgeonfish, as they were significantly more abundant in aerial cover of boulder areas and positively correlated with turfalgae substrate. These findings are consistent with other studies in Hawaii, where brown surgeonfish and saddle wrasse have been show to be dominant at shallower depths (Friedlander et al. 2003). The abundance and distribution of our study species was consistent among sites, with reef-fish strongly associated with features of the habitat at multiple spatial scales (e.g. finger coral, areas of shallow turf-rich boulder habitats). Thus, the abundance and distribution of reeffish is largely influenced by their association with features of the reef (e.g., finger coral cover, areas of shallow turf-rich boulder habitats) throughout their life.

CONCLUSIONS

In conclusion, the identification and mapping of fish habitat utilization is critical to prioritizing habitats for conservation and designing MPAs. Information on habitat use is uncommon due to the difficulty of determining the habitat requirements for multiple species at multiple spatial scales, and consequently, few MPAs include habitats important to all life stages of the targeted species. Our study addresses several gaps in the design of MPAs. Firstly, it provides a method to map and quantify the habitat use of multiple life history stages. Secondly, it identifies habitats important to vulnerable life stages of reef fish species of high commercial and cultural value. Thirdly, it provides a method to evaluate the influence of the availability and distribution of these habitats on the effectiveness of MPAs in replenishing targeted fish populations. Lastly, it identifies habitats that should be incorporated in the design and management of existing and future MPAs, and taken into account for future land-use planning and coastal development in tropical regions. Current efforts are focused on monitoring all nine existing MPAs to evaluate the effectiveness of the reserve network as a fishery management tool.

Table 1. Characteristics of reef fish species used in study.

Code	Family	Common	Trophic	Recruit ^b	Juvenil	Adult ^b	Commercial
		name	level		e ^b		value ^c
	Acanthurid						
	ae						
YT	Zebrasoma	yellow	Herbivo	color,	5 – 14	>15 cm	High
	flavescens	tang	re	shape, < 5 cm	cm		
GS	Ctenochaetu	goldring	Herbivo	color.	5 – 14	> 15 cm	High
	s strigosus ^a	surgeonfi	re	shape.	cm		8
	0	sh		$< 5 \mathrm{cm}$			
BS	Ctenochaetu	black	Herbivo		Color	Color	High
	S	surgeonfi	re				C
	hawaiiensis ^a	sh					
BrS	Acanthurus	brown	Herbivo	color,	5 - 14	> 15 cm	Low
	nigrofuscus	surgeonfi	re	shape,	cm		
		sh		< 5 cm			
	Chaetodont						
	idae						
MB	Chaetodon	multiban	Coralliv	shape,	5 - 14	> 14 cm	High
	multicinctus	d	ore	< 5 cm	cm		C
		butterflyf					
		ish					
	Pomacentri						
	dae						
AC	Chromis	agile	Planktiv		< 3 cm	> 3 cm	Low
	agilis	chromis	ore				
	Labridae						
SW	Thallasoma	saddle	Carnivor		< 5 cm	> 5 cm	Low
	<i>duperrey</i> ^a	wrasse	e				
	Cirrhitidae						
AH	Paracirrhite	arc-eyed	Carnivor		< 5cm	> 5 cm	Moderate
	s arcatus	hawkfish	e				

^aEndemic species.

^bCharacteristics used to distinguish recruits, juveniles, and adults. Information for recruits of some species was not available.

^cBased on Walsh et al. (2003)

Table 2. Description of pooled habitat types using the classification scheme in Ortiz and Tissot (2008): 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.

Habitat Category	Description	Habitat Types Included	Reef Zone	Depth Range (1
1	Deep aggregate coral-rich and sandy rubble habitats	ACL, ALC, AM, Ru, S	Reef slope	5-40
2	Mid-depth aggregate reef and boulder habitats	ALE, AEL, BLL, BLE	Reef slope and Boulder	5-25
3	Shallow turf-rich boulder habitats	BEL, PEL, Bu, Pu, Tu	Boulder & Reef flat	0-11

3. Percent area, reef length, and sampling allocation for habitat types at each study site per habitat category. N is the total number of circular plots completed. Numbers in bold indicate the total % area coverage and sampling per habitat category per site.

Site	Habitat	Habitat code	Percent area	N	
	category	iluoitut oodo	i creent area	11	
Puako	1	S	0.95	-	
		Ru	2.01	-	
		ACL	21.0	12	
		Total Habitat 1	24.0	12	
	2	AEL	8.68	3	
		Total Habitat 2	8.68	3	
	3	BEL	15.7	8	
		Tu	2.61	-	
		PEL	2.56	-	
		Bu	46.5	4	
		Total Habitat 3	67.4	12	
Total Area (ha)			104	27	
Anaehoomalu	1	S	30.0	2	
		ACL	12.0	9	
		AM	4.50	8	
		ALC	1.52	-	
		Total Habitat 1	48.2	19	
	2	ALE	16.5	5	
		AEL	8.19	-	
		BLE	15.9	-	
		Total Habitat 2	40.6	5	
	3	BEL	<1.00	6	
		Bu	12.1	-	
		Total Habitat 3	12.0	6	
Total Area (ha)			524	30	
Wawaloli	1	Ru	6.00	2	
		AM	1.00	3	
		Total Habitat 1	7.00	5	
	2	BLE	7.00	3	
		Total Habitat 2	7.00	3	
	3	BEL	49.0	10	
		PEL	27.9	5	
		Pu	8.67	-	
		Total Habitat 3	85.6	15	
Total Area (ha)			36.1	23	
Honokohau	1	S	2.00	-	
	-	Ru	2.00	-	
		AM	2.00	8	
		Total Habitat 1	6.00	8	
	2	BLL	26.0	11	
	-		= - • • •		

Total Area (ha)			112	35
		Total Habitat 3	68.0	16
		Bu	<1.00	-
		Pu	28.0	-
		PEL	29.0	8
	3	BEL	11.0	8
		Total Habitat 2	26.0	11

Species	Life Stage	Test	df	Site (S)	Habitat (H)	S*H

Table 4. Results of ANOVA and Kruskal-Wallis tests comparing the density of recruits, juvenile, and adults for seven reef-fish species among study sites and habitats. KW and TA indicate where a Kruskal-Wallis and a two-way ANOVA were conducted, respectively. S*H represents site x habitat interactions. Bold p-values are those significant at p < 0.05.

