Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing

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ABSTRACT: Over the past 4 decades, Hawaii has developed a system of Marine Life Conservation Districts (MLCDs) to conserve and replenish marine resources. These MLCDs vary in size, habitat quality, and management regimes, providing an excellent opportunity to test hypotheses concerning marine protected area (MPA) design and function using multiple discreet sampling units. Digital benthic habitat maps for all MLCDs and adjacent habitats were used to evaluate the efficacy of existing MLCDs and adjacent habitats using a spatially explicit stratified random sampling design. Most fish assemblage characteristics (e.g. species richness, biomass, number of individuals) were highest in colonized hard bottom habitats (>10% live coral cover), followed by uncolonized hard bottom habitats (<10% live coral cover), macroalgae, and sand, respectively. Although biomass was low in sand habitats, apex predators accounted for 62% of the biomass on sand within MLCDs, highlighting the importance of this habitat in reserve design. Within habitats, values for assemblage characteristics were typically higher for MLCDs compared with adjacent areas, emphasizing the importance of protection from fishing irrespective of habitat. Rugosity explained much of the variability in species richness and biomass across all locations. Overall, MLCDs protected from fishing, with high habitat complexity and good habitat quality (e.g. high coral cover and low macroalgae cover), had higher values for most fish assemblage characteristics. Integrating mapping and assessment of reef fish habitat utilization patterns allowed for a robust approach to MPA evaluation and can help inform decisions about MPA design and effectiveness, as well as helping to define essential fish habitat and ecosystem function.

KEY WORDS: Marine protected areas · Fish habitat utilization · Habitat complexity · Hawaii · Overfishing

INTRODUCTION

Coral reef fisheries resources are facing overexploitation and severe depletion worldwide (Jackson et al. 2001, Pandolfi et al. 2005) and Hawaii is no exception. Declines in fish abundance and size, particularly around the more populated areas of the state, are likely the result of years of chronic overfishing (Friedlander & DeMartini 2002). Factors contributing to the decline of inshore fisheries include a growing human population, destruction or disturbance to habitat, introduction of new and overly efficient fishing techniques (e.g. inexpensive monofilament gill nets, SCUBA, GPS), and loss of traditional conservation practices (Friedlander et al. 2003a).

Diversity, quality, and areal extent of habitat are among the most important environmental determinants of coral reef fish distribution, abundance, and

diversity (Bellwood & Hughes 2001). Many reef fishes depend upon coral reefs and their adjacent habitats for food, as well as shelter (Parrish 1989, Beukers & Jones 1997). Habitat complexity provides refuges and barriers that fragment the area, resulting in more abundant and heterogeneous assemblages (Sebens 1991).

In Hawaii, structurally complex habitats have been shown to harbor higher fish diversity and biomass compared to habitats with lower complexity (Friedlander & Parrish 1998, Friedlander et al. 2003a). Loss and degradation of important habitats due to coastal development, sedimentation, pollution, and the impacts of non-native aquatic organisms have contributed to the decline of coral reef fishes in Hawaii, as well as the entire coral reef ecosystem (Hunter & Evans 1995, Smith et al. 2002). Therefore, it is vital to understand the importance of habitat to ecosystem function and the changes that occur to these ecosystems as a result of the loss of habitat.

Ecosystem-based management requires a better understanding of the spatial patterns and processes that regulate ecosystem function, both to ensure the sustainability of fisheries and to maintain non-fisheries benefits of the ecosystem to society (Pikitch et al. 2004). In Hawaii, management units are typically on the scale of an island or the entire state and resource evaluation should therefore be conducted on a similar scale. A seascape perspective that couples the distribution of habitats and species habitat affinities at scales commensurate with ecosystem processes is valuable in understanding fish habitat utilization patterns (Kendall et al. 2003), and is useful in defining essential fish habitat (Clark et al. 2004) and biologically relevant boundaries for marine protected areas (MPAs) (Christensen et al. 2003, Friedlander et al. 2003b). Defining and understanding the mosaic of habitats and their connection within the ecosystem are critical if MPAs are to be effective in retaining productive populations within their borders (Appeldoorn et al. 2003, Christensen et al. 2003). A better understanding of the habitat requirements and life histories of the species of interest and the extent to which these habitats interact at larger spatial scales is critical if ecosystem science and management are to be effective (Sladek Nowlis & Friedlander 2004, Monaco et al. 2005).

Hawaii established its first MPA in 1968; since then numerous protected areas have been established with varying levels of protection, ranging from complete 'no-take' areas to areas that allow a wide variety of activities to occur within their boundaries (Table 1). The objective of the present study was to take the first step in evaluating the effectiveness of existing MPAs in Hawaii by using a spatially explicit sampling design to define and quantify fish habitat

utilization patterns across varying levels of habitat quality and protection from fishing. This approach will help to identify the ecological processes and management regimes that result in productive fish populations while providing policy makers with access to the necessary information to make informed decisions concerning MPA design and function at local, national, and international levels.

MATERIALS AND METHODS

Benthic habitat mapping. The National Oceanic and Atmospheric Administration (NOAA) acquired and visually interpreted orthorectified aerial photography, IKONOS satellite imagery, and hyperspectral imagery for the near-shore waters (to 30 m depth) for approximately 65% of the main Hawaiian Islands (MHI) (Coyne et al. 2003). Habitat features were delineated at a scale of 1:6000 with a minimum mapping unit (MMU) of 0.4 ha. Visual interpretation of the imagery was guided by a hierarchical classification scheme. Habitat types were defined in a collapsible hierarchy ranging from broad classes (unconsolidated sediment, macroalgae, coral reef hard bottom, and other), to more detailed categories (e.g. algae, volcanic rock boulders, pavement, etc.), and finally to percent cover of specific features (e.g. 50 to 90% macroalgae cover). In the present study, fish assemblage characteristics were analyzed at the habitat class level to clarify the ecological interpretation and management implications. The resulting digital benthic habitat maps (available at http://ccma.nos.noaa.gov/products/biogeography/hawaii_cd/index.htm) were characterized by a high degree of spatial and thematic accuracy, which was calculated to be 90% (Kappa and Tau = 0.86) for the major class level and 80% at the most detailed level of the classification scheme (Coyne et al. 2003).

