COUPLING ECOLOGY AND GIS TO EVALUATE EFFICACY OF MARINE PROTECTED AREAS IN HAWAII

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Abstract. In order to properly determine the efficacy of marine protected areas (MPAs), a seascape perspective that integrates ecosystem elements at the appropriate ecological scale is necessary. Over the past four decades, Hawaii has developed a system of 11 Marine Life Conservation Districts (MLCDs) to conserve and replenish marine resources around the state. Initially established to provide opportunities for public interaction with the marine environment, these MLCDs vary in size, habitat quality, and management regimes, providing an excellent opportunity to test hypotheses concerning MPA design and function using multiple discrete sampling units. Digital benthic habitat maps for all MLCDs and adjacent habitats were used to evaluate the efficacy of existing MLCDs using a spatially explicit stratified random sampling design. Analysis of benthic cover validated the a priori classification of habitat types and provided justification for using these habitat strata to conduct stratified random sampling and analyses of fish habitat utilization patterns. Results showed that a number of fish assemblage characteristics (e.g., species richness, biomass, diversity) vary among habitat types, but were significantly higher in MLCDs compared with adjacent fished areas across all habitat types. Overall fish biomass was 2.6 times greater in the MLCDs compared to open areas. In addition, apex predators and other species were more abundant and larger in the MLCDs, illustrating the effectiveness of these closures in conserving fish populations within their boundaries. Habitat type, protected area size, and level of protection from fishing were all important determinates of MLCD effectiveness with respect to their associated fish assemblages. Although size of these protected areas was positively correlated with a number of fish assemblage characteristics, all appear too small to have any measurable influence on the adjacent fished areas. These protected areas were not designed for biodiversity conservation or fisheries enhancement yet still provide varying degrees of protection for fish populations within their boundaries. Implementing this type of biogeographic process, using remote sensing technology and sampling across the range of habitats present within the seascape, provides a robust evaluation of existing MPAs and can help to define ecologically relevant boundaries for future MPA design in a range of locations.

Key words: biogeography; essential fish habitat; GIS; Hawaii; MPA efficacy; spatial ecology.

INTRODUCTION

Coral reef ecosystems are facing overexploitation and severe depletion on a global scale (Jackson et al. 2001, Bellwood et al. 2004, Pandolfi et al. 2005). Although pollution, coastal development, invasive species, and global climate change all impact coral reefs, fishing exerts the most direct and pervasive influence on these and other marine ecosystems (Jennings and Kaiser 1998, Jackson et al. 2001). Fishing down of marine food webs has been occurring for more than a century and this has led to large-scale changes throughout the world's oceans (Pauly et al. 1998, Pauly et al. 2001). The most dramatic decline has been the loss of large apex predators (Myers and

Worm 2003, 2005) and the progressive shift toward harvest of lower trophic groups that has led to large changes to coral reef ecosystems worldwide (Jennings and Polunin 1996, Russ and Alcala 1996, Beets 1997, Ault et al. 1998).

The poor performance of conventional fisheries management has led to increased interest among marine resource managers in marine protected areas (MPAs), areas of the sea that regulate human activities (Roberts and Polunin 1993, Bohnsack 1998, National Research Council 2001, Russ 2002, Sladek Nowlis and Friedlander 2005). Within the broader category of MPAs are no-take marine reserves, that create an off-limits population, which in theory (Beverton and Holt 1957, Polacheck 1990, DeMartini 1993, Sladek Nowlis and Roberts 1999) and empirically (McClanahan and Kaunda-Arara 1996, Roberts et al. 2001, Russ et al. 2004, Abesamis and Russ 2005) have been shown to conserve fish stocks within their boundaries and provide fisheries benefits outside these protected areas. MPAs

TABLE 1. Summary characteristics of State of Hawaii Marine Life Conservation Districts (MLCD) and the University of Hawaii Marine Laboratory Refuge.

Protected area	Area (km^2)	Year established	Use	Protection from fishing	Permitted activities
Oahu					
Hanauma Bay	0.41	1967	high	high	complete no-take
Pupukea	0.72	1983† (2003)	mod	mod	pole-and-line from shore; harvest of seaweed, *Selar crumenophthalmus* (Nov–Dec) and *Decapterus* spp. (Aug–Sep)
Waikiki	0.31	1988	high	high	complete no-take
Moku o Loe‡	0.30	1967	low	high	scientific collecting and propagation
Hawaii					
Kealakekua Bay	1.24	1969	high	mod	hook and line 60%; thrownet 60%; *Selar crumenophthalmus* and *Decapterus* spp. 60%; crustaceans 60%
Lapakahi	0.54	1979	low	low	hook and line 90%; thrownet 90%; liftnet for *Decapterus* spp. 90%
Waialea Bay	0.14	1985	low	low	hook and line; netting
Old Kona airport	1.06	1992	mod	mod	thrownet from shore, pole and line from shore, sea urchin collecting without scuba 1 Jun–1 Oct
Waiopae	0.26	2000	mod	high	complete no-take
Lanai					
Manele-Hulopoe	1.12	1976	mod	mod	hook and line from shore; all fishing except spear, trap, and net (other than thrownet) 50%
Maui					
Molokini Shoal	0.36	1977	high	high	trolling in 60% of MLCD
Honolua-Mokuleia Bay	0.18	1978	mod	high	complete no-take

Notes: "Use" denotes the level of use as classified by Hawaii Department of Land and Natural Resources, Division of Aquatic Resources (Hawaii Division of Aquatic Resources 1992). Protection from fishing is based on qualitative ranking of regulations, not on enforcement of these regulations. Percentages are the percentage of total areas where permitted activity is allowed.

† Pupukea MLCD modified rules and expanded boundaries in 2003.

‡ University of Hawaii Marine Laboratory Refuge.

also have many non-fisheries benefits, such as protecting biodiversity and ecosystem structure, serving as biological reference areas, and providing nonconsumptive recreational activities (Bohnsack 1998, Roberts 2005).

Despite the extensive advocacy and widespread implementation of MPAs, there are significant gaps in the science of MPA design and function (Botsford et al. 2003, Sale et al. 2005). In order to more effectively evaluate and design MPAs, a seascape approach is necessary to characterize ecosystem patterns at scales that are commensurate with the resources and their users (Sala et al. 2002, Monaco et al. 2005). MPAs need to be viewed in the larger context of the entire ecosystem and their design needs to consider the habitat requirements and life histories of the species of interest, as well as the extent to which these habitats interact at larger spatial scales (Sladek Nowlis and Friedlander 2004). 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).

Remote sensing has been used to develop benthic habitat maps of coastal marine environments at large spatial scale for over 30 years (Mumby et al. 1997, Green et al. 2000; reviewed by Mumby et al. 2004). Digital benthic habitat maps derived from high-resolution aerial photography have been used to help define spatial and temporal distributions by life stage of fishes and invertebrates, determine species habitat affinities, and understand ecological connections among habitats (Monaco et al. 1998). Coupling the distribution of habitats and species habitat affinities using geographical information system (GIS) technology elucidates species habitat utilization patterns for a single species and/or assemblages of animals (Rubec et al. 1999, Kendall et al. 2003, Ault et al. 2005). This integrated approach is useful in quantitatively defining essential fish habitat (Clark et al. 2003) and defining biologically relevant boundaries of marine protected areas (Christensen et al. 2003, Friedlander et al. 2003b).

