Project Final Report

I.   **Effects of Habitat and Life History Characteristics on Marine Reserve Effectiveness**

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II.   **Abstract**

A network of Marine Protected Areas (MPAs) in West Hawai'i has been shown to vary in its effectiveness to replenish depleted aquarium fish stocks. To determine the abundance and distribution of habitat needed to better design and manage MPAs along West Hawai'i, underwater video transects, existing remote sensing data and a benthic classification scheme were used to interpret and map reef habitats at a spatial scale of 10-100's m (mesohabitats). A stratified monitoring effort was carried out to quantify ontogenetic habitat use by the primary aquarium reef fish, yellow tang (*Zebrasoma flavescens*) in existing MPAs. Rugosity, microhabitat features (1–10m scale), abundance and size of fish were quantified in a total of 115 circular plots. In addition, mesohabitat features (10-100m scale) were assessed in order to determine accuracy of mapping efforts. Visual categorization and mapping of habitat was accurate and consistent with the habitats quantified on a microhabitat scale. Patterns of abundance of reef fish and the distribution of benthic substrates were distributed along distinct habitat types at each site. Reef morphology and the distribution of coral species among sites was strongly associated with wave exposure. Ontogenetic shifts in habitat use by reef fish were significant at all study sites. Recruits and juveniles of the yellow tang showed strong patterns of mesohabitat and microhabitat selection among sites by associating with deep aggregate coral rich areas and patches of finger and cauliflower coral while the distribution and abundance of adults varied greatly within and among sites. The development of the meso-scale habitat map made it possible to quantify undocumented patterns of ontogenetic habitat use and in turn provide some insight into the processes driving the population dynamics of reef fish and effective management of MPAs.

III.   **Executive Summary**

In 2000, a network of nine fish replenishment areas (FRAs) was established on the west coast of the Big Island of Hawai'i (hereafter, West Hawai'i) in response to declines of reef fishes taken by aquarium collectors. FRAs are marine protected areas (MPAs) in Hawai`i that prohibit the collecting of live fish for the aquarium trade.

Five years of monitoring in these areas has revealed significant increases in overall abundance of aquarium fish after the closure of FRAs (Walsh et al. 2004). However, FRAs varied in their degree of effectiveness to replenish fish populations, with four of the nine areas

displaying significant increases in the primary aquarium fish yellow tang, *Zebrasoma flavescens* (Tissot et al. 2004; Walsh et al. 2004). The effectiveness of the FRA network in West Hawai'i has been linked to high levels of newly recruiting fish (Tissot et al. 2004, Walsh et al. 2004) and the abundance of microhabitat features, in particular the finger coral (*Porites compressa*), important for the survival of juvenile aquarium reef fish (Tissot and Hallacher 2003). These results suggest that the abundance and spatial variation of habitat is an important factor influencing the effectiveness of the West Hawaii MPA network to replenish aquarium fish. However, research examining fish-habitat association has only been conducted at the microhabitat level (1-10 m's). This project developed a novel approach to evaluate the spatial variation of habitats at the meso-scale level (1-100 m's) in relation to the ontogenetic variation of targeted aquarium reef fish in two exisiting FRAa 's (Honokohau and Anaehoomalu) and adjacent MPAs (Wawaloli and Puako).

In 2004 ,development of a multi-scale habitat map based on larger-scale benthic habitat maps and aerial photographs of the Big Island of Hawaii (Coyne et al. 2001), Light Detection and Ranging Technology (LIDAR) data, 41 in-situ geographically referenced underwater video (UV) surveys was completed for all sites. A total of fourteen mesohabitat types were defined using a hierarchical classification scheme using six categories of physical substratum, based on the lithology and geomorphology of the seafloor, and four categories of biological substratum.

A stratified monitoring effort was carried out to quantify habitat use and distribution of reef fish through the life history stages of reef fish. Fish abundance at each location was assessed using the stationary visual survey method of Bohnsack and Bannerot (1986) from May 31 to July 30, 2005. A total of 115 circular plots were surveyed within each mesohabitat type at each site. Within each plot all fish were counted and sized as recruits (< 5cm), juveniles (>5 cm and <14 cm) and adults (> 14cm). In addition, rugosity and microhabitat features (1–10m scale) were quantified using a 10 m trasenct. Mesohabitat features (10-100m scale) were assessed within each plot in order to determine accuracy of mapping effort.

To evaluate the spatial variation of habitats in relation to the ontogenetic variation of habitat use by aquarium reef fish, we use ArcGIS software and a multivariate detrended correspondence analysis to explore role of habitat and life history traits on FRA effectiveness. Analyses indicated several important conclusions. Patterns of abundance of reef fish and the distribution of benthic substrates were distributed along distinct habitat types at each site. Reef morphology and the distribution of coral species among sites was strongly associated with wave exposure. Ontogenetic shifts in habitat use by reef fish were significant at all study sites. Recruits and juveniles of the yellow tang showed strong patterns of mesohabitat and microhabitat selection among sites by associating with deep aggregate coral rich areas and patches of finger and cauliflower coral while the distribution and abundance of adults varied greatly within and among sites. In addition to these microhabitat associations, recruit and juvenile density was highest within wave-exposed sites having a lower abundance of finger coral substratum compared to wave-sheltered sites. Recruitment variation among sites may be the result of several factors such as differential post-settlement mortality.

Findings suggest that both micro and meso-scale habitat characteristics may influence the effectiveness of MPAs. Other factors such as differential post-settlement mortality, variation in

larval supply, food and refuge availability can also contribute to the effectiveness of MPA to replenish targeted populations of reef fish. Based on current results, it is important that continued monitoring in West Hawaii continues. Long-term data and continued monitoring of existing sites will provide in insight into what factors contribute to the effective replenishment of targeted reef fish.

IV.   Purpose

A. Problems or impediments: None

B. Objectives

Our objective is to examine the ontogenetic patterns of habitat use by the yellow tang, a species which comprises the majority of the catch for the aquarium trade in West Hawai'i (Walsh et al. 2004) using the new classification scheme introduced in this paper and, a combination of remote sensing and in situ approaches. The results of this project are critical in enhancing our understanding of the ecological processes governing the distribution and abundance of coral reef fish.   In turn, this will aid in the designation and implementation of marine protected areas as a fisheries management tool and provide a model system that can be applied to MPA design throughout the state of Hawai`i and other regions.

The objectives of this proposal are to determine:

1. At what scale can we relate and quantify and describe habitat types to observed spatial life history characteristics of reef fish?

2. What are the effects of habitat on the life history assemblages of reef fish and how does it influence FRA effectiveness?