Sample design. Sampling was conducted in Hawaii's 11 Marine Life Conservation Districts (MLCDs) (Fig. 1), the University of Hawaii Marine Laboratory Refuge (MLR), and adjacent, comparable habitats. For all analyses, the MLR was combined with the MLCDs, and all further references to MLCDs include the MLR. Locations for assessment were determined using a stratified random sampling approach where random points were assigned to each of 4 major habitat strata (colonized hard bottom [CHB], uncolonized hard bottom [UCH], unconsolidated sediment [UCS], and macroalgae [MAC]) using ArcView 3.2. Uncolonized hard bottom was defined as habitat having <10% live coral cover. Within each major habitat type, sampling was further stratified by management regime (MLCD, Fisheries Management Area [FMA], and open access). FMAs comprised a heterogeneous group of manage-

Table 1. Characteristics of the state of Hawaii Marine Life Conservation District (MLCD) and the University of Hawaii Marine Laboratory Refuge. Use: level of use as classified by Hawaii Division of Aquatic Resources (1992). Protection from fishing based on qualitative ranking of regulations, not on enforcement of these regulations. Percentage of total area allocated for permitted activities is listed for specific gear types and species

Protected area	Hectares	Year established	Use	Protection from fishing	Permitted activities
Oahu					
Hanauma Bay	40.8	1967	High	High	Complete no-take
Pupukea	72.5	1983[a] (2003)	Mod	Mod	Pole-and-line from shore Harvest of seaweed, *Selar cumenophthalmus* (Nov–Dec) and *Decapterus* spp. (Aug–Sep)
Waikiki	31.4	1988	High	High	Complete no-take
Moku o Loe, Univ. of Hawaii Marine Laboratory Refuge	29.6	1967	Low	High	Scientific collecting and propagation
Hawaii					
Kealakekua Bay	123.6	1969	High	Mod	Hook and line: 60% Throw net: 60% *Selar cumenophthalmus* and *Decapterus* spp.: 60% Crustaceans: 60%
Lapakahi	54.0	1979	Low	Low	Hook and line: 90% Throw net: 90% Lift net for *Decapterus* spp.: 90%
Waialea Bay	14.1	1985	Low	Low	Hook and line Netting
Old Kona Airport	105.9	1992	Mod	Mod	Throw net from shore, pole and line from shore, sea urchin collecting without scuba from 1 Jun to 1 Oct
Waiopae	26.2	2003	Mod	High	Complete no-take
Lanai					
Manele-Hulopoe	111.7	1976	Mod	Mod	Hook and line from shore All fishing except spear, trap, and net (other than throw net): 50%
Maui					
Molokini Shoal	35.7	1977	High	High	Trolling in 60% of MLCD
Honolua-Mokuleia Bay	18.2	1978	Mod	High	Complete no-take

[a]Pupukea MLCD modified rules and expanded boundaries in 2003

ment areas that were designed to reduce user conflicts through gear restrictions or rotational closures.

Location points, in either latitude and longitude or Universal Transverse Mercator (UTM) coordinates, were downloaded into a GPS. Once in the field, 2 divers navigated to waypoints using GPS and conducted a single 25 m transect. The direction of each transect was determined randomly along the isobath of that GPS point except in cases where that direction caused the transect to traverse multiple habitats. In those situations, transects were run within a habitat polygon at a similar isobath stratum.

Fish sampling methodology. Fish assemblages at each location were quantified using standard underwater visual belt transect survey methods (Brock 1954). A diver swam a 25 m transect at a constant speed and identified to the lowest possible taxon all fishes visible within 2.5 m to either side of the center-line (125 m² transect area). Swimming duration varied from 10 to 15 min, depending on habitat complexity and fish abundance. At the beginning of the survey, the diver visualized out as far as possible to enumerate all individuals potentially leaving the sampling area. In this manner, we were able to partially account for the behavior that targeted species acquire in areas frequented by spearfishers (Kulbicki 1998). To ensure consistency in data collection, surveys were only conducted if visibility was greater than 10 m (i.e. double the transect width).

Total length (TL) of fish was visually estimated to the nearest cm. Length estimates of fishes from censuses were converted to weight using the following length–weight relationship: $W = aSL^b$, where the parameters a and b are constants for the allometric growth equa-
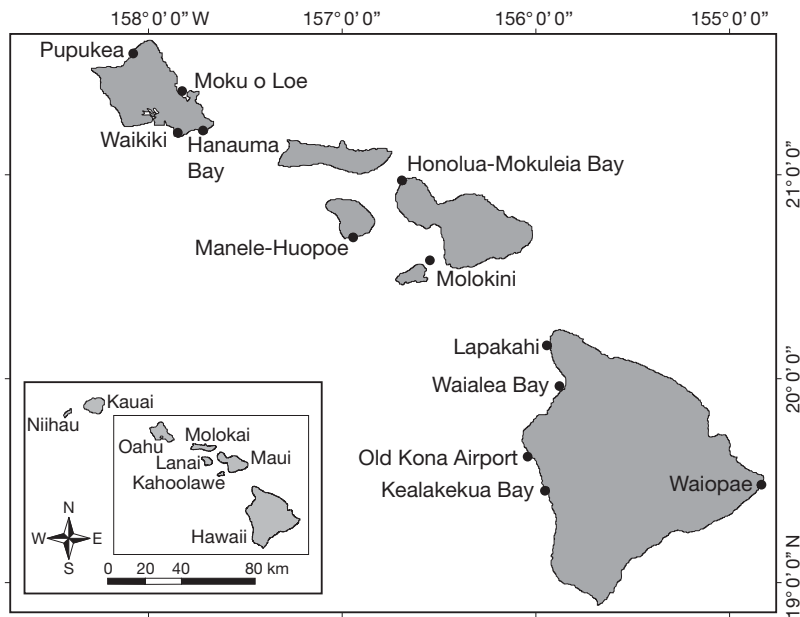
Fig. 1. Locations of Marine Life Conservation Districts (MLCDs) and Moku o Loe, the University of Hawaii Marine Laboratory Refuge (MLR)

tion, SL is standard length in mm, and *W* is weight in grams. TL was converted to SL by multiplying SL to TL-fitting parameters obtained from FishBase (www.fishbase.org) and other published and web-based sources. Length–weight fitting parameters were available for 150 species commonly observed on visual fish transects in Hawaii (Hawaii Cooperative Fishery Research Unit unpubl. data). In the cases where length–weight information did not exist for a given species, the parameters from similar bodied congeners were used. All biomass estimates were converted to metric tons per hectare (t ha^{-1}) to facilitate comparisons with other studies in Hawaii. Fish taxa were categorized into 3 trophic guilds (herbivores, secondary consumers, and apex predators) according to various published sources (e.g. Friedlander & DeMartini 2002) and FishBase (www.fishbase.org). Estimates of the abundance of apex predators from visual transects often have high variance associated with them, so some care is necessary when interpreting the results from this trophic group.