In Hawaii, declining fisheries resources (Shomura 1997, Friedlander and DeMartini 2002, Tissot and Hallacher 2003) and overall marine ecosystem degradation (Hunter and Evans 1995, Smith et al. 2002) has led to a call for the expanded use of MPAs as a tool to more effectively manage these resources. Hawaii established its first MPA over 30 years ago, and since that time numerous protected areas have been established, with varying levels of protection, ranging from complete "no-take" areas to areas that have allowed a wide variety of activities to occur within their boundaries (Table 1). Criteria for designation of MLCDs included (1) the marine life and its potential for increase, (2) its pristine state, (3) compatibility with existing uses within and adjoining the MLCD, (4) geological features that provide well defined boundaries for enforcement, and (5) the site's ability to support public safety and accessibility from the shoreline (Hawaii Division of Aquatic Resources 1992). Candidate sites

TABLE 2.   Error matrix demonstrating the user's, producer's, and overall accuracy for the four major habitat strata (colonized hard bottom [CHB], uncolonized hard bottom [UCH], unconsolidated sediment [UCS], and macroalgae [MAC]).

Habitat type	CHB	UCH	UCS	MAC	Total	User's accuracy (%)
CHB	387	24	11	3	425	91
UCH	4	60	3	5	72	83
UCS	11	2	226	7	246	92
MAC	2	13	6	169	190	89
Total	404	99	246	184		
Producer's accuracy (%)	96	61	92	92		

Note: Values for CHB, UCH, UCS, MAC, and Total are the total number of field reference points in each habitat type. Overall accuracy is 90.2%.

were nominated through public recommendations, legislative mandate, biological surveys, and other means.

Owing to the diversity of existing MPAs in Hawaii, it is critical that the efficacies of these areas are evaluated to ensure the effective design of future MPAs in the state. However, to have the capability to address the effectiveness of MPAs, the first step in this process is to define species habitat utilization patterns across varying levels of habitat quality and protection from fishing. The objective of this study was to evaluate existing MPAs in Hawaii using a spatially explicit sampling design to help identify the ecological processes and management regimes that result in productive fish populations within their borders.

METHODS

Benthic habitat mapping

The National Oceanic and Atmospheric Administration (NOAA) acquired and visually interpreted ortho-rectified aerial photography, IKONOS satellite imagery, and hyperspectral imagery for the near-shore waters (to 25 m depth) of the majority 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 of 0.004 km². Visual interpretation of the imagery was guided by a hierarchical classification scheme that defined and delineated benthic polygon types based on habitat classifications that included ecologically-relevant locational (backreef, forereef, lagoon, and so forth) and typological (patch reef, spur and groove, colonized pavement, and so forth) strata. Habitats were defined in a collapsible hierarchy ranging from four broad classes (unconsolidated sediment, macroalgae, coral reef and hard bottom, and other), to more detailed categories (e.g., emergent vegetation, seagrass, algae, individual patch reefs, uncolonized volcanic rock), to patchiness of some specific features (e.g., 50–90% cover of macroalgae). The major product of this effort is a series of GIS-based benthic habitat maps that are characterized by a high degree of spatial and thematic accuracy.

Accuracy of the benthic habitat stratum used to guide the sampling design was quantified for each of the four habitat classes using an error matrix (Table 2; colonized hard bottom [CHB], uncolonized hard bottom [UCH], unconsolidated sediment [UCS], and macroalgae [MAC]). The matrix is represented by rows and columns that

correspond to an individual benthic habitat class, with each cell containing the total sample sites for that particular habitat class (Mumby and Green 2000). A total of 933 accuracy assessment points were entered into the error matrix and the user's, producer's and overall accuracy were calculated. The producer's accuracy represents the probability that a particular habitat class is classified correctly from the imagery and is based on errors of omission (Mumby and Green 2000). The user's accuracy is dependent upon actual field verification and is based on errors of commission (Naesset 1996, Stehman 1997). Errors of commission are considered errors of inclusion and occur when an area is included in a habitat class when it did not belong in that particular habitat class (Congalton and Green 1999). For example, user's accuracy represents the probability of an area classified as aggregated coral on the map but is in fact aggregated coral in situ. Therefore, the user's accuracy may provide the most relevant measure of accuracy to evaluate the habitat maps for use in a stratified random sampling design. The user's accuracy for the habitat maps used to guide this sampling design ranged in value from 83% to 92%. UCS and CHB had the highest user's accuracy values at 92% and 91%, respectively. UCH had the lowest user's accuracy of 83%. The overall accuracy of the final mapped product prepared from the visual interpretation of imagery for the main eight Hawaiian Islands 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 (data *available online*).[6]

Sample design

Sampling was conducted in all 11 MLCDs (Fig. 1), the University of Hawaii Marine Laboratory Refuge (MLR), and adjacent habitats. For all analyses, the MLR was combined with the MLCDs and all further references to MLCDs include the MLR. Locations of assessment sites were determined using a stratified random sampling approach where random points were assigned to each of four major habitat strata (colonized hard bottom [CHB], uncolonized hard bottom [UCH], unconsolidated sediment [UCS], and macroalgae [MAC]) using Arcview 3.2 (ESRI, Redlands, California, USA). Uncolonized hard

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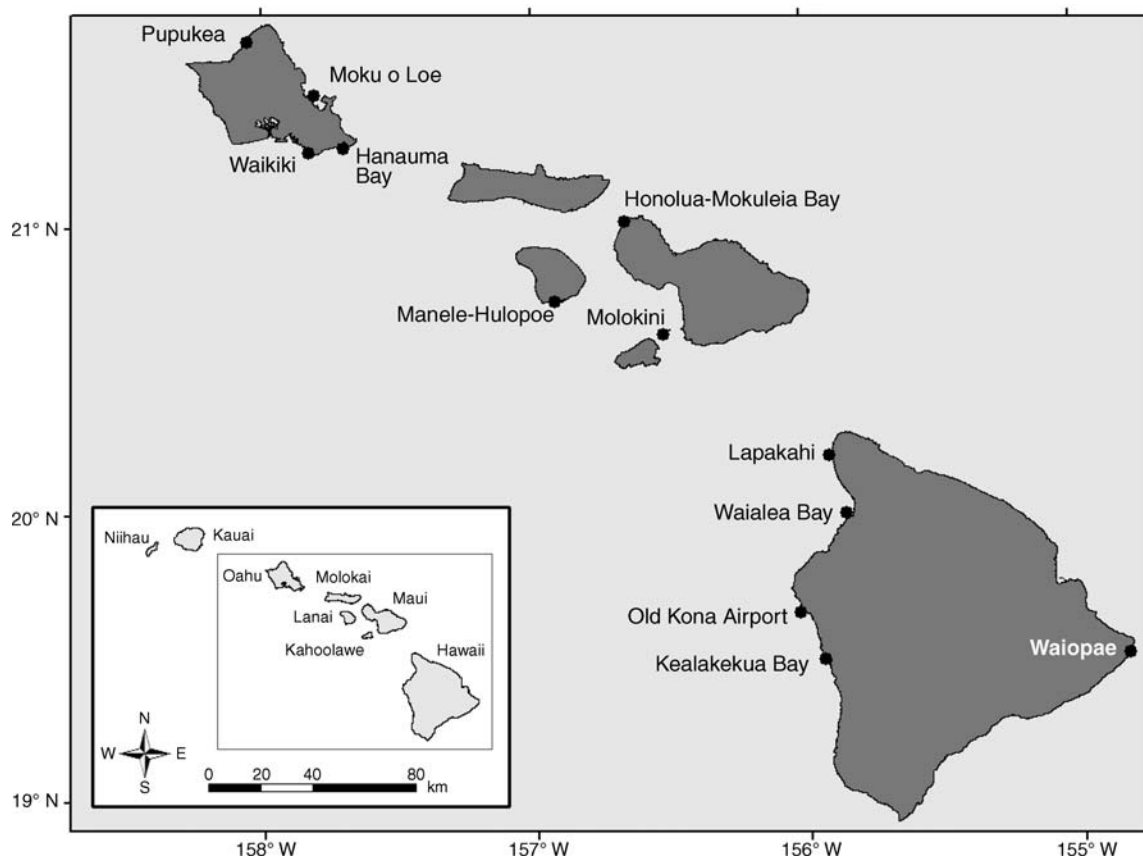[6] ⟨http://ccma.nos.noaa.gov/products/biogeography/hawaii_cd/index.htm⟩