V.   Approach

A. Methods

We developed a fine-scale assessment of benthic habitats in two FRAs and adjacent closed-control areas. We documented and evaluated the spatial variation of habitats in relation to the ontogenetic variation in habitat use of yellow tang.

Study sites

We examined two FRAs, and their paired adjacent MPAs, that varied in their effectiveness to replenish aquarium fish stocks (Fig. 1). One pair of study sites was located at Honokohau (19° 40.26'N, 156° 01.82'W) and Wawaloli (19° 42.53'N, 156° 02.99'W). Wawaloli is an MPA where aquarium collecting has been prohibited since 1991 (Department of Land and Natural Resources, 1996). Honokohau was frequented and impacted by aquarium collectors until its closure in 1999 as an FRA. Both sites are located on the south central coast of West Hawai'i where they are heavily exposed to swells and wave energy.   The second pair of sites was located at Puako (19 °58.19'N, 155° 50.93'W) and Anaeho`omalu Bay (19° 57.17'N, 155° 51.97'W).

Puako is an MPA where the collection of aquarium fishes has been prohibited since 1991 (Department of Land and Natural Resources, 1996). Anaeho`omalu Bay was frequented and impacted by aquarium collectors until its closure in 1999 as an FRA. These sites are located on the sheltered northern coastline of West Hawai'i. Five years of monitoring in these sites revealed that the Honokohau FRA has not shown a significant increase in replenishing fish stocks compared to Anaeho`omalu FRA, which has shown a significant 79 % increase (Tissot et al. 2004).

(1) At what scale can we relate and quantify and describe habitat types to observed spatial life history characteristics of reef fish?

Habitat is a key feature influencing fish abundance and diversity on coral reefs (Friedlander and Parrish 1998, Friedlander et al. 2003), and in Hawaii has been shown to be an important predictor of FRA effectiveness at local scales (Tissot et al 2004) and abundance of juvenile yellow tang in particular (Tissot et al 2003). However, most MPA studies have not examined habitat quality, abundance and distribution, which is important at both local and landscape scales (Thorrold and Williams 1996). Because habitat characteristics are known to play an important role in affecting the community structure of coral reef fishes in Hawaii (Friedlander and Parrish 1998), these fish-habitat relationships must be evaluated on a scale consistent with the patterns of both the resources and their users (Friedlander and Parrish 1998). Hence, it is imperative to evaluate ontogenetic habitat shifts on a scale consistent with the structuring patterns of habitat used displayed by species of reef fish.

In 2004, using NOAA aerial photographs and LIDAR data, a meso-scale (10-100s of meters) *in situ* assessment was conducted using a GPS-referenced video transect method that incorporates using underwater video to record habitats across randomly-placed samples perpendicular to the coast for all study areas. Habitat type was categorized from videotape using a three code combination, the first letter indicating the primary physical structure as defined by NOAA (Coyne et al 2001) [i.e. pavement (P), sand (S), rubble (R), aggregate reef (A), boulder (B)}, the second letter and third letter indicating the dominant substratum on the primary physical structure: finger coral (*Porites compressa*) (C)*,* lobe coral (*Porites lobata*) (L), cauliflower coral (*Pocillopora meandrina*) (E) and mixed areas of lobe, finger and cauliflower coral (M) . The primary biotic substratum was defined as coral species covering less than 80% and more than 50% of the area viewed. The secondary biotic substratum was defined as covering less than 50% and more than 10% of the area viewed). Habitat types were described to coral species level and the lowest structure level on a scale of 10 to 100s of meters using dominant structure and substratum types (i.e., BEL represented at least 50% cover by boulders with at least 50% covered by cauliflower coral and at least 10% lobe coral).

NOAA's habitat digitizer extension in ArcGIS was used to create a contour of the habitats displayed along the line features. Random surveys were done within each site to assess the accuracy of the mapping effort (**Fig 2**). These benthic maps served as a reference to examine spatial variation in habitat use of aquarium reef fish.

(2) What are the effects of habitat on the life history assemblages of reef fish and how does it influence FRA effectiveness?

Targeted reef fish from the aquarium trade occupy different habitats during juvenile and adult stages. For example, newly recruited yellow tang have been observed to are most abundant in finger coral dominated habitats at 10-20m depths (Walsh 1985) while large reproductive adults are more common in shallower (5-8 m) areas with higher algal abundance. Consequently it is critical to evaluate ontogenetic habitat shifts as a mechanism structuring coral reef assemblages and consequently reserve function for targeted aquarium reef fish.

To meet our second objective, a stratified monitoring effort was carried out to quantify habitat use of reef fish throughout their life history. Using underwater video transect surveys and GIS, habitat use and distribution of selected species in FRA's (with various level of effectiveness) and adjacent MPA's were assessed. A GPS-referenced rapid-survey technique (Friedlander and Brown 2003) that incorporates randomly-placed samples with each habitat type (Bohnsack and Bannerot 1986) to estimate the abundance of fishes and the associated benthic community (e.g., corals, macroalgae, etc.) will be used. From these data, we developed habitat-stratified estimates of fish abundance and distribution at each study site. ArcGIS allowed the overlay of NOAA's 1999 broad-scale benthic habitat maps with a higher resolution habitat-based assessment map spatially relevant with the patterns of habitat used by reef fish through each life history stage.

Habitat use and the distribution of yellow tang compromising 80% of the aquarium reef fish harvest was determined. All fishes were categorized into size classes and life history stage (recruit, juvenile and adult) on randomly placed 78 m^2 circular plots on each of archived broad scale habitat types for each of the study sites. One complete rotation was made for each plot and size estimates of fish were verified using a cm-scaled underwater slate. The diver periodically calibrated estimates of the sample radius with a 10 m transect line marking the circumference of the circle and also used for analysis of microhabitat features. For the purpose of analysis, recruits were generally individuals less than five centimeters in size. The division was based on the transparent characteristic coloration, size and behavior of recent recruits. Juveniles refer to individuals of 5.0 to 14.0 cm and adults refer to individuals greater than 14.0 cm in length. Adult size ranges were based on behavior and estimates of size at first reproduction (J. Claisse, unpublished data).

After counting fish, depth, rugosity and microhabitat types were estimated for each plot using a 10 m transect line. Depth was recorded systematically along the center, and lateral east, west, north and south edges of the circular plot. The five depth readings produce 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 each 10 m transect. A ratio of the distance between the length of the transect and the length of the tape was used as an index of rugosity.