goldring	recruit	KW		H = 5.2	H = 23.4	
surgeonfish			_	p = 0.15	p < 0.0001	_
	juvenile	KW	_	H = 4.98	H = 30.0	_
			_	p = 0.17	p < 0.0001	_
	adult	TA	6, 102	F = 1.80	F = 0.25	F = 0.80
				p = 0.15	p = 0.78	p = 0.58
black	juvenile	TA	6,102	F = 0.82	F = 0.68	F = 2.04
surgeonfish				p = 0.48	p = 0.51	p = 0.06
	adult	TA	6, 102	F = 0.36	F = 0.39	F = 0.56
				p = 0.79	p = 0.68	p = 0.76
brown	recruit	TA	6, 102	F = 2.62	F = 2.62	F = 3.02
surgeonfish				p = 0.05	P = 0.07	p < 0.01
	juvenile	TA	6, 102	F = 0.77	F = 1.47	F = 1.91
				p = 0.51	p = 0.23	p = 0.08
	adult	KW	_	H = 0.59	H = 11.1	_
				p = 0.89	p < 0.01	
multiband	recruit	KW	_	H = 2.92	H = 5.08	_
butterflyfish				p = 0.40	p = 0.07	
	juvenile	KW	_	H = 6.42	H = 11.0	_
				p = 0.09	p < 0.01	
agile chromis	juvenile	KW	_	H = 4.26	H = 19.13	_
				p = 0.23	p < 0.01	
	adult	KW	_	H = 2.20	H = 14.82	_
				p = 0.53	P = 0.19	
saddle wrasse	juvenile	KW	_	H = 5.87	H = 14.82	_
				p = 0.12	p < 0.0001	
	adult*	TA	2, 102	F = 2.43	F = 5.46	F = 1.85
				p = 0.07	p < 0.01	p = 0.09
arc-eye	juvenile	KW	_	H = 6.20	H = 5.05	_
hawkfish				p = 0.10	p = 0.08	
	adult*	TA	6, 102	F = 1.45	F = 0.13	F = 0.96
				p = 0.23	p = 0.87	p = 0.45

* Indicates where a log (x+1) transformation was used.

FIGURE CAPTIONS

Figure 1. Location of study areas along the west coast of the island of Hawaii. Boundaries represent area extending from the highwater mark on shore to a depth of 600ft Figure 2. Sampling locations and benthic habitat map of the Puako MPA study area. Figure 3. Ordination of habitats: (A) relative to recruits, juveniles, and adults of eight species at all study sites (B) on the two axes of the detrended correspondence analysis. Species are coded by their common name: goldring surgeonfish (GS), black surgeonfish (BS), brown surgeonfish (BrS) multiband butterflyfish (MB), agile chromis (AC), saddle wrasse (SW), arc-eye hawkfish (AH). Arrows indicate direction of ontogenetic shift in habitat use of recruits, juveniles, and adults for each species.

Figure 4. Percentage (mean + SE) of habitats and reef area and length of MPAs relative to population sizes corrected for length of three managed species: goldring surgeonfish (GS), black surgeonfish (BS), and multiband butterflyfish (MB). Underlined numbers indicate highest observed recruit, juvenile, and adult density of each species among sites.

Figure 5. Population size of recruits, juveniles, and adults of goldring surgeonfish (GS), black surgeonfish (BS), and multiband butterflyfish (MB) at each study site. Sites are ordered from north to south (left to right). Underlined numbers indicate greatest observed number of recruits, juveniles, and adults for each species among sites.

FIGURES









- Deep aggregate coral-rich and sandy rubble habitats (ACL, ALC, AM, Ru, S) $oldsymbol{\circ}$
- Mid-depth aggregate reef and boulder habitats (ALE, AEL, BLL, BLE)
- Δ Shallow turf-rich boulder habitats (BEL, PEL, Bu, Pu, Tu)



Deep aggregate coral-rich and sandy rubble habitat
Mid-depth aggregate reef and boulder habitat
Shallow turf-rich boulder habitat



Reef area (ha)	104.3	524.8	36.1	112.5
Length (km)	3.3	6.8	2.0	2.7



Fig. 4



Fig. 5

REFERENCES

- Bird, C. 2003. Ecological analysis of digital photographs. Available from http://www.photogrid.netfirms.com [accessed 3 October 2005].
- Botsford, L.W., Micheli, F., Hastings, A. 2003. Principles for the design of marine reserves. Ecol. Appl. Suppl. **13** (1): S25-S31.
- Brook, A.J., Holbrook, S.J., Schmitt, R.J. 2007. Patterns of microhabitat use by fishes in the patch-forming coral *Porites rus*. Raffles. B. Zool. Suppl. **14**: 245-254.
- Capitini, C.A., Tissot, B.N., Carroll, M.S., Walsh, W.J., and Peck, S. 2004. Competitive Perspectives in Resource Protection: The Case of Marine Protected Areas in West Hawaii. Soc. Natur. Resour. 17: 763-778.
- Christensen, J.D., Jeffrey, C.F.G., Caldow, C., Monaco, M.E., Kendall, M.S., and Appledorn, R.S. 2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf Car. Res. 14 (2): 9-27.
- Cook, R.R., and Auster, P.J. 2007. Use of Simulated Annealing for Identifying Essential Fish Habitat in a Multispecies Context. Conserv. Biol. 19 (3): 876-886.
- Coyne, M.S., Monaco, M.E., Anderson, M., Smith, W., and Jokiel, P. 2001. Classification scheme for benthic habitats: main eight Hawaiian Islands Biogeography program. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Silver Spring, M.D.
- Coyne, M. S., Battista, T.A., Anderson, M., Waddell, J., Smith, W., Jokiel, P., Kendall, M.S., and Monaco, M.E. 2003. NOAA Technical Memorandum NOS NCCOS CCMA 152 (On-line). Benthic Habitats of the Main Hawaiian Islands. Available from http://biogeo.nos.noaa.gov/projects/mapping/pacific/. Silver Spring, M.D: National Oceanic and Atmospheric Administration.
- Dahlgren, C.P., and Eggleston, D.B. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology. **81**(8): 2227-2240.
- Department of Land and Natural Resources (DLNR). 1996. Hawaii fishing regulations Division of Aquatic Resources, DLNR, Honolulu, H.I.
- Eggleston, D.B. 1995. Recruitment in Nassau grouper *Epinephelus striatus*: post-settlement abundance, microhabitat features, and ontogenetic habitat shifts. Mar. Ecol. Prog. Ser. **124**: 9-22.
- ESRI. 2002. Environmental Science Research Institute: ET Spatial Techniques: ET GeoWizards for ArcGIS, Pretoria, South Africa.
- Friedlander, A.M., and Parrish, J.D. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian Reef. J. Exp. Mar. Biol. Ecol. **224**: 1-30.