Fig. 1. Locations of Marine Life Conservation Districts (MLCDs) and Moku o Loe, the University of Hawaii Marine Laboratory Refuge (MLR), Hawaii, USA.

bottom was defined as habitat having <10% live coral cover. Within each major habitat type, sampling was further stratified by management regime (MLCD and MLR, Fisheries Management Area [FMA], and open access). FMAs comprise a heterogeneous group of management 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 for use in the field. Once in the field, two divers navigated to waypoints using GPS and conducted a single 25-m transect. 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. The Waikiki study area on Oahu is given as an example to show the spatial coverage of sampling locations by habitat type and management regime (Fig. 2).

Fish sampling methodology

Fish assemblages at each location were quantified using standard underwater visual belt transect survey methods (Brock 1954, 1982). A diver swam a 25 × 5 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 centerline (125-m^2 transect area). Swimming duration varied from 10–15 min, depending on habitat complexity and fish abundance. At the beginning of the survey, the fish counter visualized out to the end of the transect and enumerated all individuals that were potentially leaving the census area. In this manner, we were able to partially account for the behavior that targeted species acquire in areas that are frequented by spearfishers (Kulbicki 1998).

Nomenclature followed Randall (1996). Total length (TL) of fish was estimated to the nearest centimeter. Length estimates of fishes from visual censuses were converted to mass using the following length–mass relationship: $M = a\mathrm{SL}^b$ where the parameters a and b are constants for the allometric growth equation, SL is standard length in millimeters, and M is mass in grams. Total length was converted to standard length (SL) by multiplying standard length by total length-fitting parameters obtained from FishBase (*available online*).[7] Length–mass fitting parameters were available for 150 species commonly observed on visual fish transects in
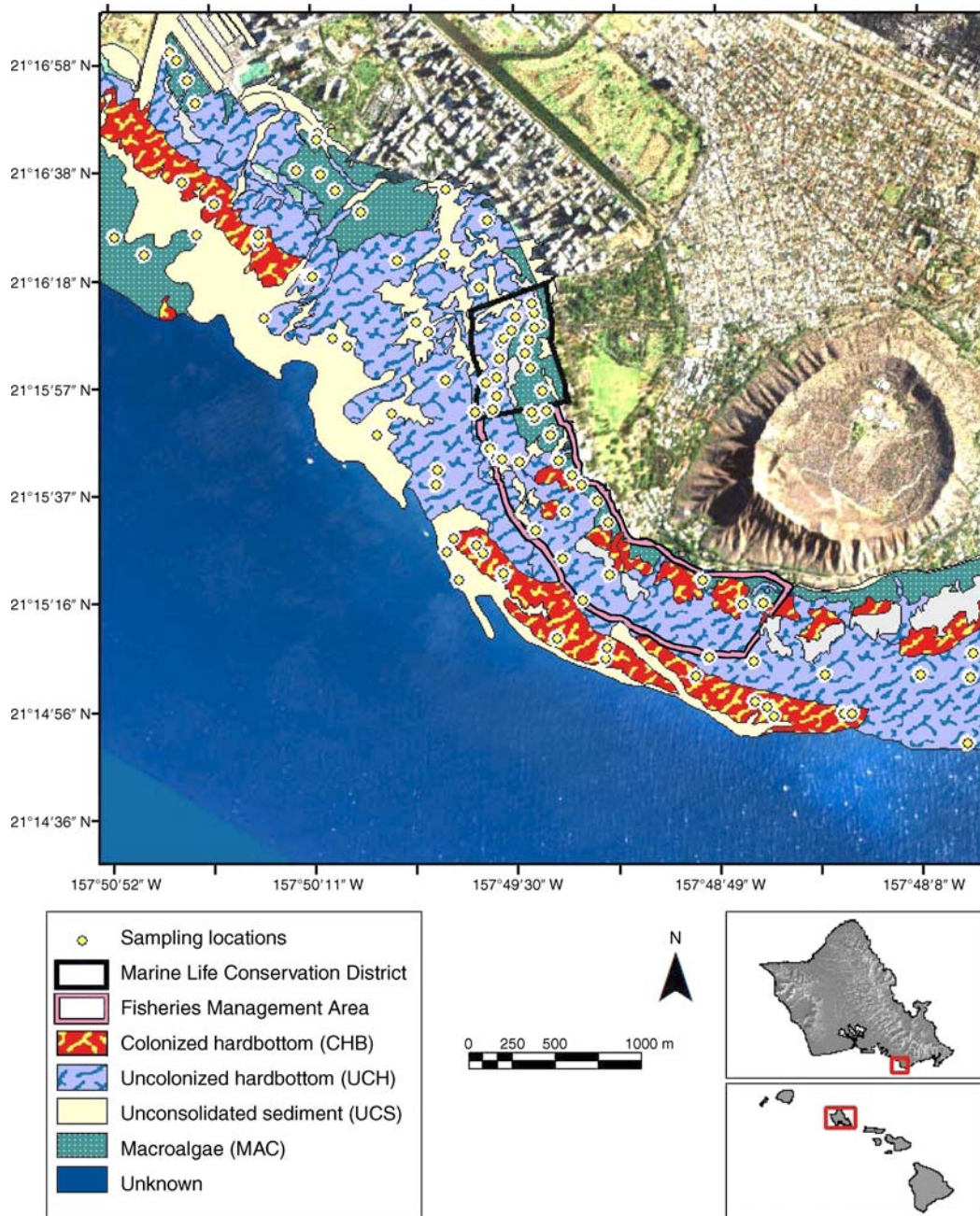
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[7] ⟨www.fishbase.org⟩

Fig. 2. Sampling locations and benthic habitats for the Waikiki study area including the Waikiki MLCD and Waikiki-Diamondhead Fisheries Management Area (FMA). The map corresponds to NAD 1983 UTM Zone 4. Data were provided by the State of Hawaii, Office of Planning and NOS Biogeography Team.

Hawaii (Hawaii Cooperative Fishery Research Unit, *unpublished data*). This was supplemented with information from other published and Web-based sources. In the cases where length–mass 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 square kilometer (Mg/km^2) to facilitate comparisons with other studies worldwide. Finally, fish taxa were categorized into three trophic

guilds (herbivores, secondary consumers, and apex predators) according to various published sources (Friedlander and DeMartini 2002, DeMartini et al. 2005) and FishBase. Based on previous work in Hawaii, these three trophic groupings worked well to document differences in fish assemblages due to habitat and fishing (Friedlander and DeMartini 2002). Finer trophic groupings (e.g., planktivores) were not analyzed separately due to the patchy distribution of these groups.

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 four major habitat types. A technique developed by Bros and Cowell (1987) using the standard error of the mean 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 sample size does not substantially increase power (decreasing standard error of the mean) is taken as the minimum suitable number of samples.