A Sony underwater digital camera was used to take 10 photoquadrats along each 10 m transect, 1 m above the substrate. Each of 1,150 images was projected on to a rectangular grid using Photogrid software (Bird 2003). Percent cover for substratum types was quantified under 20 random points on each grid. These substratum types included C (finger coral), L (lobe coral), E (cauliflower coral), PH (finger coral holes/crevices), Cr (coralline crustose), S (sand), R (coral rubble), TU (turf algae on boulders) and TR (turf algae on rubble). Percentage cover of microhabitat substratum was calculated as the percentage of the points on each transect occupied by the same substratum category at each site.

The overall accuracy of the benthic habitat maps was calculated by dividing the total correct determinations by the total number of assessments. Aerial cover of mesohabitats were derived from the newly created benthic maps and marine managed areas shape file developed by the Hawaii Department of Land and Natural Resources, Division of Aquatic Resources (DLNR 2003). Plots were sampled along fourteen representative mesohabitat types at each site, for a total of 115 plots (Table 1). Using ArcGIS 8.3x, the percentage cover of the primary substratum of mesohabitat features was calculated as the percentage area of each category at each site.

Detrended Correspondence Analysis (DCA) was used to describe associations between qualitative mesohabitat type classification and the quantitative microhabitat data. A matrix of plot samples classified by mesohabitat type (115 plots) and quantified microhabitat substratum (percent cover at each plot) was used in the analysis. DCA produces graphical ordination that shows the similarity between observations (mesohabitat types) and variables (microhabitat substratum) derived from a frequency table (SAS Institute 2000). Observations with similar frequencies appear close together, and 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 78 m^2 plot at each site and standardizing it to number of individuals per 50 m^2.

Habitat assessments were made for the distribution pattern and distinctive habitat uses of recruits, juveniles and adult. The final product of this section was a GIS-referenced composite map of distribution and habitat use by recruit, juvenile and adults by designated zones across the study sites.

B. Project Management

Aspects of the study are the result of cooperative interaction between WSU, UHH and DAR personnel. UH Scientific Divers, all UHH student divers specifically trained for the project using Quantitative Underwater Ecological Survey Techniques (QUEST) [12], assist in field data acquisition. Equipment for the project, including Scuba equipment, transect lines, differential GPS, a research vessel, and underwater digital video cameras were available through DAR, UHH, and WSU. Data entry and verification, image analysis of habitat surveys, experimental design, field implementation and database management was developed and handled by WSU.

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

VI.   Findings

A. Accomplishments and findings:

Habitat Classification and Mapping

Mapping of all four study sites was completed in 2004 (Fig. 3 a-d). The overall accuracy of circular plot assessments of classified meso-scale habitat types was 93.3%. Patchy boulder areas with low to high coral cover and aggregations of finger and lobe coral located in ecotones were less accurate, in part due to their patchy nature and their location in areas that transition from one mesohabitat type to the next.

The Detrended Correspondence analysis (DCA) revealed good correspondence between the visual assessment of mesohabitat types and the microhabitat categories quantified at each mesohabitat type among all sites (Fig. 4a). The proportion of variation explained by the canonical dimensions was 0.36 and 0.23 for the first and second axes, respectively. For example, aggregations of finger and lobe coral habitats (ACL) grouped closely with lobe coral (L), finger coral (C) and finger coral holes/crevices (PH) substratum categories. These results demonstrate that these habitat types can be visually categorized and mapped using the novel methodology used in this project.

Spatial Variation

Sites

The DCA reveals a spatial gradient separating north sheltered sites, Anaeho'omalu and Puako, from the south central exposed locations, Honokohau and Wawaloli (Fig. 4a,c). Shallow boulder turf algae rich habitats with patchy areas rich in coral were characteristic of exposed sites compared to the aggregations of deep coral rich habitats dominating the northern sheltered sites (Fig. 4a,b). Overall, of the four sites mapped, Honokohau and Wawaloli were predominantly composed of pavement and boulder substratum, while Puako and Anaehoomalu were predominantly boulder and aggregations of coral rich habitats and some had a mixture of sand and rubble substratum

Biological substratum varied greatly from site to site (Fig. 5). Puako was dominated mostly by finger coral (26.8%), lobe coral (11.3%) and turf algae (13.8%), while finger coral (26.8%), turf algae (14.6%) and sand (12.7%) were the dominant substrates in Anaeho`omalu. Honokohau and Wawaloli displayed greater abundance of coralline crustose and turf algae. Although finger coral was abundant in Wawaloli (11.4%) and Honokohau (19.6%), distribution of this substratum is distributed along patches of reef along boulder and pavement substrates (Fig. 4a-b).

Size Class Habitat Use

Correspondence analysis revealed significant associations among the sizes of tang and mesohabitat types at each site (Fig. 6a-c,7a-d) (Chi-square, all p < 0.01). Overall, recruits were strongly associated with deep reef aggregations of finger and lobe coral and/or patchy areas of mixed coral cover at the reef slope, juveniles used habitat ranging from deep high finger and lobe coral cover to shallow boulder turf algae rich habitats and adults were mostly associated with shallow boulder turf algae rich with low coral cover habitats along the reef edge and reef flat. These patterns varied greatly in Honokohau and Wawaloli with recruits and juveniles being distributed along shallower habitats having patchy areas of finger and cauliflower coral substratum (Fig 7c-d) while Puako and Anaeho`omalu had recruit and juveniles associating with aggregate areas of finger and cauliflower coral habitats (Fig 7 a-b). The distribution of adults varies on all sites.

VII.   Evaluation

A. Attainment of project goals and objectives

Project goals and objectives have been largely attained.

B. Recommendations

Findings suggest that both micro and meso-scale habitat characteristics may influence the effectiveness of MPAs. Other factors such as differential post-settlement mortality, variation in larval supply, food and refuge availability can also contribute to the effectiveness of MPA to replenish targeted populations of reef fish.

The integration of remote sensed data combined with in-situ benthic methods provided a useful quantitative approach for the description of habitats at two spatial scales, encompassing a range of ecological scales important to the life stages of targeted reef fish in West Hawai'I (Fig 8).   Habitat characterization and mapping at multiple spatial scales reveals undocumented patterns of ontogenetic habitat use and provides a baseline against which the efficacy of MPAs to enhance resource abundance can be tested, implemented and monitored.

We advocate for continued mapping of the West Hawaii MPA network and monitoring of recruitment to help better understand the effects of habitat and dynamics of recruitment processes important for the effective management of fishery resources.

C. Dissemination of Findings

Scientific Publications

Ortiz DM and BN Tissot. 2006 Ontogenetic Patterns of Habitat Use by a Coral Reef Fish in an MPA Network: A Multi-Scaled Remote Sensing and In-Situ Approach. Marine Ecology Progress Series (in revision).