- Friedlander, A.M., Brown, E.K., Jokiel, P.L., Smith, W.R., and Rodgers, KS. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22: 291-305.
- Friedlander, A.M., Brown, E., and Monaco, M.E. 2007. Coupling Ecology and GIS to Evaluate Efficacy of Marine Protected Areas in Hawaii. Ecol. Appl. **17**(3): 715-730.

Gladstone, W. 2007. Requirements for marine protected areas to conserve the biodiversity of rocky reef fishes. Aquat. Conserv. **17**: 71-87.

- Hastings, A., and Botsford, L.W. 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science. **284**: 1537-1538.
- Hixon, M.A. 1991. Predation as a process structuring coral-reef fish communities. Pages 475-508. *In* P.F. Sale (ed.) The Ecology of Fishes on Coral Reefs. Academic Press; San Diego, C.A.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. Scan. J. Stat. 6: 65-70.
- Jones, G.P. 1991. Postrecruitment Processes in the Ecology of Coral Reef Fish Populations: A Multifactorial Perspective. Pages 294-328. *In* The Ecology of Fishes on Coral Reefs. P. Sale (ed). Academic Press, Inc., San Diego, C.A.
- Lecchni, D., and Galzin, R. 2005. Spatial repartition and ontogenetic shifts in habitat use by coral reef fishes (Moorea, French Polynesia). Mar. Biol. 147 (1): 47-58.
- Lecchini, D. 2006. Highlighting ontogenetic shifts in habitat use by nocturnal reef-fish. C. R. Biol. **329** (4): 265-270.
- Murray, S.N., Ambrose, R.E., Bohnsack, J.A., Botsford, L.W., Carr, M.H., Davis, G.E., Dayton, P.K., Gotshall, D., Gunderson, D.R., Hixon, M.A., Lubchenco, J., Mangel, M., MacCall, A., McArdle, D.A., Ogden, J.C., Roughgarden, J., Starr, R.M., Tegner, M.J., and Yoklavich, M.M.1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. Fisheries 24: 11-25.
- Ortiz, D.M., and Tissot, B.N. 2008. Ontogenetic Patterns of Habitat Use by Reef-Fish in an MPA Network: A Multi-Scaled Remote Sensing and In-Situ Approach. Mar. Ecol. Prog. Ser. 365: 217-232.
- Pimentel, R.A. 1979. Morphometrics, the multivariate analysis of biological data. Kendall-Hunt, Dubuque.
- Randall, J.E. 2007. Reef and shore fishes of the Hawaiian Islands University of Hawai'i Sea Grant College Program, Honolulu, H.I.

- Roberts, C.M. 1995. Rapid build-up of fish biomass in a Caribbean marine reserve. Conserv. Biol. **9**: 816-826.
- Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H.P., Ruckelshaus, M., and Warner. R.R. 2003. Ecological criteria for evaluating candidate sites for marine reserves. Ecol. Appl. 13: S199–S214.
- Sala, E., Aburto-Oropeza, O., Paredes, G., Parra, I., Barrera, J.C., and Dayton, P.K. 2002. A general model for designing networks of marine reserves. Science **298**: 1991-1993.
- Sale, E., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C., Planes, S., Polunin, N.V.C., Russ, G.R., Sadovy, Y.J., and Steneck, R.S. 2005. Critical science gaps impede use of no-take fishery reserves. Trends. Ecol. Evol. 20 (2): 74-80.
- SAS Institute. 2000. JMP Statistics and Graphics Guide. Version 4.00 SAS Institute Inc, Cary, N.C., U.S.A.
- Syms, C. 1995. Multi-scale analysis of habitat association in a guild of blennoid fishes. Mar.Ecol. Prog. Ser. **125**: 31-43.
- Tissot, B.N., and Hallacher, L.E. 2003. The effects of aquarium collectors on coral reef fishes in Hawaii. Conserv. Biol. 17(6): 1759-1768.
- Tissot, B.N., Walsh, W.J., and Hallacher, L.E. 2003. Evaluating the effectiveness of a marine reserve in West Hawaii to improve management of the aquarium fishery. NOAA Technical Report.
- Tissot, B.N., Walsh, W.J., and Hallacher, L.E. 2004. Evaluating the effectiveness of a marine reserve network in Hawaii to increase the productivity of an aquarium fishery. Pac. Sci. 58 (2): 175-188.
- Tupper, M. 2007. Identification of nursery habitats for commercially valuable humphead wrasse *Cheilinus undulates* and large groupers (Pisces: Serranidae) in Palau. Mar. Ecol. Prog. Ser. 332: 189-199.
- Walsh, W.J. 1984. Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. PhD dissertation, University of Hawaii, Honolulu, H.I.
- Walsh, W.J. 1985. Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. Bull. Mar. Sci. 36: 357-376.
- Walsh, W.J. 1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Environ. Biol. Fish. 18 (4): 257-276.

- Walsh, W.J., Cotton, S.P., Dierking, J., and Williams, I.D. 2003. The Commercial Marine Aquarium Fishery in Hawai'i 1976-2003. In Friedlander A.M. (ed) Status of Hawai'i's Coastal Fisheries in the New Millennium. Proceedings of a Symposium sponsored by the American Fisheries Society, Hawai'i Chapter. pp. 132-159.
- Walsh, W.J., Tissot, B.N., and Hallacher, L.E. 2004. A Report on the Finding and Recommendations of Effectiveness of the West Hawaii Regional Fishery Management Area. Department of Land and Natural Resources, Honolulu, H.I.
- Ward, T.J., Vanderklift, M.A., Nicholls, A.O., and Kenchington, R.A. 1999. Selecting Marine Reserves Using Habitats and Species Assemblages as Surrogates for Biological Diversity. Ecol. Appl. 9 (2): 691-698.
- Watson, R.A., Carlos, G.M., and Samoilys, M.A. 1995. Bias introduction by the non random movement of fish in visual transect surveys. Ecol. Model. 77: 205-214.
- Williams, I. D., W.J. Walsh, J. T. Claisse, B.N. Tissot, K. A. Stamoulis. 2009. Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. Biological Conservation 142: 1066-1073.
- Wood, E.M. 1985. Exploitation of coral reef fishes for the aquarium trade. Marine Conservation Society, Herefordshire, U.K.
- Zar, J.H. 1984. Biostatistical analysis. Prentice Hall, N.J.

MANUSCRIPT 3:

EVALUATING THE EFFICACY OF AN MPA NETWORK DESIGN IN HAWAII

Abstract

We examined the spatial characteristics of coral reefs associated with an effective network of marine protected areas (MPAs) in West Hawaii. The geomorphology of protected reefs, area and number 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 collected aquarium species in Hawaii. Locations with large areas rich in living coral and turfcovered boulders at a range of depths, as well as retention features important for settlement, juvenile survivorship, and adult reproduction supported higher abundances of each of the life stages of yellow tang. Furthermore, recruitment rate and years of closure influenced the effectiveness of the network, with MPAs receiving consistent recruitment showing significant increases of yellow tang as years of protection increased. Guidelines for designing MPA networks should depend on the life history and spatial requirements of the species being protected. Consequently, 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.