For number of species per transect, high and low standard error of the mean began to level off and converge at approximately four samples in the CHB and UCS habitats and approximately eight samples for the MAC and UCH habitats. For number of individuals per transect, high and low standard error of the mean began to converge at six samples in the UCS habitat and nine samples in the CHB, UCH, and MAC habitats. Given this set of results, nine to 10 samples per habitat appeared to be adequate to control the standard error of the mean for number of individuals and number of species per transect and was the minimum sample size used per habitat and management stratum in this study.

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, percent coverage, and Shannon-Weaver diversity but all subsequent surveys were conducted using the in situ planar point intercept quadrat method (Reed 1980) due to the long post processing time (~2 h for one transect) and low taxonomic resolution of some substrate categories (e.g., macroalgae) using video. A previous study in Hawaii comparing these two methods found no significant differences between the two methods in characterizing the benthic assemblages (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 nonoverlapping video frames from each transect with 50 randomly selected points per frame. 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 × 5 m segments with quadrats randomly allocated within each segment. 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 determined at the intersection of standard deviation and sampling time as a function of number of points per quadrat (10, 25, or 50) (Friedlander et al. 2006). Each

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 down to the species level 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.

To measure reef rugosity or surface relief, a chain of small links (1.3 cm per link) was draped along the full 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 of $r = cd/ld$.

Data analysis

Differences in habitat quality were examined using two approaches. First, a permutation-based hypothesis testing analysis of similarities (ANOSIM in PRIMER 5.0 [Primer-E Ltd., Plymouth, UK]) was used for the comparison of hard-bottom benthic assemblages between the MLCDs and the adjacent open access area (Clarke and Gorley 2001, Clarke and Warwick 2001). This procedure generates an R statistic that is on a scale from 0 or negative value (identical assemblages) to 1 (completely dissimilar assemblages). The resulting P value indicates the probability that the two assemblages come from a similar distribution (Clarke and Warwick 2001). Second, differences in topographical complexity (rugosity) between MLCDs and the corresponding open areas were compared using a Student's t test. Each MCLD comparison was conducted individually and raw values were used in the analysis since the data conformed to the assumptions of normality and homogeneity of variances. Sand habitats and FMA samples were excluded from both analyses because they were not present at all of the sites. The criterion for significance for these comparisons was $P = 0.05$, adjusted for multiple tests by the Bonferroni correction ($P = 0.05/m$), where m is the number of comparisons within the series (Manly 1991).

Biomass was $\ln(x + 1)$-transformed prior to statistical analysis to conform to the assumptions of parametric statistics (Zar 1999). Normality was tested using a Shapiro-Wilk W test ($P < 0.05$) while a Bartlett's test ($P < 0.05$) was used to examine homogeneity of variance. Percent substrate cover data were arcsine-square root transformed prior to statistical analyses (Zar 1999). Species diversity was calculated from the Shannon-Weaver diversity index (Ludwig and Reynolds 1988): $H' = S (p_i \times \ln[p_i])$, where p_i is the proportion of all individuals counted that were of species i.

The MLR was combined with all MLCDs for all analyses and all references to MLCDs in the results section include the MLR. Comparisons of fish species richness, biomass, and diversity among management strata and habitat types were conducted using one-way

TABLE 3. Sampling allocation by habitat type and management regimes.

Island and location	Code	Management regime	CHB	MAC	UCH	UCS	Total
Hawaii							
Waiopae	WAIO	MLCD	14		15		29
Waiopae	WAIO	Open	14		14		28
Kealakekua	KEA	FMA	29				29
Kealakekua	KEA	MLCD	22			12	34
Kealakekua	KEA	Open	13				13
Lapakahi	LAP	MLCD	15		13		28
Lapakahi	LAP	Open	13		13		26
Old Kona Airport	OKA	FMA	12		10	10	32
Old Kona Airport	OKA	MLCD	10		11		21
Old Kona Airport	OKA	Open	10		10		20
Waialea	WAI	MLCD	11		13	10	34
Waialea	WAI	Open	17		14	15	46
Lanai							
Manele	MAN	MLCD	12		11	10	33
Manele	MAN	Open	19		10	11	40
Maui							
Honolua	HON	MLCD	15		12	10	37
Honolua	HON	Open	13	12	23	15	63
Molokini	MOL	MLCD	23			15	38
Molokini	MOL	Open	15		2	15	32
Oahu							
Hanauma	HAN	MLCD	12		10	11	33
Hanauma	HAN	Open	11	11	15	10	47
Moku o Loe (Kaneohe Bay)	KBAY	MLR	20	10			30
Kaneohe Bay	KBAY	Open	30	24	10	10	74
Pupukea	PUP	MLCD	9		15	11	35
Pupukea	PUP	Open		12	15	11	38
Waikiki	WAIK	FMA		9	11		20
Waikiki	WAIK	MLCD			11	10	21
Waikiki	WAIK	Open	14	17	16	11	58
Total			373	106	273	187	939

Note: Values for CHB, MAC, UCH, UCS, and Total are the number of fish and benthic transects conducted in each habitat type and management regime (see *Methods: Benthic habitat mapping* for explanations of habitat codes). Empty cells represent habitats that were not present in the study area at a minimum mapping unit of ≥ 0.004 km^2. Kaneohe Bay (in parentheses) is the location of the Moku o Loe University Marine Laboratory Refuge. Management types are Marine Life Conservation Districts (MLCD), Fisheries Management Areas (FMA), and open access.

analysis of variance (ANOVA). Analysis of trophic biomass among management strata was performed in a similar manner. Unplanned comparisons between pairs were examined using the Tukey-Kramer hsd (honestly significant difference) test for ANOVAs ($\alpha = 0.05$). The correlation between the ratio of fish biomass inside vs. outside MLCDs and the human population density per kilometer of island shoreline was tested using the nonparametric Spearman Rho correlation coefficient (Siegel and Castellan 1988). The correlation of overall rank size of MLCDs with various fish assemblage characteristics (species richness, biomass, diversity, and number of individuals ≥ 15 cm) was tested using Kendall's coefficient of concordance (Daniel 1990).

Fish size spectra were described for each management stratum using least-squares regression to relate log$_{10}$-transformed numerical densities against body length in 5-cm size classes. Lengths were first standardized to the midpoint of the size distribution for each management stratum in order to remove the correlation between slope and intercept (Dulvy et al. 2004, Graham et al. 2005). Estimates were restricted to fish ≥ 15 cm TL to examine the adult component of the assemblage, which is the majority (by mass) of the fisheries harvest, and to eliminate the influence of recent recruitment on size distributions. Size spectra were compared among management strata using least squares analysis of covariance (ANCOVA). Unplanned multiple comparisons were tested using Tukey's hsd test ($\alpha = 0.05$).

Nonmetric multi dimensional scaling (MDS) analysis using PRIMER v5 (Clarke and Gorley 2001) was conducted to examine fish assemblage structure among habitats and management regimes. The data matrix consisted of mean fish biomass by species for each major habitat within each management stratum 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.

RESULTS

Sampling effort and map accuracy

A total of 939 spatially independent surveys were conducted between 22 January 2002 and 22 December

TABLE 4. Pairwise ANOSIM test comparisons between the hard-bottom benthic assemblages in the MLCDs and the adjacent areas open to fishing.