Scientific Presentations

Ortiz DM and BN Tissot.Western Society of Naturalist. November 2004 (California). Effects of Habitat and Life History characteristic on MPA effectiveness: A multi-scale remote sensing and in-situ approach.

Ortiz DM and BN Tissot. Western Society of Naturalist. November 2005 (California). Evaluating spatial variation in habitats in relation to ontogenetic variation in a reef fish in an MPA network in Hawaii.

Ortiz DM and BN Tissot .Ocean Science Meeting. February 2006 (Hawaii). Evaluating patterns of ontogenetic variation in habitat use of a coral reef fish in an MPA network in Hawaii: a multi-scale remote sensing and in-situ approach.

Ortiz DM and BN Tissot. WSU Vancouver Research Showcase. April 2006 (Washington). Habitat use of a coral reef fish in an MPA network in Hawaii.

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VIII. Signature Investigator must sign and date Project Final Report

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<u>Dr. Brian N. Tissot (P.I.)</u>

Table 1. Area coverage, sampling allocation, characteristics and description of meso-scale habitats for 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. Classification scheme based on present study: A = aggregate reef; M = mixed; B = boulders; P = pavement; E = cauliflower coral *(P. meandrina)* ; L = lobe coral *(P. lobata)*; C = finger coral *(P. compressa)*; u = uncolonized; T = scattered coral rock; S = sand.

Site	Habitat code	Area (h)	n	Rugosity	Mean Depth (m)		Description
					Depth	SE	
Puako	ACL	21.93	12	1.37	8.96	2.05	aggregate reef with finger and lobe coral cover
	AEL	9.06	3	1.22	8.73	0.77	aggregate reef with cauliflower and lobe coral cover
	BEL	16.38	8	1.22	3.60	1.52	colonized boulders with cauliflower and lobe cover
	Bu	48.52	4	1.25	1.88	0.39	uncolonized boulders
	PEL	2.67	-	-	-	-	colonized pavement with cauliflower and lobe coral cover
	Ru	2.10	-	-	-	-	uncolonized rubble
	S	0.99	-	-	-	-	Sand
	Tu	2.73	-	-	-	-	scattered coral rock
Total		104.45	27				
Anaehoomalu	ACL	156.84	9	1.24	9.89	2.19	aggregate reef with finger and lobe coral cover
	AEL	0.01	-	-	-	-	aggregate reef with cauliflower and lobe coral cover
	ALC	1.97	-	-	-	-	aggregate reef with lobe and finger coral cover
	ALE	214.35	5	1.31	8.53	2.45	aggregate reef with lobe and cauliflower coral cover
	AM	58.31	8	1.18	8.68	2.20	aggregate reef with mixed cover
	BEL	7.00	6	1.62	3.62	1.03	colonized boulders with cauliflower and lobe coral cover
	BLE	205.62	-	-	-	-	colonized boulders with lobe and cauliflower coral cover
	Bu	156.43	-	-	-	-	uncolonized boulders
	S	390.35	2	1.16	11.40	2.60	Sand
Total		524.87	30				
Wawaloli	BEL	17.71	10	1.20	11.96	3.02	colonized boulders with cauliflower and lobe coral cover
	BLE	2.58	3	1.15	10.73	1.47	colonized boulders with lobe and cauliflower coral cover
	AM	0.46	3	1.24	14.39	1.47	aggregate reef with mixed cover
	PEL	10.08	5	1.16	4.23	1.57	colonized pavement with cauliflower and lobe coral cover

	Pu	3.13	-	-	-	-	uncolonized pavement
	Ru	2.22	2	1.14	15.63	1.05	uncolonized rubble
Honokohau	AM	36.98	23	12.19	1.31	1.25	aggregate reef with mixed cover
	BEL	12.01	8	6.71	1.82	1.27	colonized boulder with cauliflower-lobe coral cover
	BLL	28.89	11	8.76	1.62	1.30	colonized boulders with lobe coral cover
	Bu	0.55	-	-	-	-	uncolonized boulders
	PEL	32.30	8	5.02	1.51	1.21	colonized pavement
	Pu	31.76	-	-	-	-	uncolonized pavement
	Ru	2.84	-	-	-	-	uncolonized rubble
	S	2.12	-	-	-	-	Sand
Total		112.56	35				

Table 1 (Contd.)