Fish sample size analysis. A pilot study was conducted in the Waikiki area to determine optimal sample size to adequately characterize the number of species and number of individuals per transect among the 4 major habitat types for each management regime in each study area. A technique developed by Bros & Cowell (1987) using the standard error of the mean (SEM) to resolve statistical power was used for this analysis. This method uses a Monte Carlo simulation procedure to generate a range of

sample sizes versus power. The sample size at which further increases in number of replicates does not substantially increase power (decreasing SEM) is taken as the minimum number of samples.

For number of species per transect, high and low SEM began to level off and converge at ca. 4 samples in the CHB and UCS habitats and ca. 8 samples for the MAC and UCH habitats. For number of individuals per transect, high and low SEM began to converge at 6 samples in the UCS habitat and 9 to 10 samples in the CHB, UCH, and MAC habitats. Given this set of results, 9 to 10 samples per habitat appeared to be adequate to control the SEM for number of individuals and number of species per transect and was the targeted sample size used per habitat and management stratum in each survey area.

Benthic survey techniques. On completion of the fish survey, benthic cover was assessed along the same 25 m transect line. During the first survey period (Waikiki area), digital video transects were used to measure coral species richness and percent coverage, but all subsequent surveys were conducted using the *in situ* planar point intercept quadrat method (Reed 1980) due to the long post-survey processing time (ca. 2 hr for 1 transect) and low taxonomic resolution of some substrate categories (e.g. macroalgae) using video. It should be noted that previous comparisons between methods showed no statistical difference in the overall benthic assemblage structure (Brown 2004).

For the video method, each transect was videotaped from a perpendicular angle at a height of 0.5 m above the substrate. Total area sampled along each transect was 12.8 m^2. Image analysis was conducted using 20 randomly selected non-overlapping video frames from each transect with 50 randomly selected points per frame. Based on previous analysis, this level of effort adequately characterized the substrate (Brown et al. 2004). Percent cover was tabulated for coral (by species), macroinvertebrates, and other benthic substrate types (coralline algae, turf algae, macroalgae, and sand).

For the *in situ* visual quadrats, each transect was stratified into 5 m segments with a single quadrat randomly allocated within each segment (N = 5). Twenty-five randomly selected intersections were marked on a 1 m^2 quadrat grid and used for substrate identification within each 5 × 5 m segment (n = 125 points per transect). Sample size was optimized by comparing

standard deviation versus sampling time as a function of number of points per quadrat (10, 25, or 50). Each point-intersection was identified using substrate categories of sand, coralline algae, turf algae, macroalgae, and coral. Coral and macroinvertebrates were identified to species level. Limitations of *in situ* methodology precluded taxonomic resolution of algae to species, so algae were identified to genera. Percent cover values for each substrate category and coral species were derived by dividing the number of occupied points by the total number of intersections (25) within each quadrat.

Rugosity methods. To measure reef rugosity or surface relief, a small link chain (1.3 cm per link) was draped along the length of the centerline of each transect (Risk 1972). Care was taken to ensure that the chain followed the contour of all natural fixed surfaces directly below the transect centerline. A ratio of distance along the reef surface contour (cd) to linear horizontal distance (ld) gave an index of spatial relief or rugosity (r): r = cd/ld.

Data analysis. For the purposes of this study, results focused on the entire fish assemblage rather than individual fish species. Number of individuals and biomass were $\ln(x+1)$ transformed prior to statistical analysis to conform to the assumptions of normality and homogeneity of variances (Zar 1999). Percent substrate cover data were arcsine-square root transformed prior to statistical analyses (Zar 1999). Non-metric multi dimensional scaling (MDS) analysis coupled with an analysis of similarities (ANOSIM) test were conducted using PRIMER v. 5 (Clarke & Gorley 2001) to examine fish biomass among habitats and management regimes. The data matrix consisted of mean fish biomass by species for each major habitat within each management strata at each overall location. A Bray-Curtis similarity matrix was created from the $\ln(x+1)$ transformed mean fish biomass matrix prior to conducting the MDS.

Fish assemblage characteristics among habitat types were compared using a Kruskal-Wallis rank sum test with Dunn's test for unplanned multiple comparisons. Within habitat types, fish assemblage characteristics were compared using Wilcoxon rank sum tests. Comparisons of individual trophic groups between management regimes and within habitat types was also compared using Wilcoxon rank sum tests.

To evaluate size-related differences between management regimes within habitats, we developed size spectra for each habitat and management strata (Dulvy et al. 2004). Size spectra were based on mean numerical density (no. ha^{-1}) for each 5 cm TL size class (10 to 65 cm for CHB and UCH, 10 to 50 cm for MAC and UCS), and described using least squares regression to relate $\log_{10}$-transformed numerical densities to body length. Size spectra were standardized by rescaling the midpoint of the length range to zero to remove the correlation between the slopes and intercept (Dulvy et al. 2004). Within each habitat type, an ANCOVA was conducted between the 2 regression models (MLCD and open area). Differences in the least square means (LSM) between management regimes were tested using Tukey's HSD.