Island and site	R	P
Hawaii		
Waiopae	0.107	0.005
Kealakekua	0.295	**0.002**
Lapakahi	0.043	0.066
Old Kona Airport	0.030	0.276
Waialea	−0.019	0.714
Lanai		
Manele-Hulopoe	0.110	0.005
Maui		
Honolua	−0.002	0.483
Molokini	0.161	0.006
Oahu		
Hanauma	0.040	0.168
Kaneohe Bay	0.083	0.027
Pupukea	0.327	**0.001**
Waikiki	0.066	0.123

Notes: FMAs and sand habitats are omitted from this analysis because they were not present at all sites. The scale of R values is from 0 or negative values (identical faunas) to 1 (dissimilar faunas). P values for the test are shown in bold when $P \leq 0.004$ (from a Bonferroni correction, $P = 0.05/12$).

2004 (Table 3). Of this total, 40% were in CHB, 29% were in UCH, 20% were in UCS, and 11% were in MAC. On average, ~9.3 ± 5.6 km (mean ± SD) of linear shoreline was surveyed for each protected area and its adjacent habitat. MLCDs comprised 40% of the samples, while 52% were conducted in open areas, with the remaining 8% in FMAs.

Comparisons of habitat characteristics

Benthic assemblages were generally similar between the MLCDs and the corresponding areas open to fishing based on ANOSIM comparisons (Table 4). Even though P values for two comparisons were significant (Kealakekua, Hawaii and Pupukea, Oahu), the small R statistics (<0.35) indicated that these benthic assemblages were still relatively similar to their adjacent open-access areas. The rugosity measurements also indicated that the topographical complexity of the hard-bottom habitats for the majority of sites (nine out of 12 or 75%) was statistically equivalent between the MLCDs and the adjacent open areas (Table 5). Three sites, however, Pupukea MLCD, Hanauma Bay MLCD, and Honolua Bay MLCD had statistically higher rugosity values than their corresponding open access areas.

Fish assemblage characteristics among major habitat types and management regime

Results of one-way ANOVAs revealed that within major habitat types, species richness, biomass, and diversity were, in most cases, higher in the MLCDs, followed by FMAs, and open areas (Table 6). Species richness and diversity were significantly higher ($P < 0.05$) in the MLCDs compared to open areas in all major habitats except MAC. Biomass in the MLCDs and the MLR was significantly higher than both the FMA and open areas in all habitats except macroalgae. Among all hard-bottom habitats (CHB, UCH, MAC), overall species richness and diversity were both 1.4 times greater in MLCD compared with open areas, while overall fish biomass was 2.6 times greater in MLCDs compared to open areas among all habitats.

Size spectra among management regimes

Size spectra analysis was used to compare size structure of fish assemblages among management regimes on hard-bottom habitats (Fig. 3). There was a significant difference

TABLE 5. Student's t test comparisons of topographical complexity (rugosity, mean with SD in parentheses) on the hard-bottom habitats between the MLCDs and the corresponding areas open to fishing.

Island and site	MLCD	Open	t	P
Hawaii				
Waiopae	33.27 (3.34)	32.07 (3.38)	1.34	0.183
Kealakekua	33.29 (6.50)	34.35 (4.98)	0.53	0.597
Lapakahi	35.11 (2.10)	34.83 (4.62)	0.29	0.773
Old Kona Airport	37.68 (3.23)	38.29 (2.43)	0.68	0.501
Waialea	30.09 (3.85)	30.78 (5.76)	0.61	0.545
Lanai				
Manele-Hulopoe	33.92 (7.83)	31.79 (5.70)	1.35	0.182
Maui				
Honolua	32.01 (5.96)	28.30 (3.15)	4.07	**<0.001**
Molokini	33.41 (7.00)	33.60 (8.93)	0.10	0.919
Oahu				
Hanauma	30.93 (5.05)	28.16 (2.51)	3.24	**0.002**
Kaneohe Bay	36.34 (8.81)	36.19 (7.81)	0.07	0.941
Pupukea	33.72 (6.00)	29.90 (4.39)	3.12	**0.003**
Waikiki	29.62 (2.43)	29.87 (3.25)	0.24	0.807

Notes: FMAs and sand habitats are omitted from this analysis because they were not present at all sites. P values for the test are shown in bold at a critical $P \leq 0.004$ (from a Bonferroni correction, $P = 0.05/12$).

TABLE 6. Comparisons of fish assemblage characteristics among management regimes by major habitat type.

Characteristic and habitat	MLCD	FMA	Open	F	df	P	Multiple comparisons
Species richness							
CHB	21.15 (0.47)	20.95 (0.93)	18.58 (0.46)	8.3	2, 372	<0.001	MLCD, FMA, Open
UCH	18.44 (7.10)	15.00 (6.63)	12.85 (7.05)	19.5	2, 272	<0.001	MLCD, FMA, Open
MAC	6.62 (4.65)	8.00 (3.46)	5.13 (5.00)	1.9	2, 105	0.152	FMA, MLCD, Open
UCS	2.33 (3.34)	0.90 (0.99)	1.06 (1.68)	6.0	2, 186	0.003	MLCD, FMA, Open
Biomass							
CHB	97.06 (99.21)	63.65 (41.00)	50.19 (37.45)	26.1	2, 372	<0.001	MLCD, FMA, Open
UCH	87.77 (79.78)	39.32 (33.17)	30.46 (38.13)	36.7	2, 272	<0.001	MLCD, FMA, Open
MAC	12.45 (21.01)	10.81 (1.73)	4.01 (6.79)	5.5	2, 105	0.005	MLCD, FMA, Open
UCS	18.32 (70.04)	0.83 (1.83)	1.80 (11.25)	5.2	2, 186	0.006	MLCD, FMA, Open
Diversity							
CHB	2.19 (0.41)	2.24 (0.31)	2.06 (0.41)	6.3	2, 372	0.002	MLCD, FMA, Open
UCH	2.17 (0.44)	2.05 (0.39)	1.81 (0.63)	13.3	2, 272	<0.001	MLCD, FMA, Open
MAC	1.29 (0.65)	1.61 (0.40)	1.04 (0.74)	1.6	2, 105	0.050	FMA, MLCD, Open
UCS	0.52 (0.70)	0.16 (0.35)	0.21 (0.45)	7.3	2, 186	<0.001	MLCD, Open, FMA

Notes: Values are means (with SD in parentheses) for all transects in each stratum: CHB, colonized hard bottom; UCH, uncolonized hard bottom; MAC, macroalgae; and UCS, unconsolidated sediments (sand). Statistical values of one-way ANOVA are shown for each habitat type. Tukey's hsd tests were used for unplanned multiple comparisons among management strata. Underlined management strata are not significantly different ($\alpha = 0.05$). Biomass (Mg/km^2) was $\ln(x + 1)$-transformed for statistical analysis.

in size spectra of $\log_{10}$(no. fish/km^2) by standardized size class (TL in cm) for all fishes among management regimes ($F_{2,26} = 10.4$, $P < 0.001$) with MLCDs having higher intercept values compared with the other two management regimes (MLCD > FMA = Open, $\alpha = 0.05$). The slope (rate of decline) appeared smallest for the MLCDs but was not significantly different ($P > 0.05$) from the other two management regimes.

Comparisons between individual protected areas and areas open to fishing

A ratio of fish biomass (Mg/km^2) on all hard-bottom habitats (UCH, CHB, and MAC) inside protected areas (MLCDs) compared with outside adjacent areas, excluding FMAs, was developed to examine how effective each protected area was relative to the adjacent open area in conserving fish biomass (Fig. 4). Biomass in the Hanauma Bay MLCD was 8.4 times higher than along the adjacent south shore Oahu areas. The MLCDs with the smallest differences in biomass ratios were all only partially protected from fishing and located on the islands of Hawaii (Waialea, Kealakekua, and Lapakahi) and Lanai (Manele), which have lower human population densities than Oahu and Maui. There was a significant correlation between island human population density per km of shoreline and the ratio of biomass inside the protected area compared to the adjacent area open to fishing (Spearman rho = 0.696, $P = 0.012$).