Figure 1 Study sites
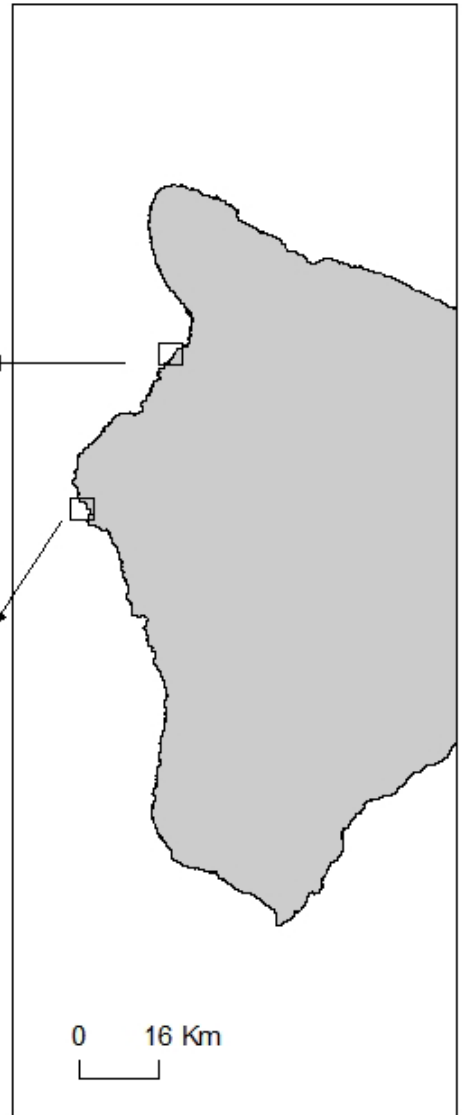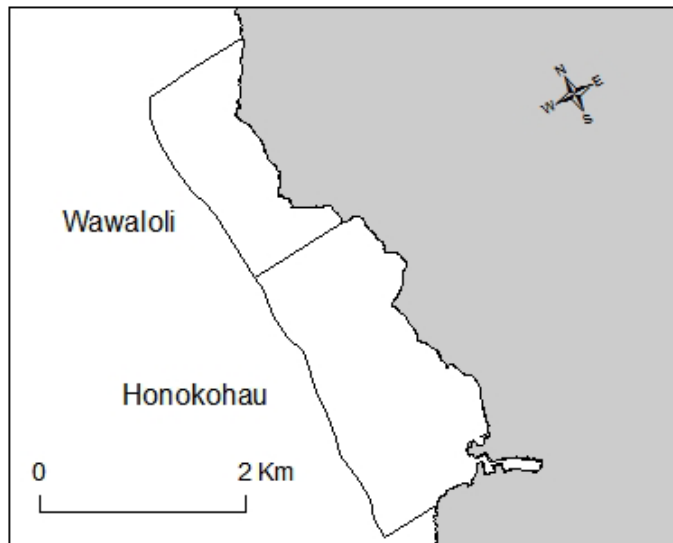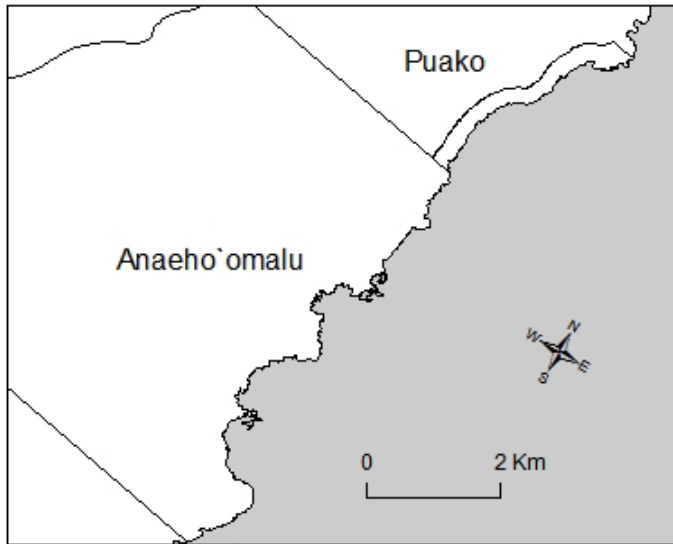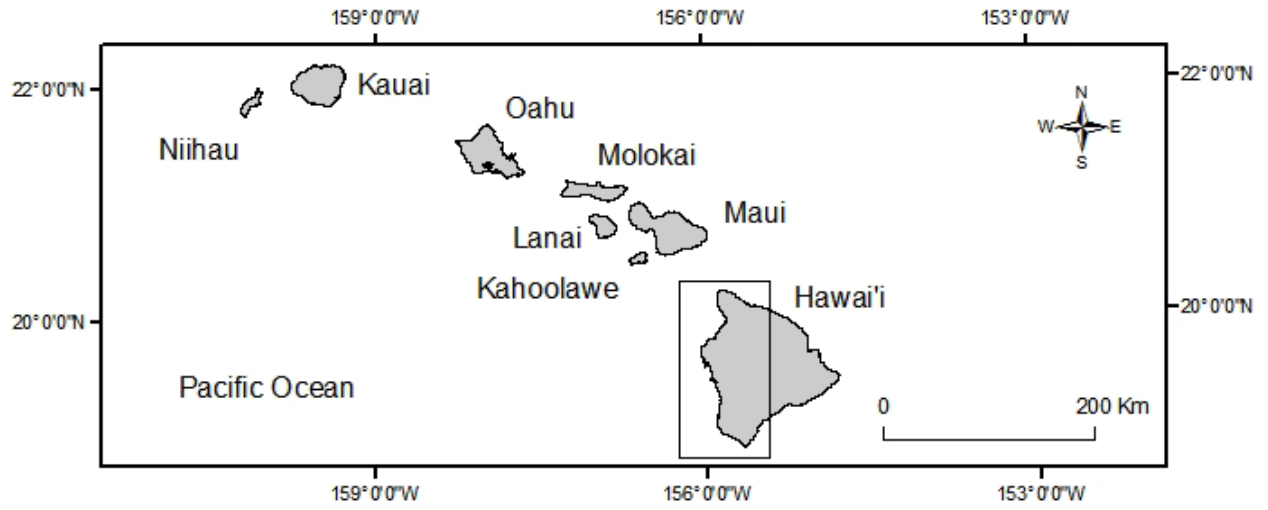
Figure 2. Description of benthic habitat mapping effort for Honokohau, Hawaii. Mapping was completed using NOAAs aerial photographs, bathymetry data, underwater video surveys transects and randomly assigned habitat assessments (a-b). The result of the mapping effort is a description of mesoscale habitats at a finer spatial scale than the benthic habitat maps developed by NOAA (c-d).
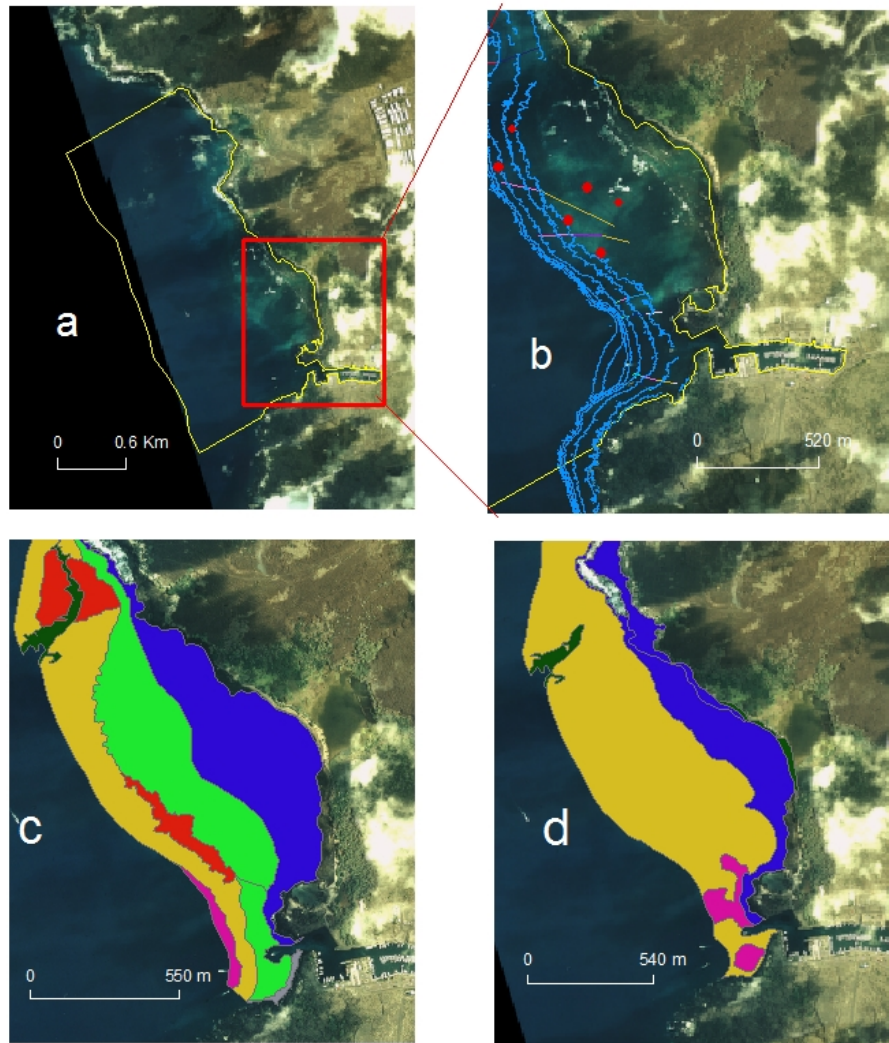