INTRODUCTION

There is increasing concern over the decline of coral reef ecosystems (Pandolfi et al. 2005), especially for species targeted by the marine ornamental fish trade (Wood 1985, Tissot and Hallacher 2003). As a result, marine protected areas (MPAs) are increasingly being used as a tool for ecosystem-based fisheries management (Hastings and Botsford 1999, Roberts et al. 2001). Although the number of MPAs has increased, there have been a concomitant increase in our understanding and development of a general theory about MPA effectiveness and design (Agardy 2000, Jameson et al. 2002, Sala et al. 2002, McLeod et al. 2009).

Evaluation of the effectiveness of MPAs in relation to fisheries conservation has been widely studied yet very few attempts have been made to determine the sources of variability that result in some managed areas failing to meet their target goals (Botsford et al. 2003). Several studies have documented the many benefits of MPAs, including the increase in abundance of harvested fishes within MPA boundaries and the enhancement of fishes in outside areas by spillover (Roberts and Polunin 1991, Russ and Alcala 1996, Russ 2002, Halpern 2003) and seeding (Almany et al. 2007, Planes et al. 2009). However, other empirical studies have shown that some MPAs have either positive or no effects on fish populations (Gerber et al. 2002, Russ 2002, Halpern 2003, Baskett et al. 2007, Claudet et al. 2008). The reason why some MPAs appear to be effective and others do not is largely unknown, which has resulted in a paucity of information on which resource managers can base MPA design (Botsford et al. 2003).

Previous studies have relied on modeling to develop criteria on which to base MPA design. For example, some theoretical studies suggest that MPAs are more effective if they include key spatial characteristics such as large areas of habitat important to the life history of managed species (Sala et al. 2002, Botsford et al. 2003, Roberts et al. 2003, Baskett et al. 2007). Empirical support for these hypotheses, however, is limited as data are rarely collected before the establishment of MPAs, hindering any unequivocal measure of the effect of an MPA based on before-after comparisons (Underwood 1992, Botsford et al. 2003). In addition, data on the spatial abundance and distribution of important habitats to managed species within MPAs are often limited, making it difficult to compare the spatial design of MPAs (Sale et al. 2005). As a result, few studies are able to empirically compare the efficacy of different MPA designs in augmenting

fish populations. In order to ensure the effective ecosystem management and design of future MPAs, knowledge of the combination of key spatial characteristics of MPAs that result in productive fish populations within their boundaries is needed.

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 fish replenishment areas, were closed 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. The West Hawaii MPA network, combined with pre-existing MPAs, prohibits aquarium collection along 35.2% of the coastline. Continuous monitoring in the nine fish replenishment areas and control areas (MPAs that have been closed for more than 20 years) before and after implementation 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) and larval seeding (Christie et al. in review). 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.

Incorporating key spatial characteristics of the reef in the design of protected areas is difficult. This is because coral reef fishes associate with distinctive features of the reef at multiple spatial scales (Levin 1991), that often change with ontogeny (Dahlgren and Eggleston 2000). Previous studies have shown that reef fishes can associate with large-scale (1-10km) features, such as the geometry and size of the reef, mid-scale (10km-1km) features, such as swaths of continuous habitat types, or small scale (1-10m) features, such as substrate cover and rugosity (Friedlander and Parrish 1998, Christensen et al. 2003, Syms and Jones 2004). Even though reef fishes are often site-attached following settlement (Sale 1991) they often move from tens to hundreds of meters as they mature; when reproductively active, they can move hundreds of meters daily between sheltering and foraging locations (Walsh 1984). The use of landscape (meters to 10's of kilometers) metrics serves as an important tool for examining benthic landscapes in relation to reef-fish abundance and MPA design at all three spatial scales (1-10km, 10-100'm, and 1-10km) (Grober-Dunsmore et al. 2007).

The purpose of this study was to apply commonly used landscape metrics to investigate relationships between targeted species and the spatial characteristics of reefs in relation to the effectiveness of the MPA network in West Hawaii. Monitoring data spanning nine years (one year prior to the establishment of the network and eight years post-closure) were collected and MPA effectiveness was measured as the absolute percent change in reef-fish density inside MPAs relative to protected reference areas before and after closure (Walsh et al. 2004). The data also included information on the spatial characteristics of the reef within MPAs, using Geographic Information Systems (GIS) and landscape metrics. Therefore, these data allow for a rigorous empirical evaluation of the spatial characteristics of the reef that results in the effective replenishment of aquarium fish populations within an MPA network.

METHODS

Study area and species

The network of nine fishery replenishment areas along the West Hawaii coastline was examined (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 aquarium species which constitutes about 80% by number and 70% by value of aquarium landings from West Hawaii (Williams et al. 2009). Yellow tang is 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).

Reef geomorphology and benthic habitat mapping

Geomorphology of the reef within each of the study sites was described by previous studies (Dollar 1982, Gibbs and Cochran 2009) and by 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). 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.2). 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 1045m². 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 (B) with at least 50% covered by cauliflower coral (E) and at least 20% lobe coral (L). 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 three 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 (DC), (2) mid-depth aggregate reef and boulder habitats (MB), and (3) shallow turf-rich boulder habitats (ST) (Table 1).

Accuracy of the benthic habitat map was quantified using an error matrix, where rows and columns represented each of the reef habitat types from the benthic habitat map and field observations respectively. Each cell represented the total sites sampled for that particular reef habitat type . In 2005 and 2007, respectively, a total of 90 and 115 accuracy assessments sites

were randomly sampled within mapped reef habitat types. 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. 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 from 92% for MPAs mapped in 2005 (Anachoomalu and Honokohau) (Ortiz and Tissot 2008) to 93% in 2007 (for remaining MPAs). Assessments of 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%).

Fish and benthos sampling design

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 m² 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 individuals <5 cm in total length; juveniles were 5 to 14 cm, and adults were >14 cm. The circular plot method was chosen to randomize sample locations within a given depth strata because it both facilitated quick deployment, thus allowing

for greater replication, and limited the time spent in a survey area, thereby decreasing bias estimates due to net movement of fish (Watson et al. 1995).

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 were used to calculate a mean depth for each 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 (Risk 1972). 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 algae on rubble.