Stepwise multiple regression analyses were conducted to assess the importance of various independent variables on fish assemblage characteristics (species richness, number of individuals, and biomass). Independent variables included percent cover of live coral, macroalgae, sand, turf algae, as well as rugosity, depth, and whether the transect was protected from fishing (protected = MLCDs). Percent cover data were arcsine-square root transformed prior to analyses. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion was based on Mallows' C_p criterion, an alternative measure of total squared error defined as:

$$C_p = (\text{SSE}_p/s^2) - (N - 2p)$$

where s^2 is the mean-square error (MSE) for the full model and SSE_p is the error sum of squares for the fitted subset regression model with p parameters. If C_p is graphed with p, Mallows (1973) recommended choosing the model where C_p first approached p. The Variance Inflation Factor (VIF) was used to measure the possible collinearity among explanatory variables where a value >10 is indicative of collinearity (Kleinbaum et al. 1988). The UCS habitat was excluded from the analysis with only MLCDs since it was not found in all protected areas.

RESULTS

Sampling effort

A total of 939 spatially independent surveys were conducted between 22 January 2002 and 22 December 2004 (Table 2). Sampling depth averaged 6.2 ± 5.2 m (SD) and ranged from 0.5 to 31.8 m. On average, ca. 9.3 ± 5.6 km of linear shoreline was surveyed for each protected area and its adjacent habitat. Of the total, 40% were in CHB, 29% were in UCH, 20% were in UCS, and 11% were in MAC. MLCDs comprised 40% of the samples, while 52% were conducted in areas open to fishing, with the remaining 8% in FMAs. FMAs were excluded from further analyses owing to this small sample size, uneven distribution among the protected areas, and a lack of representative habitat types, resulting in an unbalanced design.

Table 2. Sample allocation among habitat types and management regimes. CHB: colonized hard bottom; UCH: uncolonized hard bottom; MAC: macro-algae; UCS: unconsolidated sediments (sand); FMA: Fisheries Management Area; MLCD: marine Life Conservation District

Habitat	Management	N	Avg. (±SD)	Depth (m)	
				Min.	Max.
CHB	FMA	41	8.14 (3.29)	1.52	16.46
	MLCD	163	5.67 (3.87)	0.61	19.81
	Open	169	5.67 (3.81)	0.49	15.85
UCH	FMA	21	3.06 (1.46)	0.91	5.79
	MLCD	110	3.85 (3.05)	0.49	14.94
	Open	142	5.53 (4.39)	0.49	19.11
MAC	FMA	9	0.93 (0.22)	0.46	1.22
	MLCD	21	1.20 (0.84)	0.61	4.57
	Open	76	5.08 (6.47)	0.61	22.86
UCS	FMA	10	13.26 (3.56)	7.92	18.29
	MLCD	79	8.45 (5.53)	1.52	32.00
	Open	98	8.47 (6.35)	0.61	24.08
Total		939			

Table 3. Comparisons of fish assemblage characteristics among management regimes by major habitat type (defined in Table 2). Values are means (±SD) for all transects in each stratum. CHB: N_{MLCD} = 163, N_{Open} = 169; UCH: N_{MLCD} = 110, N_{Open} = 142; MAC: N_{MLCD} = 21, N_{Open} = 76; UCS: N_{MLCD} = 79, N_{Open} = 98; Z: statistical results of Mann-Whitney rank sum tests

Habitat	MLCD	Open	Percent difference	Z	p
Species richness					
CHB	21.15 (0.47)	18.58 (0.46)	13.83	3.61	<0.001
UCH	18.44 (7.10)	12.85 (7.05)	43.50	5.64	<0.001
MAC	6.62 (4.65)	5.13 (5.00)	29.04	1.77	0.076
UCS	2.33 (3.34)	1.06 (1.68)	119.81	3.10	0.002
Numbers (no. m^{-2})					
CHB	1.16 (0.69)	1.09 (0.69)	5.95	1.22	0.224
UCH	0.82 (0.46)	0.58 (0.46)	41.82	4.03	<0.001
MAC	0.27 (0.22)	0.16 (0.23)	68.10	3.04	0.002
UCS	0.05 (0.09)	0.02 (0.05)	133.33	2.62	0.009
Biomass (t ha^{-1})					
CHB	0.97 (0.99)	0.50 (0.37)	94.00	6.66	<0.001
UCH	0.87 (0.80)	0.30 (0.38)	190.00	7.44	<0.001
MAC	0.12 (0.21)	0.04 (0.07)	200.00	1.60	0.110
UCS	0.18 (0.70)	0.02 (0.02)	800.00	4.23	<0.001

Fish assemblage characteristics

Fish assemblage characteristics varied greatly by habitat type and management strata (Table 3). Species richness was significantly different among the 4 major habitat types (H = 515.7, p < 0.001, CHB > UCH > MAC > UCS) with CHB averaging 19.8 ± 6.2 (SD) species per transect (125 m^2) compared to UCS habitats which averaged only 1.6 ± 2.6 species. Within all habitat types except MAC, species richness was signif-

icantly higher in MLCDs compared with areas open to fishing (Table 3).

Significant differences among all 4 habitat types were detected for number of individuals (H = 520.8, p < 0.001, CHB > UCH > MAC > UCS). The average number of ind. m^{-2} ranged from 1.16 ± 0.69 (SD) in CHB within MLCDs to 0.03 (± 0.07 SD) in UCS open to fishing. CHB was the only habitat type that did not show a significant difference in number of individuals between MLCDs and fished areas.

Fish biomass differed significantly among the 4 major habitat types except between MAC and UCS (H = 446.2, p < 0.001, CHB > UCH > MAC = UCS). MLCDs had significantly higher biomass than fished areas for all habitat types except MAC. Biomass was 94% higher in CHB habitats within MLCDs compared to areas open to fishing. The largest differences in biomass between management regimes within a single habitat type occurred in UCS, where biomass in the MLCDs was 8 times higher than areas open to fishing. The mid-point height of the numerical density-to-body size relationship (i.e. abundance at the mid-point of the length distribution) was significantly higher in MLCDs compared to areas open to fishing for all habitat types (Table 4, Fig. 2).

Multivariate comparison of fish assemblages

Comparison of fish assemblages (based on biomass) among all locations showed strong correlations with habitat (Fig. 3). ANOSIM found significant differences in assemblage biomass among all habitat types (ANOSIM Global R = 0.51, p < 0.001). Pairwise comparisons among habitat types found fish assemblages in the CHB and UCH habitats to be most similar in structure (Table 5). Much of the MAC habitat sampled was macroalgae growing on hard substrate, and as a result showed similarities with the other hard bottom assemblages. The fish assemblages in the UCS habitats were highly variable but distinct from the other habitat types.