Trophic comparisons

Within all hard-bottom habitats, there were significant differences in trophic biomass among management regimes ($F_{2,2255} = 10.42$, $P < 0.05$; Fig. 5). Biomass of

primary consumers was 2.9 times higher in the MLCDs compared to the open areas and 2.1 times higher than in the FMAs ($F_{2,751} = 13.38$, $P < 0.001$; MLCD > FMA = Open). Secondary consumer biomass was not significantly different ($P > 0.05$) between the MLCDs and FMAs, but both were significantly higher ($P > 0.05$) than the open areas ($F_{2,751} = 20.92$, $P < 0.001$, MLCD = FMA > Open). Apex predator biomass was 9.2 times higher in the MLCDs compared with the open areas and
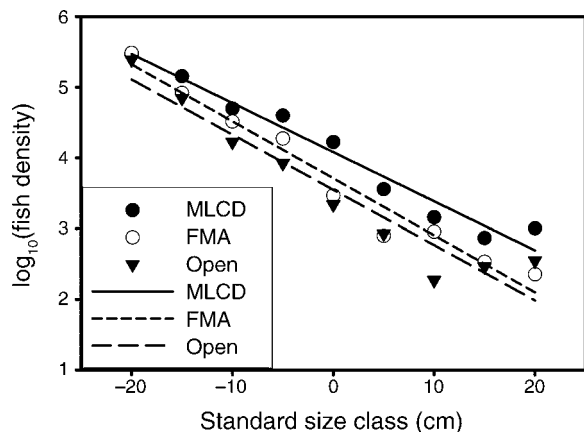

FIG. 3. Size spectra of $\log_{10}$-transformed number of fish/km^2 by standardized size class (total length, TL) for all fishes on hard bottom, in sites open to fishing, in the Marine Life Conservation District (MCLD), and in the Fisheries Management Area (FMA). ANCOVA results are: $F_{2,26} = 10.4$, $P < 0.001$, with least-square means intercept values of MLCD > FMA = open, $\alpha = 0.05$.
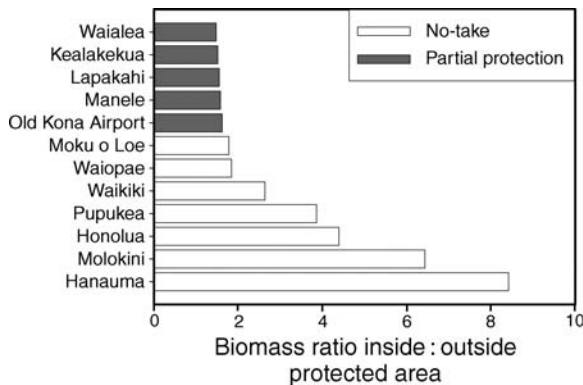
FIG. 4. Ratio of biomass (Mg/km^2) inside MLCDs and Moku o Loe Refuge vs. outside, in areas open to fishing. Data are shown from hard-bottom habitats only.

4.5 times higher than in the FMAs ($F_{2, 751} = 13.38$, $P < 0.001$; MLCD > FMA = Open).

Assemblage characteristics among protected areas

Significant differences in total species richness ($F_{11, 293} = 20.23$, $P < 0.001$), biomass ($F_{11, 293} = 6.99$, $P < 0.001$), and diversity ($F_{11, 293} = 7.22$, $P < 0.001$) were present among all MLCDs (Fig. 6). The Old Kona Airport MLCD had a significantly greater number of species than all other protected areas. Pupukea, Lapakahi, and Honolua followed in species richness, respectively, but these sites did not differ significantly ($P > 0.05$) from Molokini, Manele, Kealakekua, or Hanauma. Species richness at Waikiki, Moku o Loe, Waiopae, and Waialea was less than half that of Old Kona Airport.

The Molokini MLCD possessed the highest biomass on hard bottom among all protected areas and also had the highest biomass of apex predators (Fig. 6). Old Kona Airport, Kealakekua, Hanauma, Manele, and Honolua followed in biomass, respectively, and were all statistically indistinguishable ($P > 0.05$) from Molokini. Apex predators tended to be most abundant in these protected areas than in areas with lower total biomass. The lowest biomasses were recorded in the Waikiki MLCD, followed by Waiopae, Waialea, and Moku o Loe, respectively. Diversity was highest at Lapakahi but the top nine protected areas did not differ significantly ($P > 0.05$) from one another in species diversity. The lowest diversity in hard-bottom habitats was observed at Moku o Loe, followed by Waikiki and Waialea.

MLCD size

The amount of hard bottom within each MLCD was ranked and compared with the ranks of various fish assemblage characteristics (species richness, biomass, diversity, and number of individuals ≥ 15 cm; Fig. 7). The overall rank size of MLCDs and the MLR was significantly and positively correlated with these various fish assemblage characteristics (Kendall's coefficient of concordance $W = 0.720$, $P = 0.031$; Daniel 1990).

Multivariate comparisons of fish assemblages

Viewed in ordination space, all MLCDs, except for Waialea Bay, tended to increase up and to the right in the MDS plot relative to their corresponding open areas and FMAs (Fig. 8). The magnitude of this shift in ordination space was related to the differences observed in assemblage characteristics (i.e., areas adjacent to MLCDs with large differences in individual assemblage characteristics were farther apart in ordination space than adjacent areas with smaller differences in individual assemblage characteristics). The MLCDs clustered together towards the center and right of the plot with open areas clustering in the lower left corner. Open areas on Oahu and Maui clustered closer together in ordination space, while locations on the Kona coast of the Big Island were more similar to one another.

DISCUSSION

Results from this study show that spatial patterns of fish assemblages in Hawaii are largely driven by their habitats and level of protection from fishing. Fish assemblages varied among habitat types, with coral reef hard bottom having the highest values for most assemblage characteristics, while sand and macroalgal habitats contained low fish species richness, biomass, and diversity. Elsewhere in Hawaii, habitat characteristics, at multiple scales, have also been shown to play an important role in affecting the structure of coral reef fishes (Friedlander and Parrish 1998, Friedlander et al. 2003a).