Data Analysis

To compare the geomorphology of each reef among MPAs, we used 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. The total number of

habitat types and patches, and variability of habitat patch size and shape were also measured. We define habitat patch as an area, delineated by a polygon of a distinct habitat type. Variability of patch size was measured as the root mean square distance of the polygon parts from its center while the variability of the patch shape was measured as the standard deviation of the perimeter to area ratio for all the patches present.

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 tests (Holm 1979), with a P value of < 0.01 used for statistical significance.

To determine whether 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 tests (Holm 1979), with a *P* value of < 0.01 used for statistical significance. A one-way ANOVA was used to determine whether 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). 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.

Because reef-fish recruitment is highly variable during the summer months (Walsh 1987), and recruit densities were sampled one time during the year, the Division of Aquatic Resources (DAR) long-term monitoring data were used to supplement our study (see Williams et al., 2009). Since 1999, DAR has surveyed aquarium fish populations four to six times per year at each of the study sites. Monitoring stations were located on medium-depth reefs with moderate to high finger coral cover, a habitat important to recently settled fishes (recruits), where fishes were counted and classified as recruits (< 5cm) [for a complete description see (Tissot et al. 2004)]. For the current study, data from monitoring stations were used to generate average recruit densities of yellow tang per site from 2000 to 2008. These results were compared with the recruit densities from our 2008 survey using Spearman's rank correlation coefficient.

Population size of each life stage of yellow tang among MPAs was compared. Total population sizes per reef were estimated 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). These estimates were calculated to account for the different shoreline lengths and reef structure from shore to depth in each site.

A Canonical Correlation Analysis (CCA) (SAS 2000) was conducted to examine multivariate associations among the spatial characteristics of the reef the population size (total number of individuals) 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.

To evaluate the relationship among MPA effectiveness and the spatial characteristics of the reef, data from DAR's long-term monitoring study were used to calculate an index of effectiveness (R) calculated as the absolute percent change in reef-fish density inside MPAs relative to protected reference areas before and after closure (Walsh et al. 2004). These changes were calculated as follows:

$$\mathbf{R} = \left[\frac{\sum_{i=1}^{t_{after}} \overline{X}_{control} - \overline{X}_{FRA}}{t_{after}}\right] - \left[\frac{\sum_{i=1}^{t_{after}} \overline{X}_{control} - \overline{X}_{FRA}}{t_{before}}\right] x 100$$

Before and after differences of yellow tang densities among sites were assessed using a twosample 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 closure.

RESULTS

Reef geomorphology and habitats of MPAs

Reef geomorphology varied greatly along the West Hawaii coast (Table 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 (DC) (> 38%) and shallow turf-rich boulder (ST) (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 (MB) 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%).

Comparison of reef habitat complexity

Results of a one-way ANOVA revealed that the reef habitat complexity of DC ($F_{8,89} = 2.42$, P < 0.05), MB ($F_{3,24} = 5.37$, P < 0.01), and ST ($F_{8,74} = 3.92$, P < 0.01) varied significantly among MPAs (Fig. 3a-c). Complexity of DC in Honokohau was significantly higher (P < 0.05) than Waiakailio Bay and Hookena (Fig. 3a), and the complexity of MB was significantly higher (P < 0.05) in Anaehoomalu than S. Oneo Bay (Fig. 3b). For ST, Kaupulehu had significantly lower (P < 0.05) rugosity values than Hookena and Anaehoomalu (Fig. 3c). Overall, DC and MB were

most complex in Anaehoomalu and Honokohau respectively, while ST was most complex in Anaehoomalu, Hookena, and Milolii.

Fish density among habitats and sites

Density of recruit (*H*=15.79, *P* <0.0001), juvenile (*H*=53.95, *P* <0.0001), and adult (*H*=6.32, P < 0.05) yellow tang varied significantly among habitats (Fig. 4). Overall, recruit and juvenile densities were higher in DC and MB, while adult densities were higher in ST, but displayed broader distributions. Densities of yellow tang recruits were significantly higher (*P* < 0.05) in DC compared to MB and ST. Densities of juvenile yellow tang were also significantly higher (*P* < 0.05) in DC than in MB and ST while adult yellow tang densities were higher (*P* < 0.05) in ST relative to DC and MB. Thus, the abundance and distribution of the early life stages of yellow tang was highest in deep coral-rich areas (i.e. DC), while adults yellow tang densities varied among habitats, but had highest densities in MB and ST.

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 algae (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 coralline algae on dead finger coral (r = 0.17 - 0.32, P < 0.02), percent cover of crustose coralline algae 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 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 be positively associated with 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 were positively associated with 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 various depths.

Recruitment trends

Recruitment estimates from our study were not significantly correlated with estimates from the long-term monitoring study (r = 0.40, P > 0.06). However, the moderate r statistic (> 0.40) and comparison of recruit densities between the 2008 survey and the long-term (2000-2008) monitoring data shows that there has been consistently higher recruitment in the central (Honokohau, S. Oneo Bay, and N. Keauhou) and some southern sites (Hookena and Milolii) relative to the remaining sites.

Population size and MPA characteristics

Estimates of fish population size per reef (# / km) were conducted for each life stage among MPAs (Fig. 5). Estimates of population size for all life stages were, overall, greater in large MPAs that contained wide reefs and large areas of recruit, juvenile, and adult habitat. Recruits were most abundant in Kaupulehu and Honokohau while juvenile abundance was highest in

Anaehoomalu, Kaupulehu, S. Oneo Bay, and N. Keauhou. Adult abundance varied among sites with Anaehoomalu, Honokohau, S. Oneo Bay, and Keei having greater abundance . Overall, population size of most life stages was greater in some northern and central sites (Anaehoomalu, Kaupulehu, Honokohau, and S. Oneo Bay).

The first (CC1) and second (CC2) axes of the canonical correlation analysis (CCA) provided significant ecological contrasts for yellow tangs (Figs. 6a-b; 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.
Effectiveness of MPAs

Overall density of yellow tang increased by 74% from 1999, before MPA closure, to 2008. Among the sites, eight out of the nine MPAs experienced significant (P < 0.00) increases: Anaehoomalu (55 %), Kaupulehu (46%), Honokohau (29 %), S. Oneo Bay (10%), N. Keauhou (154 %), Keei (134 %), Hookena (44 %), and Milolii (6 %). Waiakailio Bay, however, showed significant decreases (25%) in yellow tang abundance.

Density of yellow tang varied greatly within each MPA following years of closure (Fig. 7). Yellow tang showed steady increases in all areas beginning in 2002 with most reaching higher abundances than before closure densities. Since 2006, the MPAs have shown some signs of decline, with Waiakailio Bay showing declines below the pre-closure densities.