Table 4. ANCOVA comparing size spectra (Log$_{10}$ numerical densities vs. body length class) between management regimes (MLCD vs. Open) for each habitat type (defined in Table 2). Least square means (LSM) compared using Tukey's HSD (α = 0.05)

CHB	R^2 = 0.97				LSM comparison
Source	df	MS	F	p	
Model	2	17.5	346.9	<0.001	
Length class	1	34.5	682.5	<0.001	
Management	1	0.6	11.3	0.003	MLCD (1.9) > Open (1.6)
Error	21	0.5			
UCH	R^2 = 0.95				
Source	df	MS	F	p	
Model	2	14.5	212.0	<0.001	
Length class	1	27.9	407.6	<0.001	
Management	1	1.1	16.4	<0.001	MLCD (1.9) > Open (1.5)
Error	21	0.5			
MAC	R^2 = 0.92				
Source	df	MS	F	p	
Model	2	6.4	90.9	<0.001	
Length class	1	12.2	173.5	<0.001	
Management	1	0.6	8.3	0.01	MLCD (1.7) > Open (1.3)
Error	21	0.1			
UCS	R^2 = 0.84				
Source	df	MS	F	p	
Model	2	3.1	39.0	<0.001	
Length class	1	5.5	5.1	<0.001	
Management	1	1.0	1.1	0.002	MLCD (1.4) > Open (0.9)
Error	17	0.1			

Fig. 2. Size spectra of log$_{10}$-transformed number of fish ha^{-1} by standardized size class (total length, TL) for all fishes, in sites open to fishing and in MLCDs by habitat type: (A) colonized hard bottom (CHB); (B) uncolonized hard bottom (UCH); (C) macroalgae (MAC); (D) unconsolidated sediments (sand) (UCS). ANCOVA results in Table 4

Fish assemblages (based on biomass) differed significantly between MLCDs and open areas for CHB (ANOSIM Global R = 0.15, p = 0.009) and UCH (ANOSIM Global R = 0.317, p = 0.004) habitats. Assemblages for the 2 management regimes were similar for UCS (ANOSIM Global R = 0.07, p = 0.217) and MAC (ANOSIM Global R = 0.182, p = 0.381) habitats, although a limited number of sampling locations in MAC made statistical comparisons problematic.

Factors influencing fish assemblages

Rugosity accounted for 50% of the variability in species richness among all sampling locations (Table 6A). The presence of sand and macroalgae had negative relationships with species richness and explained an additional 13 and 3% of the variability, respectively. Protection from fishing only accounted for an additional 1% of the variance in species richness. Sand had a negative relationship with number of individuals, explaining nearly 57% of the variability (Table 6B). Rugosity contributed an additional 10% to number of individuals, followed by protection from fishing (1%), live coral cover (0.8%), and turf algae (0.6%). Approximately 34% of the variability in biomass was explained by rugosity, with an additional 7% explained by protection from fishing (Table 6C). Sand and macroalgae displayed negative relationships with biomass and explained an additional 4 and 2% of the variability, respectively.

Rugosity was the most important parameter in explaining variability in species richness, and biomass, and was also important for number of individuals. As a result, rugosity was used as a covariate to examine the importance of management regimes in structuring fish assemblages. ANCOVA revealed significantly higher fish biomass in protected areas compared to open areas with similar rugosity ($F_{1,21}$ = 24.0, p < 0.001, R^2 = 0.78, LSM: MLCD > Open, Fig. 4).
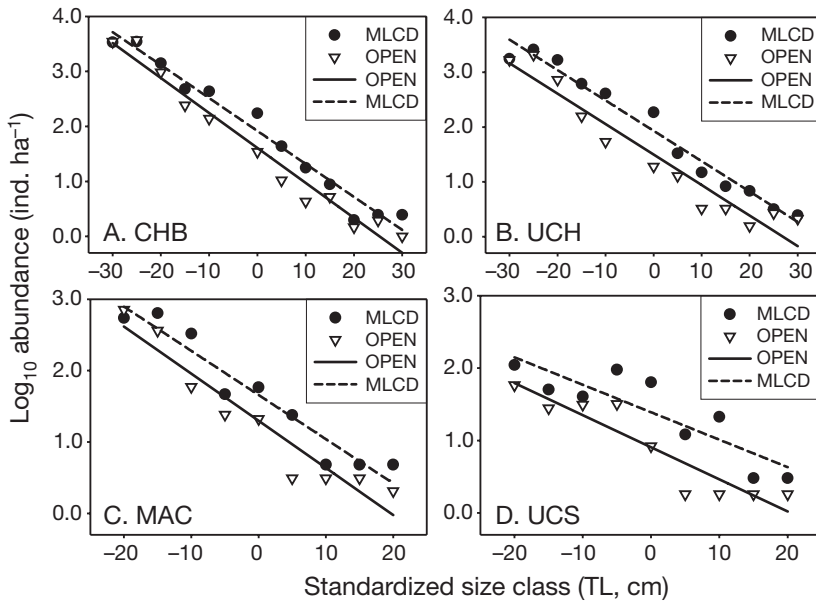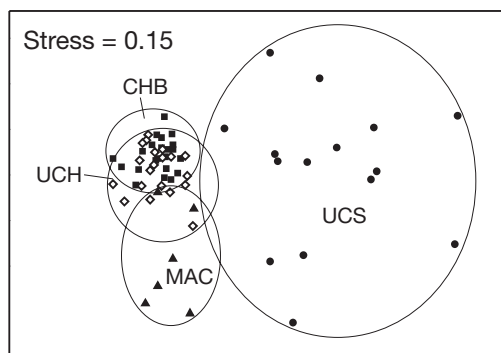
Fig. 3. Nonmetric multi-dimensional scaling plot of sampling locations by habitat type (defined in Table 2). Input values are mean fish biomass (t ha^{-1}) by species for each habitat type, N = 64. Circles encompass locations with similar habitat types showing high concordance of fish biomass levels within CHB and UCH habitats and low concordance within UCS habitats
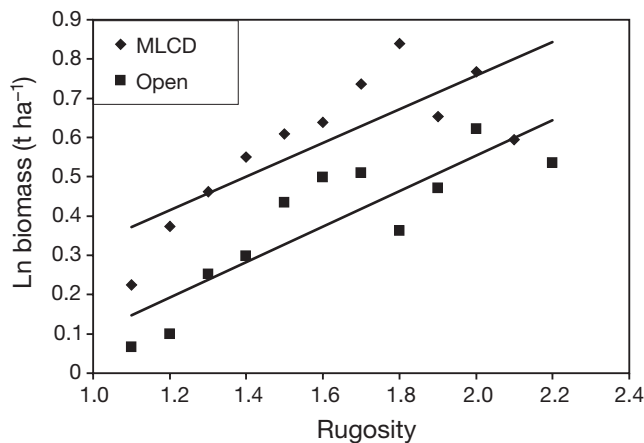