Within major habitat types, species richness, biomass, and diversity were, in most cases, nominally higher in the MLCDs, followed by FMAs, and open areas. Overall fish biomass was 2.6 times greater in MLCDs
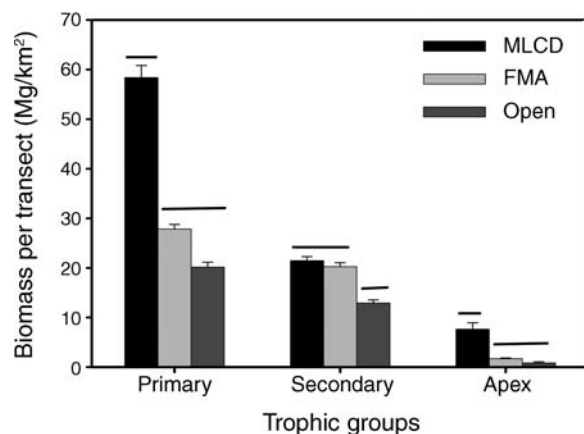

FIG. 5. Biomass per transect (Mg/km^2, mean + SE) by trophic guild and management regime (open to fishing, Fisheries Management Area [FMA], or Marine Life Conservation District [MLCD]) on hard-bottom habitats over the entire study area. One-way ANOVA results for each trophic group are in *Results: Trophic comparisons*. Horizontal lines above bars span management regimes within each trophic guild that are not significantly different at $\alpha = 0.05$ (Tukey's hsd tests).
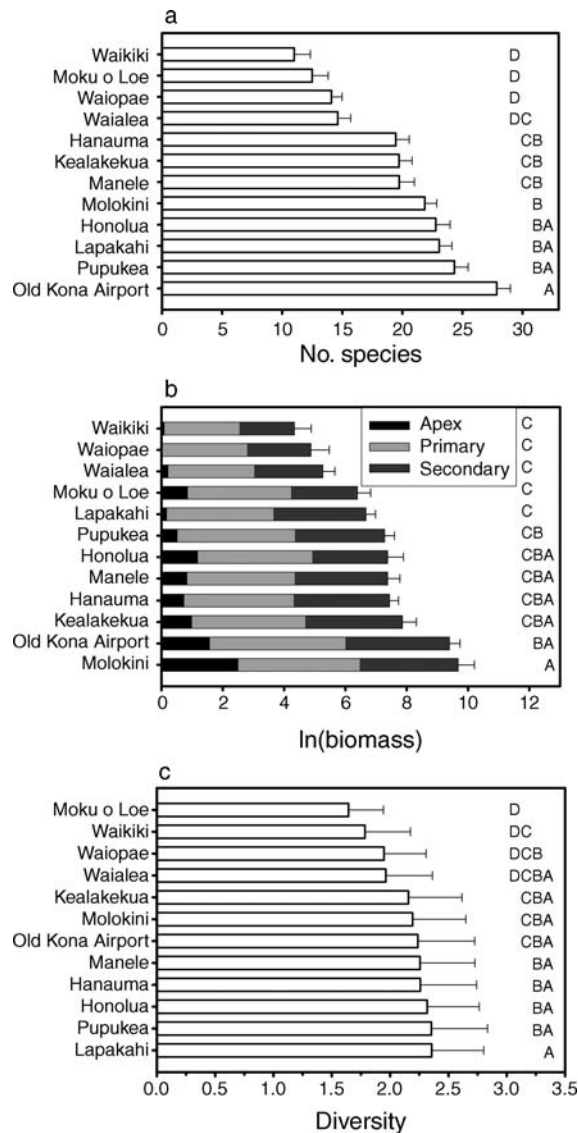
FIG. 6. Number, biomass, and diversity of fish species, on hard-bottom habitats only, among all MLCDs and the Moku o Loe Marine Laboratory Refuge; values are means + SE. (a) Number of species (one-way ANOVA, $F_{11, 293} = 20.23$, $P < 0.001$). (b) Log-transformed ($\ln[x + 1]$) biomass (originally measured in Mg/km^2) by trophic guild (one-way ANOVA, $F_{11, 293} = 13.12$, $P < 0.001$). (c) Shannon-Weaver diversity index (one-way ANOVA, $F_{11, 293} = 7.22$, $P < 0.001$). Unplanned multiple comparisons among protected areas were made with Tukey's hsd tests ($\alpha = 0.05$). Locations with the same letter listed to the right are not significantly different.

and the Moku o Loe MLR compared to open areas. Results from size spectra comparisons of fish assemblages among management regimes indicate that both the overall size of the adult fish assemblage was larger in the protected areas and the larger size classes had a greater number of individuals compared with the other management regimes. Larger individuals are important to fish population replenishment because they provide a

disproportionately greater reproductive contribution than smaller individuals, and these contributions have lower overall mortality (Berkeley et al. 2004).

One explanation for the higher fish assemblage characteristics in the MLCDs compared to their corresponding open access areas may be due to pre-existing differences in habitat quality. Indeed several of the MLCDs (e.g., Kealakekua, Honolua, Hanauma, and Pupukea) did have slightly different benthic assemblages and higher topographical complexity than the adjacent areas accessible to fishing (Tables 4 and 5). These habitat quality characteristics may have partially contributed to the higher biomass ratios seen in three of the four sites (Fig. 4).

Two lines of evidence, however, indicate that these habitat differences were not the principal factors accounting for the much higher levels of fish species richness, diversity, and biomass in the MLCDs. First, the low R statistic for the benthic assemblage comparisons indicated that any statistical differences in benthic community structure were still quite small and that the hard-bottom habitats were very similar (Clarke and Warwick 2001). Second, the majority of site comparisons (19 out of 24, 79%) did not exhibit differences in either benthic assemblage structure or rugosity. Therefore, the habitat comparisons 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. Our sampling strategy using a space-for-time substitution, also controlled for habitat quality and supported a direct contrast of fish assemblages in fished and protected areas since habitat quality was not different in most cases.

"Space-for-time" substitution has been used in many instances as an alternative to long-term studies to assess the impact of human-induced changes where pre-impact records are sparse or nonexistent (Pickett 1989). In the absence of reliable time-series data inside protected
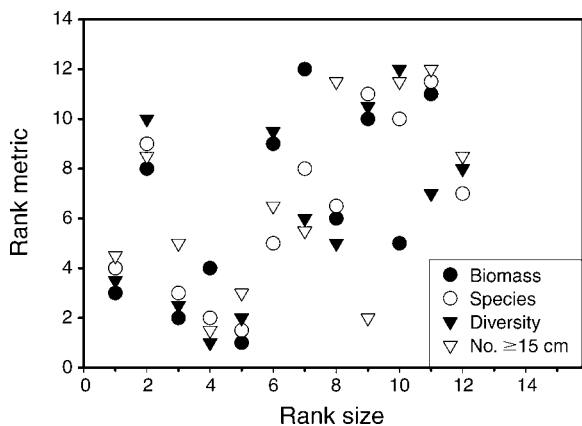

FIG. 7. Scatterplot of ranks of assemblage characteristics (biomass, species richness, diversity, number of individuals ≥15 cm) vs. ranks of MLCD size.
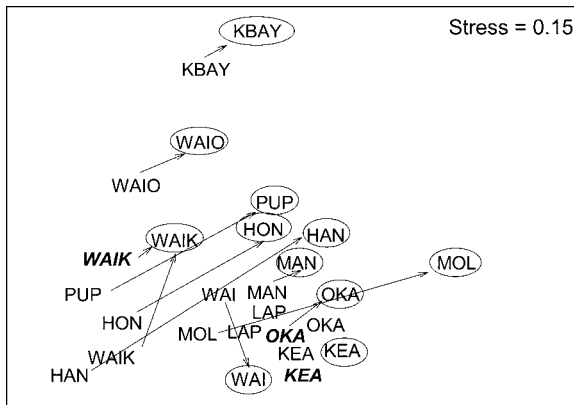
FIG. 8. Nonmetric multidimensional scaling plot of mean fish biomass for each protected area and adjacent open areas and FMAs. MLCDs and MLR are circled; open areas are in normal font, and FMAs are in bold italics. Arrows denote the direction and magnitude from open area or FMA to corresponding MLCD in ordination space. See Table 3 for key to codes.

areas, we can infer the impacts of fishing by examining the differences in fish assemblages between MLCDs and adjacent areas open to fishing. Locations with the highest human population density had the highest ratio of fish biomass inside the MLCD compared with adjacent outside areas. This is likely the most accurate estimate of fishing pressure in Hawaii since commercial fisheries catch and effort statistics only represent a small proportion of the total landings and Hawaii has no recreational fishing license (Friedlander and Parrish 1997). For the United States as a whole, recreational fisheries have been documented to comprise a large component of the total fish catch of nonindustrial species, particularly among species of concern (Coleman et al. 2004).