DISCUSSION

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 and number of reef habitats, and level of habitat complexity are associated with the significant recovery of aquarium fish populations in West Hawaii.

Physical characteristics of the reef affecting larval supply among sites were likely to have influenced recruitment patterns and recovery of fish within MPAs. The abundance of favorable recruit habitat (i.e. deep coral-rich areas) only partially explained the patterns of recruitment among sites, with some sites having moderate to high recruit densities despite small to moderate areas of recruit habitat. Instead, sites with highest recruit densities displayed physical characteristics consisting of small bays with small and narrow reefs and shallow sunken lava

benches, high in turf algae, 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 may 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 likely contributes to the retention of larvae and consequently to the patterns of recruitment in West Hawaii. Indeed, elsewhere such current patterns and retention features (i.e. eddies, bays) affecting larval supply have been shown to play an important role in explaining recruitment patterns among reef fish (Caselle and Warner 1996, Kingsford 2009).

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 coral-rich and boulder turf-rich, 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 S. Oneo Bay MPAs supported the highest number of juveniles and have 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 number, mean size and age, biomass, and potentially higher production of larvae of target species. In our study, the number of adults varied among our sites, with the Anaehoomalu, S. Oneo Bay, Keei, and Milolii MPAs supporting the highest number of adults and displaying positive increases in yellow tang densities. All sites have moderate to large areas of 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.

Differences in reef habitat complexity, as measured by rugosity, may account for additional differences in fish recovery among sites. For example, Waiakailio Bay displayed significant decreases in yellow tang compared to all other sites. This MPA is a unique site characterized by large pinnacles of sunken lava structures 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, D. Ortiz). Additionally, since 2005, Waiakailio Bay has been subjected to anthropogenic stresses from non-point pollution, such as sediment loading from coastal development (personal communication, W. Walsh), 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. However, habitat does not appear to explain all of the variability in effectiveness among MPAs. Thus, it is likely that additional factors, such as recruitment, recovery time, and low power are also important.

Recovery of reef fish in MPAs can be slow and is often dependent on recruitment (Russ and Alcala 1996b) 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 within MPAs in Kenya required decades, with densities peaking at 7-10 years and reaching stable states after 37 years of closure. For yellow tang, an acanthurid which can live up to 41 years and reach sexual maturity at 4 to 6 years old (J. Claisse, unpublished data) and have a high degree of inter-annual variation in recruitment (Tissot et al. 2004), recovery will likely vary significantly over time. For instance, 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. Williams et al. (2009) also showed that fluctuation in the densities of juvenile and adult yellow tang within MPAs strongly tracked the intensity of recruitment. 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 potentially more MPAs showing significant increases as years of protection increase and recruitment is consistent.

Detecting significant changes in abundance among MPAs is difficult due to the high variability of fish abundance in both time and space. Detecting statistically significant changes depends on the magnitude of the before-after differences in density and the number of surveys in each. For instance, the Keei MPA had shown a statistically significant 185% increase since its closure because yellow tang abundance within the MPA had increased substantially from 0.12 / m^2 in 1999 to 0.34 / m^2 in 2008. In contrast, the Anaehoomalu MPA had a non-significant 28% increase even though the number of yellow tang in the MPAs increased from 0.12 / m^2 to 0.16 / m^2 . However, the increase varied greatly over time and therefore was not significant. Thus, the ability of this study to detect statistically significant effects was limited to large changes in the abundance of the most common species.

MPA Network Design

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 juvenile/adult spillover (Palumbi 2003). As most reef fishes 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 accommodate 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 larvae, and providing MPA spacing within range of yellow tang dispersal distances, which can range to at least 184km (Christie et al. in review).

Characteristics of the West Hawaii MPA network design 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 tang, that to be effective the design of an MPA network depends on the life history and spatial requirements of the species being protected. In the case of West Hawaii, aquarium reef fishes, 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 and ontogenetic shifts in habitat use, as well as similar 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 aquarium reef fish among sites by protecting both settlement and foraging and sheltering locations for early life stages 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

boundaries where extensive fish mortality can occur due to fishing and lower quality habitats (Carr et al. 2003). Fourth, MPAs should be widely spaced (i.e. 15-30 km apart) 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.

Conclusion

Effective management and design of MPA networks requires that we understand the combination of key spatial characteristics of MPAs that result in productive fish populations within their borders. 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. Existing and future MPA networks should incorporate the recommendations outlined in this paper in order to develop spatial management practices that are effective at replenishing protected species in Hawaii and other regions.

TABLES

Table 1. Description of pooled reef habitat types using the classification scheme from Ortiz and

Tissot (2008): 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	DC	ACL, ALC, AM, BM, Ru, S	Reef slope	5-40
Mid-depth aggregate reef and boulder habitats	MB	ALE, AEL, BLL, BLE	Reef slope and Boulder	5-25
Shallow turf-rich boulder habitats	ST	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 (DC), mid-depth aggregate reef and boulder habitats (MB), and shallow turf-rich boulder habitats (ST).

Site	DC	MB	ST	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. Spatial characteristics of the reef and population size of each of the life stages of yellow tang among MPAs. Spatial characteristics of the reef are the following: total area, mean reef width, reef length, standard deviation of patch shape, standard deviation of patch size, number of reef habitats, number of habitat patches, areas of sand, areas of deep aggregations of coral-rich habitats (DC), areas of mid-depth aggregate reef and boulder habitats (MB), and areas of shallow turf-rich boulder habitats (ST). Population size of recruits, juveniles, and adult of yellow tang reflect the total number of yellow tang of each life stage within each MPA.

MPA	total area	reef	reef	patch	patch	reef	habitat	sand (ha)
	(ha)	width	length	shape	size (ha)	habitats (#)	patches	
		(m)	(km)	(ha)			(#)	
Waiakailio Bay	1,758	353	5.5	0.41	17	2	12	68
Anaehoomalu	3,341	742	6.8	0.40	14	3	78	158
Kaupulehu	4,009	529	5.1	0.54	38	2	11	28
Honokohau	320	344	2.7	0.15	7	3	14	2
S. Oneo Bay	3,101	621	8.7	0.65	30	3	27	152
N. Keauhou	742	253	3.3	0.30	10	2	14	10
Keei	816	172	7.4	0.53	21	3	16	15
Hookena	619	183	8.7	0.59	27	2	9	21
Milolii	806	358	7.6	0.57	27	3	21	42

MPA (Cont)	DC(w/out	MB (ha)	ST (ha)	recruits	juveniles	adults
	sand) (ha)					
Waiakailio Bay	81	0	68	2,402	27,684	32,054
Anaehoomalu	87	212	66	5,458	146,095	159,106
Kaupulehu	81	0	180	11,805	122,777	33,344
Honokohau	5	28	76	7,767	11,194	72,521
S. Oneo Bay	178	35	171	7,692	187,752	132,874
N. Keauhou	23	0	56	1,410	89,900	47,920
Keei	45	7	126	597	37,964	80,765
Hookena	18	0	165	856	39,395	20,087
Milolii	50	88	156	9072	93136	82,651

FIGURE CAPTIONS

Figure 1. Location of MPAs along West Hawaii. Boundaries represent area extending from the highwater mark on shore to a depth of 200 m. Values indicate the total area (ha) of the MPA within these boundaries.