Mesohabitats (Ortiz and Tissot 2005)

- Hardbottom/Uncolonized Pavement
- Reef/Aggregate Coral/Finger/Lobe/Cauliflower
- Reef/Colonized Rock/Boulder/Lobe coral
- Reef/Colonizedm/Volcanic Rock/Boulder/Cauliflower and Lobe coral
- Hardbottom/Uncolonized Volcanic Rock/Boulder
- Hardbottom/Colonized Pavement/Cauliflower and Lobe coral
- Sand

Habitats (Coyne et al. 2003)

- Hardbottom/Uncolonized Volcanic Rock/Boulders
- Reef/Aggregate Coral
- Reef/Colonized Volcanic Rock/Boulders
- Sand

Figure 3. 2005 Mesoscale habitat maps of study sites
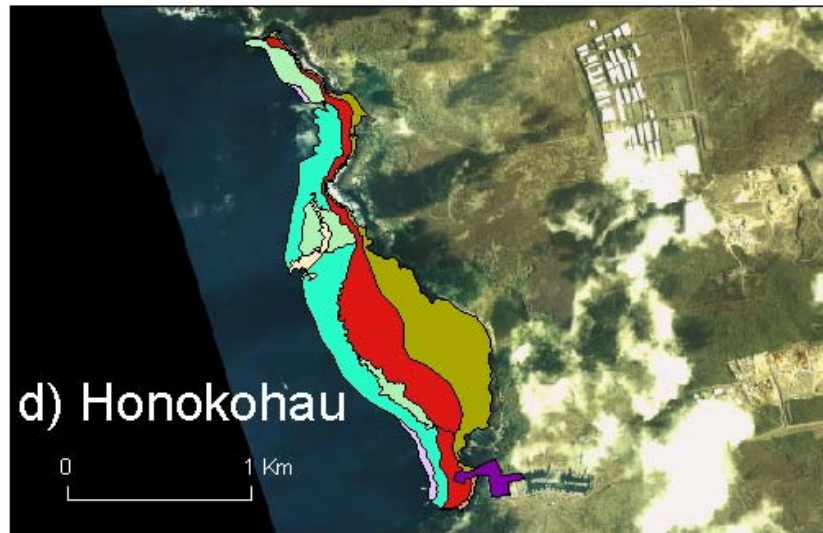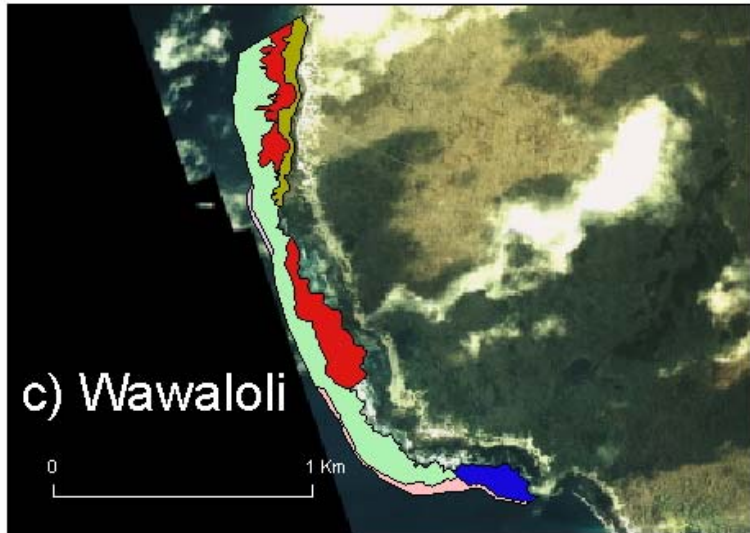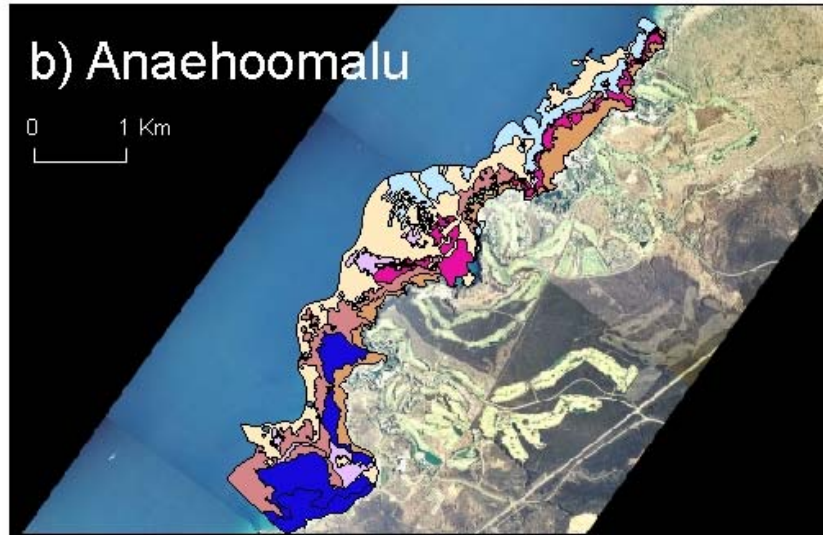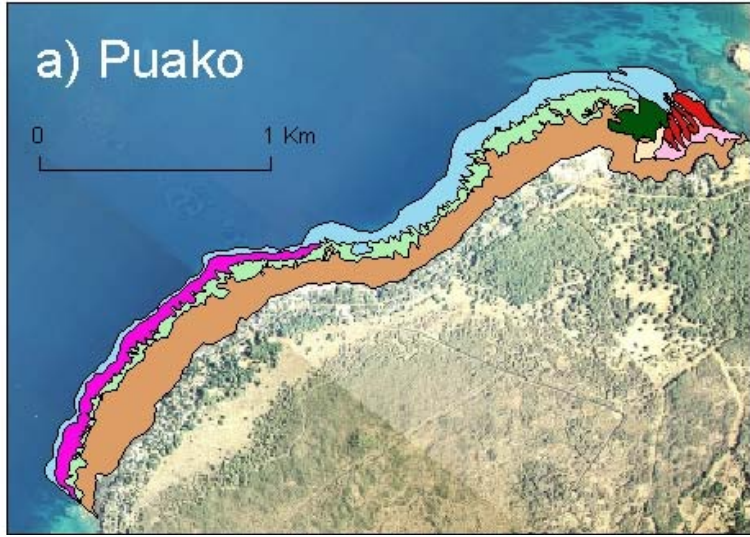
Mesohabitat classification