Fig. 4. Relationship between rugosity and ln biomass (t ha^{-1}) for hardbottom habitats within all MLCDs and areas open to fishing. $F_{1, 21} = 24.0$, $p < 0.001$, LSM intercept: MLCD > Open, ($\alpha = 0.05$)

Table 5. Similarities of fish assemblages (based on biomass) among habitat types (defined in Table 2). ANOSIM Global R = 0.51, p < 0.001. Pairwise tests results

Habitat comparison	R statistic	p	Similarity
CHB and UCH	0.126	0.003	Most
UCS and MAC	0.415	0.001	
UCH and MAC	0.643	0.001	
UCH and UCS	0.725	0.001	
CHB and UCS	0.753	0.001	
CHB and MAC	0.858	0.001	Least

Table 6. Stepwise multiple regression analyses for fish assemblage characteristics among all habitat types (defined in Table 2). Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion based on Mallow's C_p criterion for selecting a model. Percent cover data were arcsin square root transformed prior to analyses. Biomass and number of individuals ln(x+1) transformed for statistical analyses. p: no. variables; VIF: Variance Inflation Factor

Parameter	Estimate	Seq SS	F ratio	R^2	C_p	p	VIF
(A) Species richness							
Rugosity	0.54	41212.54	149.93	0.502	601.16	2	2.34
Sand	−15.34	10452.88	82.39	0.629	211.28	3	4.38
Macroalgae	−7.89	2558.54	24.40	0.661	117.36	4	1.29
Management	−1.26	989.38	49.84	0.673	82.27	5	1.07
Depth	0.21	1032.89	33.31	0.685	45.55	6	1.20
Turf algae	7.79	422.52	33.65	0.690	31.71	7	2.52
Coral cover	10.83	685.77	25.71	0.699	8.00	8	3.16
(B) Number of individuals							
Sand	−1.85	543.85	120.95	0.567	404.89	2	3.73
Rugosity	0.05	102.47	107.68	0.674	77.63	3	2.33
Management	−0.10	9.63	29.49	0.684	48.68	4	1.03
Coral cover	1.47	8.69	44.13	0.693	22.75	5	2.89
Turf algae	0.63	6.14	19.76	0.699	5.02	6	2.42
(C) Biomass							
Rugosity	0.02	35.41	141.24	0.338	235.79	2	1.60
Management	−0.09	7.26	115.92	0.408	115.54	3	1.05
Sand	−0.49	4.53	102.76	0.451	41.30	4	1.61
Macroalgae	−0.45	2.45	41.29	0.474	2.14	5	1.11

Trophic composition

Overall, primary consumers accounted for 62% of total fish biomass, followed by secondary consumers (29%) and apex predators (9%), respectively. Biomass of all trophic groups was significantly higher in the MLCDs compared with open areas for CHB, UCH and UCS habitats (Table 7A,B,D). For primary consumers, differences in biomass between the MLCDs and open areas were 51% and 27% for CHB and UCH, respectively. As to be expected, densities of this trophic group were low in UCS, accounting for only 14% of the biomass in the MLCDs and <1% in the open areas.

Apex predators showed the largest differences in biomass between MLCDs and open areas for these 3 habitat types. The most pronounced differences were in UCS, where apex predators accounted for the majority of the biomass in the MLCDs (62%), but <1% in the open areas. Numerical density of fishes was low overall in this habitat type and the few large apex predators observed may bias these results. In CHB, apex predators accounted for 12% of the total biomass within MLCDs but only 3% within open areas. Biomass of apex predators was low overall in UCH but still significantly higher (p < 0.001) in MLCDs compared to open areas.

Within MAC habitats, no significant differences were found in biomass between any trophic groups, although primary consumers were 9 times more

Table 7. Trophic comparisons of fish biomass (t ha^{-1}) among management regimes by major habitat type (defined in Table 2). Values are means (±SD) for all transects in each stratum. Z = statistical results of Mann-Whitney rank sum tests

Trophic	Mean (SD)	Percentage of total	Mean (SD)	Percentage of total	Z	p
(A) CHB	MLCD, N = 163		Open, N = 169			
Primary	0.59 (0.67)	60.9	0.29 (0.28)	58.7	5.92	<0.0001
Secondary	0.26 (0.24)	26.5	0.19 (0.18)	37.9	3.56	<0.0001
Apex	0.12 (0.48)	12.6	0.02 (0.10)	3.4	4.76	<0.0001
(B) UCH	MLCD, N = 110		Open, N = 142			
Primary	0.67 (0.70)	76.1	0.19 (0.28)	62.5	7.36	<0.0001
Secondary	0.19 (0.21)	21.3	0.11 (0.16)	37.0	4.31	<0.0001
Apex	0.02 (0.08)	2.6	<0.01 (0.01)	0.5	4.54	<0.0001
(C) MAC	MLCD, N = 21		Open, N = 76			
Primary	0.09 (0.16)	75.0	0.01 (0.05)	37.3	1.68	0.09
Secondary	0.03 (0.05)	25.0	0.02 (0.04)	59.9	0.64	0.52
Apex	<0.01 (<0.01)	<0.1	<0.01 (<0.01)	2.8	0.90	0.36
(D) UCS	MLCD, N = 79		Open, N = 98			
Primary	0.03 (0.10)	14.5	<0.01 (0.0)	0.2	3.60	<0.0001
Secondary	0.04 (0.13)	23.4	0.02 (0.11)	92.8	3.30	<0.0001
Apex	0.11 (0.65)	62.2	<0.01 (0.01)	7.0	3.42	<0.0001

abundant by weight within MLCD compared to open areas (Table 7C). High variance, small sample sizes, and overall low biomass within this habitat type contributed to the lack of statistical significance.