Figure 2. Benthic habitat maps of MPAs in West Hawaii.

Figure 3. One-way ANOVA test comparisons of rugosity within (a) deep-coral rich and sandy rubble habitats (DC), (b) mid-depth aggregate reef and boulder habitats (MB), and (c) shallow turf-rich boulder habitats (ST) between MPAs. Different letters denote significant differences of P < 0.05. Values are log-scaled for better interpretation.

Figure 4. Mean density $(\# / m^2)$ of recruit, juvenile, and adult yellow tang among reef habitats for all sites. Reef habitats include deep aggregate coral-rich and sandy rubble habitats (DC), middepth aggregate reef and boulder habitats (MB), and shallow turf-rich boulder habitats (ST). Error bars are standard error.

Figure 5. Population density (# / km) of recruit, juvenile, and adult yellow tang at each study site. Error bars are standard error.

Figure 6. 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; P < 0.00 for all axes) measures the overall association between the spatial characteristics of the reef 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. High positive loadings on

axis 2 define large MPAs with large areas of DCRH, MABH, and sand and numerous habitat patches supporting a large number of all life stages. Negative loadings on axis 2 defined smaller MPAs with smaller areas of these habitats and fewer habitat patches supporting fewer life stages. Figure 7. Changes in yellow tang abundance in MPAs from 1999-2008. Data are averaged by years and error bars are suppressed for clarity.

FIGURES



Fig. 1



Deep aggregate coral-rich and sandy rubble habitat Mid-depth aggregate reef and boulder habitat Shallow turf-rich boulder habitat





Fig. 3



Fig. 4



MPA

Fig. 5



MPA characteristics

Fig. 6



Fig. 7

REFERENCES

- Agardy, T. 2000. Information needs for marine protected areas: Scientific and societal. Bulletin of Marine Science **66** (3): 875-888.
- Almany, G. R., M. Berumen, S. R. Thorrold, S. Planes, and G. Jones. 2007. Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. Science 316:742-744.
- Baskett, M. L., F. Micheli, and S. A. Levin. 2007. Designing marine reserves for interacting species: Insights from theory. Biological Conservation **137**:163-179.

Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications **13**:S25-S31.

- Carr, M. H., J. E. Neigel, J. A. Estes, S. Andelman, R. R. Warner, and J. L. Largier. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecological Applications 13:S90-S107.
- Caselle, J. E., and R. R. Warner. 1996. Variability in recruitment of coral reef fishes: the importance of habitat at two spatial scales. Ecology **77**:2488-2504.
- Christensen, J. D., C. F. G. Jeffrey, C. Caldow, M. E. Monaco, M. S. Kendall, and R. S. Appledoorn. 2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf and Caribbean Research 14:9-27.
- Christie, M. R., B. N. Tissot, M. A. Albins, J. P. Beets, J. Yanli, S. E. Thompson, and M. A. Hixon. In Review. Larval connectivity in an effective network of marine protected areas. Science.
- Claisse, J. T., M. Kienzle, M. E. Bushnell, D. J. Shafer, and J. D. Parrish. In Review. Habitat and sex specific life history patterns of yellow tang, Zebrasoma flavescens, with implications for fisheries management using protected areas. Marine Ecological Progress Series.
- Claisse, J. T., S. A. McTee, and J. D. Parrish. 2009. Effects of age, size, and density on natural survival for an important coral reef fishery species, yellow tang *Zebrasoma flavescens*. Coral Reefs 28:95-105.
- Claudet, J., C. W. Osenberg, L. Benedetti-Cecchi, P. Domenici, J. Garcia-Charton, A. Perez-Ruzafa, F. Badalamenti, J. Bayle-Sempere, A. Brito, F. Bulleri, J. Culioli, M. Dimech, J. M. Falcon, I. Guala, M. Milazzo, J. Sanchez-Mecca, P. J. Somerfield, F. Vandeperre, C. Valle, and S. Planes. 2008. Marine reserves: size and age do matter. Ecology Letters 11:481-489.
- Coyne, M. S., M. E. Monaco, M. Anderson, W. Smith, and P. Jokiel. 2001. Classification scheme for benthic habitats: main eight Hawaiian Islands Biogeography program. *in* N.

O. a. A. A. US Department of Commerce, National Ocean Service, editor. Silver Spring, USA.

- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological Processes Underlying Ontogenetic Habitat Shifts In A Coral-Reef Fish. Ecology **81**:2227-2240.
- Dollar, S. J. 1982. Wave Stress and coral community structure in Hawaii. Coral Reefs 1:71-81.
- Eble, J., R. J. Toonen, and B. W. Bowen. 2009. Endemism and dispersal: comparative phylogeography of three surgeonfishes across the Hawaiian Archipelago Marine Biology **156**:689-698.
- ESRI. 2002. ET Spatial Techniques. ET Geowizards for ArcGIS, Pretoria.
- Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291-305.
- Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian reef. Journal of Experimental Marine Biology and Ecology **224**:1-30.
- Gerber, L. R., P. M. Kareiva, and J. Bascompte. 2002. The influence of life history attributes and fishing pressure on the efficacy of marine reserves. Biological Conservation **106**:11-18.
- Gibbs, A. E., and S. A. Cochran. 2009. An Integrated Approach to Benthic Habitat Mapping Using Remote Sensing and GIS: An Example from the Hawaiian Islands Pages 211-231 *in* X. Yang, editor. Remote Sensing and Geospatial Technologies for Coastal Ecosystem Assessment and Management Springer Berlin Heidelberg.
- Grigg, R. W. 1994. The effects of sewage discharge, fishing pressure, and habitat complexity on coral ecosystems and reef fishes in Hawaii. Marine Ecological Progress Series **103**:25-34.
- Grober-Dunsmore, R., T. K. Frazer, D. R. Lindberg, and J. Beets. 2007. Reef fish and habitat relationship in a Caribbean seascape: the importance of reef context. Coral Reefs **26**:201-216.
- Halpern, B. 2003. The impact of marine reserves: do reserves work and does reserve size matter? Ecological Applications **13**:S117-137.
- Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science **284**:1537-1538.
- Holm, S. 1979. A simple sequential rejective multiple test procedure. Scandinavian Journal of Statistics **6**:65-70.
- Jameson, S.C., M.H. Tupper, and J.M. Ridley. 2002. The three screen doors: can marine "protected" areas be effective? Marine Pollution Bulletin 44 (11): 1177-1183