Aggregate Reef/Mixed	Colonized Boulder/Cauliflower-Lobe coral
Aggregate Reef/Finger-Lobe coral	Colonized Pavement/Cauliflower-Lobe coral
Aggregate Reef/Lobe-Finger coral	Uncolonized Boulder
Aggregate Reef/Lobe-Cauliflower coral	Uncolonized Pavement
Aggregate Reef/Cauliflower-Lobe coral	Uncolonized Rubble
Colonized Boulder/Lobe-Lobe coral	Scattered Coral rock
Colonized Boulder/Lobe-Cauliflower coral	Sand

Figure 4 Results of correspondence analysis among sites and habitats. a. Correspondence plot of sites. b.Correspondence plot of microhabitat substrate associations among mesohabitat types. c. Correspondence plot with inferred wave exposure regime classification for each sampling site
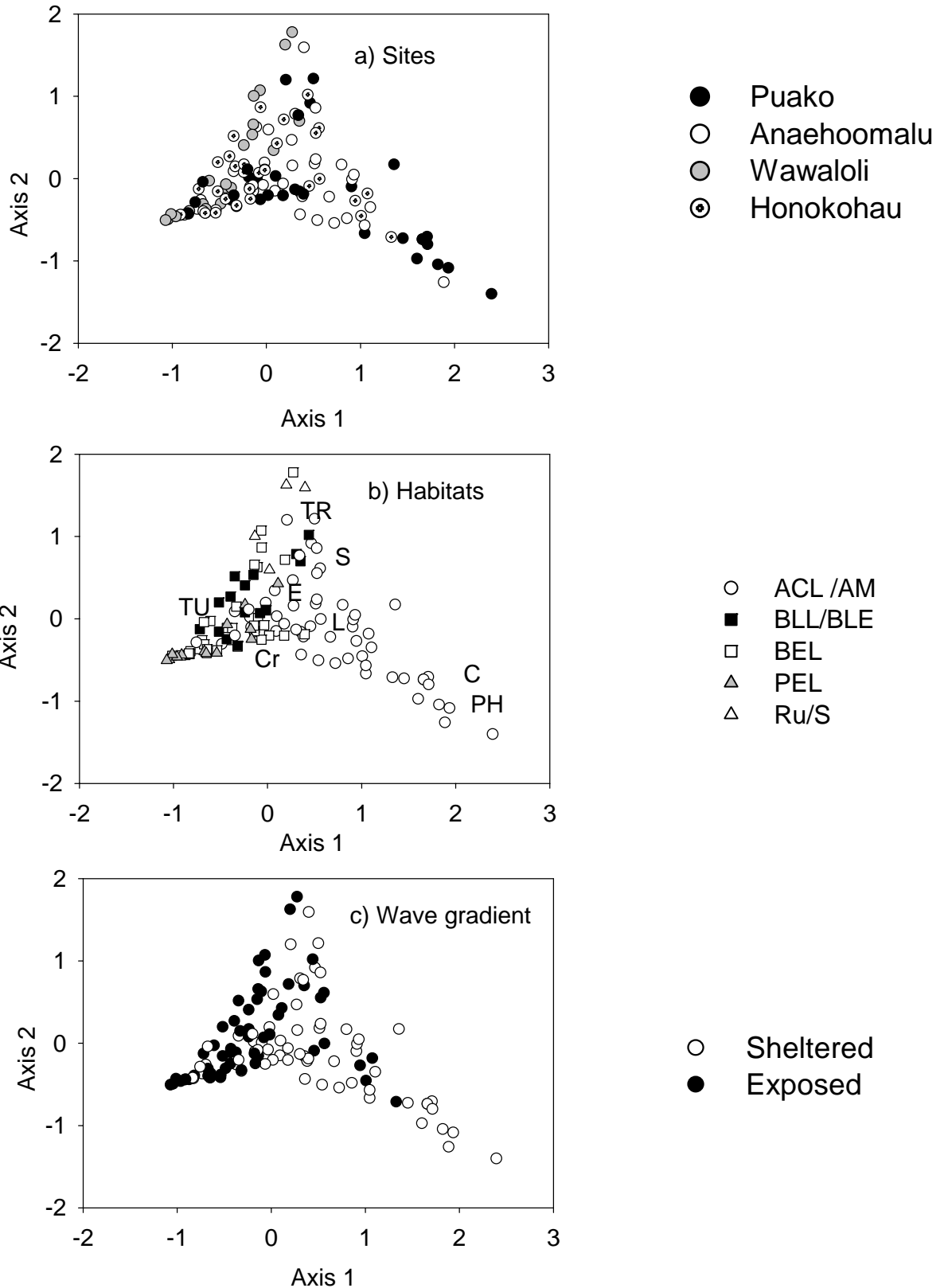