Herbivore biomass showed a significant negative relationship with macroalgal cover for both MLCDs ($r = -0.70$, $p = 0.011$) and open areas ($r = -0.82$, $p = 0.0011$) (Fig. 5). The highest macroalgae cover in the MLCDs was found at Waikiki and Moku o Loe, where invasive algae such as *Gracilaria salicornis* and *Kappaphycus* spp. have proliferated. The Waiopae MLCD
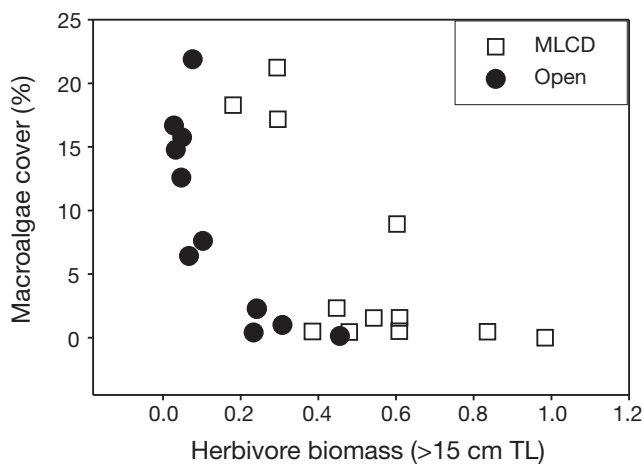

Fig. 5. Comparison of mean percent macroalgae cover and mean herbivore biomass (t ha^{-1}) within protected (MLCD) and open (Open) areas

also had high macroalgae cover dominated by cyanobacteria that was likely associated with cesspools from adjacent shoreline homes.

Factors influencing fish assemblages among MLCDs

Within the protected areas, depth explained nearly 64% of the variance in species richness, while sand on hard bottom habitats (<0.4 ha MMU) contributed an additional 13.4% and had a negative relationship with species richness (Table 8A). Rugosity accounted for 62.5% of the variability in number of individuals and was the only parameter included in the model selection (Table 8B). Nearly 52% of the variance in fish biomass within MLCDs was explained by rugosity. The variance in depth, which describes larger scale measures of habitat complexity or rugosity, explained 8.2% of the variability in biomass. Macroalgae was negatively correlated with biomass and explained an additional 11.9% of the variability in this parameter (Table 8C). There were no significant correlations between age of the protected areas and fish biomass, species richness, or number of individuals (Spearman's rho: p > 0.05 for all).

DISCUSSION

Unique fish assemblages were observed among different habitat types and between different fisheries management regimes within specific habitat types. CHB and UCH habitats had more species, more individuals, and higher biomass than MAC and UCS habitats. Within habitat types, assemblage characteristics were typically higher for MLCDs compared with adjacent fished areas emphasizing the importance of protection from fishing regardless of habitat type. Although habitat quality in a few MLCDs is higher than adjacent areas, overall comparisons between all MLCDs and adjacent areas showed little difference and suggest that differences in fish assemblage structure between MLCDs and open access areas were not attributed to differences in habitat quality, but rather differences in other factors, such as fishing pressure (Friedlander et al. 2007).

Apex predators have been severely overexploited in the MHI (Friedlander & DeMartini 2002) and this trophic group showed the greatest difference in abun-

Table 8. Stepwise multiple regression analyses for fish assemblage characteristics among all MLCDs. Input values are means for each location. UCS was excluded due to the absence of this habitat type in many MLCDs. Probability to enter the model was 0.25 and probability to leave was 0.10. Model selection criterion based on Mallow's C_p criterion for selecting a model. Percent cover data were arcsine-square root transformed prior to analyses. Biomass and number of individuals ln(x+1) transformed for statistical analyses. VIF: Variance Inflation Factor

Parameter	Estimate	Seq SS	F ratio	R^2	C_p	p	VIF
(A) Species richness							
Depth	1.38	190.15	13.40	0.639	0.56	2	1.19
Sand	−27.57	39.96	5.34	0.774	−0.62	3	1.19
(B) Number of individuals							
Rugosity	0.10	0.81	16.68	0.625	−1.37	2	1.00
(C) Biomass							
Rugosity	0.03	0.22	3.58	0.516	−0.02	2	1.50
Macroalgae	−1.81	0.05	5.60	0.635	0.02	3	1.52
Variance in depth	0.01	0.04	2.32	0.717	0.67	4	2.12

dance and biomass between MLCDs and fished areas. These predators and other large, mobile species may not be adequately surveyed using underwater visual census (UVC) techniques, and methods such as longlines and hook-and-line fishing are often used to estimate abundance for these species (Pikitch et al. 2005). Despite limitations to the method, UVCs have been found to be significantly and positively correlated with various fishing methods (e.g. longlining, line fishing) for reef fish stocks in New Caledonia (Kulbicki et al. 2000); we therefore feel that UVCs provide a robust relative comparison of predator biomass among sampling strata.

Although overall biomass was low in sand habitats, apex predators accounted for 62% of the biomass in this habitat within MLCDs. This highlights the importance of sand as a corridor for apex predators and the need to include sand habitats into reserve design. These corridors may provide transit pathways among hard bottom habitats or serve as important feeding locations for these top predators.

Several of the MLCDs (e.g. Waiopae, Moku o Loe) included shallow water habitats that were identified as important nursery areas for a number of fishes that make ontogenetic movements into deeper water habitats with age (Friedlander et al. 2007). Elsewhere in Hawaii, DeMartini (2004) has identified backreef, lagoonal patch reef, and other sheltered habitats as nursery areas for juveniles.