- Johnson, A. G., C. Glenn, W. C. Burnett, R. Peterson, and G. Wilkins. 2006. Ultrahigh resolution aerial infrared imagery and geochemical groundtruthing of submarine groundwater plumes from arid west Hawaii. Geophysical Research Abstracts **8**:05441.
- Kingsford, M. J. 2009. Contrasting patterns of reef utilization and recruitment of coral trout (Plectropomus leopardus) and snapper (Lutjanus carponotatus) at ONe Tree Island, southern Great Barrier Reef. Coral Reefs **28**:251-264.
- Kohler, K. E., and S. M. Gill. 2006. Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computer & Geosciences 32:1259-1269.
- Levin, P. S. 1991. Effects of microhabitat on recruitment in a Gulf of Maine reef fish. Marine Ecology Progress Series **75**:183-189.
- McClanahan, T. R., N. A. J. Graham, J. M. Calnan, and M. A. MacNeil. 2007. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. Ecological Applications 17:1055-1067.
- McLeod, E., R. Salm, A. Green, and J. Almany. 2009. Designing marine protected area networks to address the impacts of climate change. Frontiers in Ecology and the Environment 7:doi:10.1890/070211.
- Ortiz, D. M., and B. N. 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 Ecological Progress Series **365**:217-232.
- Ortiz, D. M., and B. N. Tissot. In Review. Evaluating Habitat Structure in Relation to the Effectiveness of an MPA Network to Replenish the Aquarium Fishery in West Hawaii. Canadian Journal of Fisheries and Aquatic Science.
- Pandolfi, J. M., J. B. C. Jackson, N. Baron, R. H. Bradbury, H. M. Guzman, T. P. Hughes, C. V. Kappel, F. Micheli, J. C. Ogden, H. P. POssingham, and E. Sala. 2005. Are U.S. coral reefs on the slippery slope to slime? . Science 307:1725-1726.
- Parrish, J. D., and J. T. Claisse. 2006. Post-settlement life history of key coral reef fishes in a Hawaiian marine protected area network. NOAA Final Project Report, Honolulu, HI
- Pimentel, R. A. 1979. Morphometrics, the multivariate analysis of biological data, Kendall-hunt, Dubuque, IA.
- Planes, S., G. Jones, and S. R. Thorrold. 2009. Larval dispersal connects fish populations in a network of marine protected areas. Proceedings of the National Academy of Sciences USA 106:5693-5697.
- Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Research Bulletin **153**:1-6.

- Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. A. McArdle, H. P. Possingham, M. Ruckelshaus, and R. R. Warner. 2003. Ecological criteria for evaluating candidate sites for marine reserves. Ecological Applications 13:S199-S214.
- Roberts, C. M., J. A. Bohnsack, F. Gell, J. P. Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294:1920-1923.
- Roberts, C. M., and N. V. C. Polunin. 1991. Are marine reserves effective in management of reef fisheries? Reviews in Fish Biology and Fisheries 1:65-91.
- Russ, G. R. 2002. Yet another review of marine reserves as reef fisheries management tools. Pages 421-443 *in* P. F. Sale, editor. Coral reef fishes dynamics and diversity in a complex ecosystem. Academic Press, San Diego, California, USA.
- Russ, G. R., and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. Marine Ecology Progress Series **132**:1-9.
- Russ, G. R., and A. C. Alcala. 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations Oecologia **138**:622-627.
- Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. Science **298**:1991-1993.
- Sale, P. F. 1970. Distribution of larval Acanthuridae off Hawaii. Copeia 1970:765-766.
- Sale, P. F., editor. 1991. The ecology of fishes on coral reefs. Academic Press, San Diego, CA.
- Sale, P. F., R. K. Cowen, B. S. Danilowicz, G. P. Jones, K. C. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, J. Y. Sadovy, and R. S. Steneck. 2005. Critical science impedes use of no-take fishery reserves. Trends in Ecology and Evolution 20:74-80.
- SAS. 2000. JMP Statistics and graphics guide. *in*, SAS Institute, Cary, NC.
- SHOALS, L. B. 2002. acessed March 2005,. http://shoals.sam.usace.army.mil/hawaii/pages/Hawaii_Data.htm.
- Syms, C., and G. P. Jones. 2004. Habitat structure, disturbance and the composition of sanddwelling goby assemblages in a coral reef lagoon. Marine Ecological Progress Series 268:221-230.
- Tissot, B. N., and L. E. Hallacher. 2003. Effects of Aquarium Collectors on Coral Reef Fishes in Kona, Hawai'i. Conservation Biology **17**:1-10.

- Tissot, B. N., W. J. Walsh, and L. E. Hallacher. 2004. Evaluating the effectiveness of a marine reserve network in Hawaii to increase the productivity of an aquarium fishery. Pacific Science **58**:175-188.
- Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. J. Exp. Mar. Biol. Ecol **161**:145-178.
- Walsh, W. J. 1984. Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. PhD Dissertation. University of Hawaii, Honolulu, H.I.
- Walsh, W. J. 1985. Reef fish community dynamics on small artificial reefs: the influence of isolation, habitat structure, and biogeography. Bulletin of Marine Science **36**:357-376.
- Walsh, W. J. 1987. Patterns of recruitment and spawning in Hawaiian reef fishes. Environmental Biology of Fishes **18**:257-276.
- Walsh, W. J., B. N. Tissot, and L. E. Hallacher. 2004. A report on the finding and recommendations of effectiveness of the West Hawaii Regional Fishery Management Area. Department of Land and Natural Resources, Honolulu, HI.
- Watson, R., G. Carlos, and M. Samoilys. 1995. Bias introduction by the non random movement of fish in visual transect surveys. Ecological Modelling **77**:205-214.
- Wedding, L., A. M. Friedlander, McGranaghan, M., R. S. Yost, and M. E. Monaco. 2008. Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. Remote Sensing of Environment 112:4159-4165.
- Williams, I. D., W. J. Walsh, J. T. Claisse, B. N. Tissot, and K. A. Stamoulis. 2009. Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. Biological Conservation doi:10.1016/j.biocon.2008.12.029.
- Wood, E. M. 1985. Exploitation of coral reef fishes for the aquarium trade. United Kingdom, Heredfordshire.
- Zar, J. H. 1984. Biostatistical analysis. Prentice Hall, New Jersey.