Figure 5 . . Percent cover of the seven most abundant microscale habitat substrates for each site: C (finger coral), L (lobe coral), PH (finger coral holes/crevices), E (cauliflower coral), Cr (coralline crustose), TU (turf algae), S (sand).
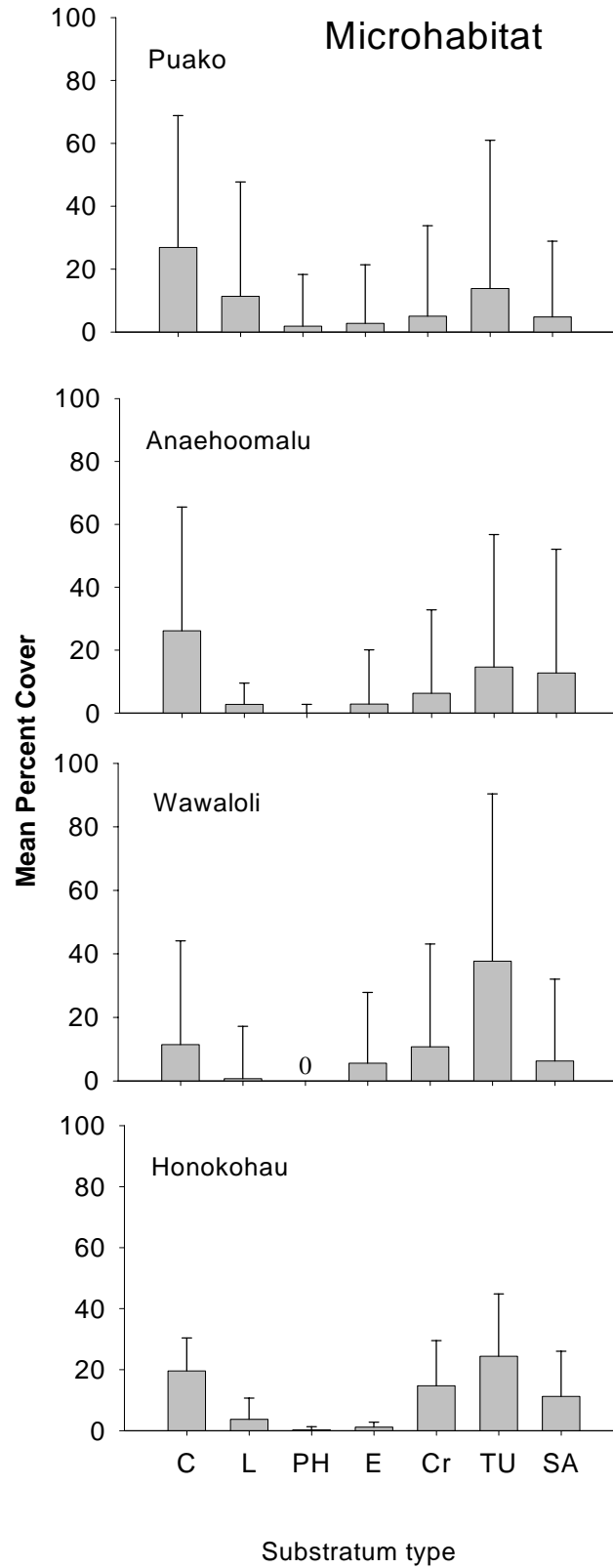
Figure 6a-c. Correspondence analysis of yellow tang recruits, juveniles and adults abundance in relation to study sites and spatial gradients.
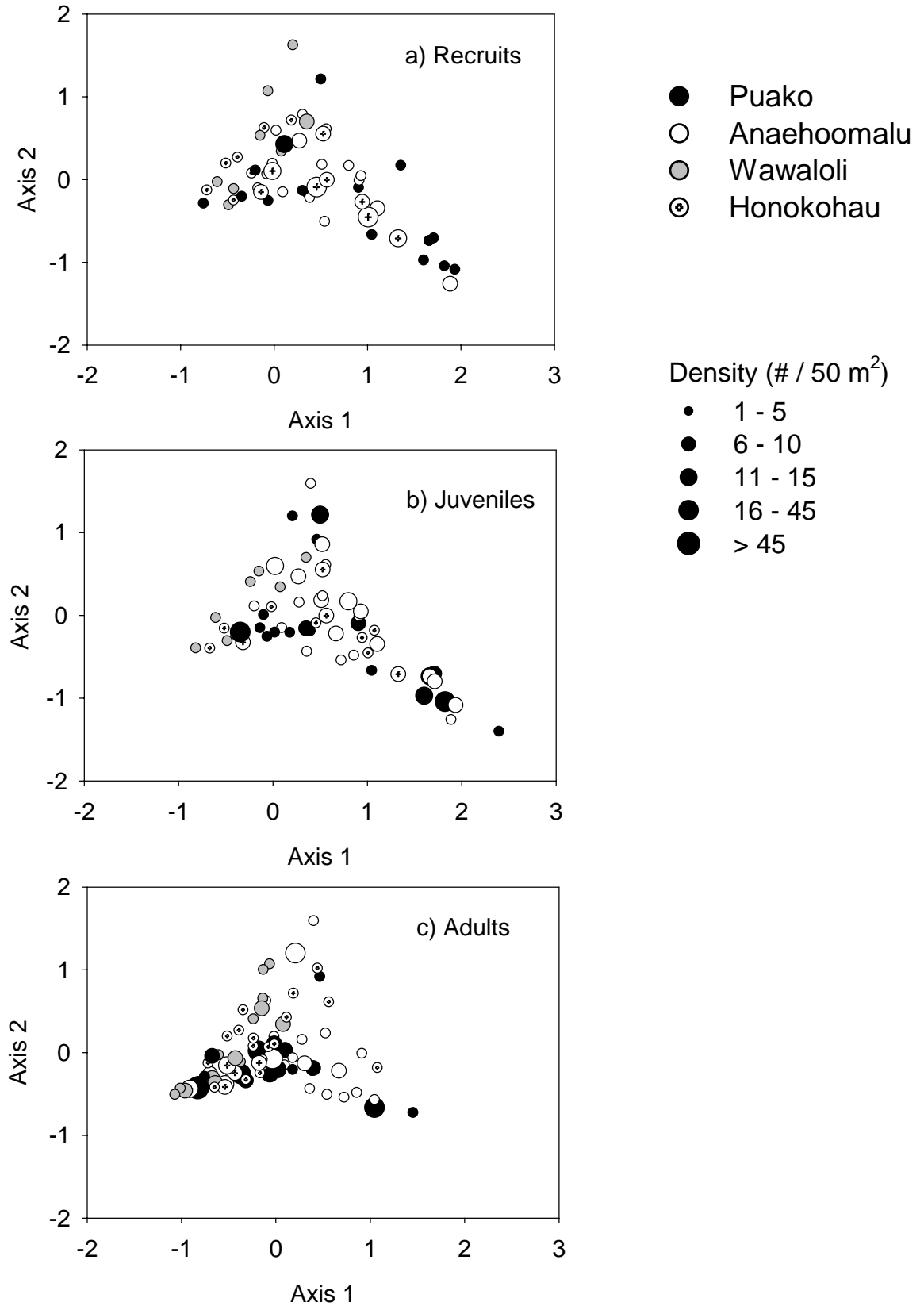
Figure 7. Mean (± 1 SE) density of recruits, juveniles and adults of Yellow tangs along habitats at each study site. Sites are ordered from north to south (top to bottom). Habitats are ordered from deep to shallow depths (left to right).