Rugosity explained the majority of the variability in species richness and biomass and also provides an important contribution to variation in number of individuals. When compared among areas of similar rugosity, protected areas harbored significantly greater biomass than areas open to fishing. Within MLCDs, rugosity explained most of the variability in number of

individuals (62%) and biomass (52%). Variance in depth reflects a larger scale measure of complexity and explained slightly more than 8% of fish biomass among MLCDs.

MLCDs with greater depth ranges had greater species richness compared to shallower protected areas with narrower depth ranges. A broader depth range encompasses a greater range of habitat types, microhabitat variability, and reef complexity that harbors more diverse fish assemblages. The exclusion of deeper habitats from some MLCDs makes organisms that utilize these habitats for diel and ontogenetic movement vulnerable to exploitation.

Macroalgae cover had a negative relationship with a number of fish assemblage characteristics. There were strong negative relationships between the biomass of large herbivores and macroalgae cover for both MLCDs and areas open to fishing. The higher herbivore biomass in protected areas partially accounted for the lower overall macroalgae cover observed in these areas compared with fished areas. Macroalgae overgrows and reduces the structural complexity of the reef (Williams & Polunin 2001); in particular, introduced and invasive algae have proliferated around the urban areas of Oahu and Maui (Smith et al. 2002) exacerbating the problem that overfishing of herbivores has created in these areas. Reduced biomass of herbivorous fishes as a result of overfishing is thought to contribute to the increase in macroalgae cover observed on many reefs around the world (Hughes 1994, Jackson et al. 2001), but is only one of many factors leading to phase shifts from coral to macroalgae on coral reefs (Hughes 1994).

Despite the fact that MPAs in Hawaii have been in existence since the 1960s, no comprehensive assessment has been conducted until now. Many MLCDs in Hawaii were initially established to support the State of Hawaii's conservation and education objectives, not to enhance fish stocks or conserve ecosystems. As a consequence, most are currently too small to provide these benefits. Their small size and limited habitat types do not allow for the entire fish assemblage to function in a natural manner (Friedlander et al. 2007). In addition, many of these MLCDs do not incorporate the range of habitats and depths that tend to have higher species richness and diversity. Inclusion of deeper habitats not only enhances the biodiversity of the protected area, but also protects critical habitats for larger-bodied fishes that undergo ontogenetic movements to deeper habitats with age (Lindeman et al. 2000).

The concept of essential fish habitat (NOAA 1996) and the principles behind developing MPAs necessitate examination of greater spatial ranges than those at which typical experiments are conducted. The results of this study suggest that for future MPAs in nearshore waters in Hawaii to be effective, they should contain CHB habitats (live coral cover >10%) with low macroalgal cover (<10%), high topographical complexity (rugosity >1.5), access to UCS habitats, and a wide range of depths (e.g. 0 to 30 m).

Analysis of reef fish distribution among all habitats available in the seascape is critical to developing better informed resource management solutions. Habitat plays an important role in structuring fish assemblages, yet most studies of marine reserves fail to measure habitat quality (Côte et al. 2001). In a review of 89 marine reserve studies, Halpern (2003) acknowledged that differences in habitat characteristics among reserves made comparisons and analyses difficult. In one of the few studies to examine reserve habitat, McClanahan (1994) found that given equal habitat quality, reserves in Kenya had significantly more species than non-reserve areas.

The landscape process approach focuses in large part on providing corridors to link networks of protected areas (Rosenberg et al. 1997). Marine reserve networks have the greatest chance of including all species, life stages, and ecological linkages if they encompass representative portions of all ecologically relevant habitat types in a replicated manner (Sala et al. 2002). Habitats are a good surrogate for species, so a system of protected areas that incorporates all habitat types is likely to also provide refuge for most species (Ward et al. 1999, Sala et al. 2002, Friedlander et al. 2003b). In fact, habitats are generally a better focus for protected area design than species because they are easier to map and are more closely tied to the ecological processes that should ultimately be conserved (Sladek Nowlis & Friedlander 2005).

Recently, spatially explicit biogeographic assessments have provided robust analytical results to strengthen the sustainable management of marine resources within and adjacent to MPAs (Monaco et al. 2005, Monaco et al. 2007). A logical progression of events leading to the establishment of an MPA would first include an assessment of the function of available habitats relative to managed fishery resources. The high variance in fish assemblage characteristics among different habitat types and the unique fish assemblages associated with these different habitats means that sampling and analyses need to be stratified by habitat for more robust statistical comparisons.

MPA design must consider the habitat requirements and life histories of the species of interest as well as the extent of fishing pressure in the adjacent area.

Enforcement must be effective to achieve the goals of the MPAs, and the design of the protected area should consider how to maximize enforcement. Future protected area design in the MHI needs to incorporate a mosaic of habitats to support viable reef fish populations. Complex habitats will harbor higher biomass and greater species richness. Shallow nearshore habitats are necessary for recruit settlement and juvenile survival, while deeper habitats are important foraging, sheltering, and spawning sites for large adults. To more effectively sample organisms across the seascape and examine habitat utilization patterns, complementary methods that incorporate movement patterns and alternative sampling methods need to be employed (Chapman et al. 2005).

CONCLUSIONS

This study demonstrates that certain habitat qualities (e.g. high rugosity, large depth range, and low macroalgal cover) in addition to protection from fishing appear essential to enhancing fish assemblages in Hawaii. By identifying essential fish habitat and other sensitive and important habitats, MPAs can be designed to maximize protection for vulnerable life stages (Lindeman et al. 2000). Exclusion of these essential habitats would most certainly impose a bottleneck at which population and growth potential might be compromised (Christensen et al. 2003).

Conservation and ecosystem issues will dominate fisheries management in coming years. Hopefully this will focus a greater amount of effort on conserving entire ecosystems and the variety of all habitats that constitute them. The integration of mapping and monitoring of coral reef ecosystems and reef fish habitat utilization patterns can help managers make informed decisions about MPA design and effectiveness, as well as helping to define essential fish habitat and ecosystem function. Spatial information is often underutilized owing to the lack of capability to explore spatial and temporal relationships between species distributions and environmental gradients across large spatial scales (Battista & Monaco 2004). The approach taken in this study, which attempts to make a functional match between habitats and fishes to be preserved, is appropriate for selecting, evaluating, and managing reserves and should aid in decisions regarding existing and future MPAs.

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