Based on biomass ratios inside and outside MLCDs, all protected areas appear to conserve fish biomass, in varying degrees, within their borders compared to adjacent areas open to fishing. The large difference in fish biomass inside vs. outside the Hanauma Bay MLCD (more than eight times) can likely be attributed to high fishing pressure in the areas outside the MLCD. Biomass in Molokini Shoals MLCD was more than six times higher than the nearby "control" areas along south Maui but these areas may not represent true comparisons with the MLCD owing to the unique offshore habitat of Molokini. Other MLCDs with large differences in biomass relative to their adjacent controls included, Honolua on Maui (more than four times higher), and Pupukea (3.8 times higher) and Waikiki (2.5 times higher) on the island of Oahu. These locations are situated near large human populations and therefore may experience high fishing pressure in the open areas adjacent to the MLCDs. As noted above, poor habitat quality in some of these adjacent may have contributed to lower fish biomass.

MLCDs on the islands of Lanai (Manele) and Hawaii (Waialea, Kealakekua, Lapakahi, and Old Kona Airport) all had relatively small differences in the ratio of fish biomass inside the MLCD compared to the adjacent open areas. Lower fishing pressure and the good habitat quality (low macroalgal cover and high habitat complexity) outside the MLCDs may explain these relatively small differences. In addition, all five areas have management strategies that only partially protect against fishing. Partial protection has been shown to be less effective than complete no-take reserves in Hawaii (Friedlander et al. 2003a, Williams et al. 2006) and elsewhere, as well (Wallace 1999, Reed 2002).

Highest values and ranks for fish assemblage characteristics were associated with larger MLCDs. Molokini Shoals MLCD had the highest fish biomass observed among all MLCDs, followed by Old Kona Airport, Kealakekua Bay, and Hanauma Bay. Molokini also had the greatest biomass of apex predators among all areas with sharks and jacks accounting for more than 99% of apex predator biomass. Species richness, biomass, and diversity were low at Waikiki, Moku o Loe, Waiopae, and Waialea. Low values for the Moku o Loe MLR and the Waiopae MLCD can be attributed to their habitats. The Moku o Loe MLR consists of a single, 30-ha, patch reef, while the Waiopae MLCD is comprised of a series of shallow tide pools.

Apex predators (sharks and jacks) accounted for only 2% of total fish biomass in the areas open to fishing but 9% in the MLCDs. Jacks are a prized target species in Hawaii's coastal fisheries (Holland et al. 1996, Meyer et al. 2001) and the lack of apex predators in fished areas has severe implications for ecosystem function (Graham et al. 2003, Dulvy et al. 2004). The small size of most of Hawaii's protected areas limits their effectiveness for larger, more mobile predators (Friedlander and DeMartini 2002) but some evidence suggests that these fishes may benefit from well designed MPAs (Holland et al. 1996).

MLCDs, FMAs, and open areas showed greater concordance in fish assemblage structure with each other than with other locations under similar management regimes. The two locations with the most dissimilar fish assemblages among all others were Kaneohe Bay (KBAY) and Waiopae (WAIO). Kaneohe Bay is the only embayment with a barrier reef and extensive patch reef system in the MHI and the Waiopae area consists of shallow tidepools that are dominated by small-bodied fishes. Owing to the unique barrier and patch reef system of Kaneohe Bay (Jokiel et al. 2004), the fish assemblage structure is dominated by herbivores, especially small parrotfishes (Friedlander et al. 2003a). The Waiopae area consists of a sunken lava bench with a series of shallow tide pools. The fish assemblage in this habitat is dominated by juveniles and small-bodied individuals. Owing to the unique habitat at these two locations, it is not surprising that the associated fish assemblages are so dissimilar to other locations in the MHI.

MLCDs in Hawaii were established to support the State of Hawaii's conservation and education objectives, not to enhance fish stocks. As a consequence, most of the MLCDs in Hawaii are currently too small to provide any fisheries benefits. Their small size and limited habitat types do not allow for the entire fish assemblage to function in a natural manner compared to larger and relatively pristine areas such as the northwestern Hawaiian Islands (NWHI). Mean fish biomass on hard-bottom habitats in fished areas in the MHI is 6.8 times less than in the NWHI and within MLCDs, biomass is still 2.7 times less than in the NWHI. The biomass of predators in protected areas in the MHI is also 19 times less than those observed on unfished reefs in the NWHI (Friedlander and DeMartini 2002).

MLCDs currently account for 0.03% of the total reef area of the MHI (Gulko et al. 2000). In order for these protected areas to provide any fisheries benefits, 20–30% of the reef area needs to be protected from exploitation (Sladek Nowlis and Roberts 1999, Sladek Nowlis and Bollermann 2002) but larger areas have been proposed by some models (Lauck et al. 1998, Mangel 1998). An effective reserve network design will protect populations and enhance non-protected populations through larval dispersal (Roberts et al. 2003, Shanks et al. 2003). Self-replenishment can be achieved by reserves of sufficient size to contain a substantial amount of larval dispersal, or by networking reserves at suitable distances such that propagules produced by populations in one reserve replenish populations in other reserves (Cowen 2002, Swearer et al. 2002, Palumbi 2003).

Despite the fact that marine protected areas in Hawaii have been in existence since the 1960s, up until now there has not been a comprehensive assessment of them. The small size and shallow depth range of these protected areas limit their effectiveness for biodiversity conservation and fisheries replenishment. Future protected area design in the MHI needs to incorporate a mosaic of habitats necessary 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. In addition to these hard-bottom habitats, sandy areas are important corridors for the movement of predators and other vagile species between hard-bottom habitats. Adjacent habitats provide coral reefs with a net gain in energy through feeding guilds that shelter on the reef by day and forage in the surrounding habitats at night (Ogden 1988). The synergy of these habitats provided needed space in an otherwise crowded biotope, the coral reef (Parrish 1989).

It is now becoming evident that to conserve marine biodiversity, maintain fisheries, and deliver a broad suite of ecosystem services over a long time frame, an ecosystem-based management approach is necessary (Pikitch et al. 2004, Rosenberg and McLeod 2005). A more holistic approach to place-based management will require comprehensive ocean zoning if we are to resolve the mismatches between spatial and temporal scales of governance and ecosystems (Agardy 2005, Crowder et al. 2006). To achieve ecosystem-based management, a spatially explicit GIS approach will be required to better understand the patterns and processes that regulate ecosystem function, both to ensure the sustainability of fisheries and to maintain the non-fisheries benefits of the ecosystem to society (Babcock et al. 2005).

In this study, a biogeographic process using GIS technology and sampling across the range of habitats present within the seascape has allowed for a robust assessment of MPAs for which future management decisions can be based. Legislation recently aimed at limiting, or outright prohibiting additional MPAs in Hawaii was withdrawn, in part because of our findings that showed that MPAs in Hawaii have been successful to varying degrees despite their small size and lack of adequate scientific design. Our approach is easily repeatable and should provide a framework for the evaluation of existing MPAs at other locations, leading to more effective management and ultimately, better conservation of marine ecosystems.

Literature Cited

Abesamis, R. A., and G. R. Russ. 2005. Density-dependent spillover from a marine reserve: long-term evidence. Ecological Applications 15:1798–1812.

Agardy, T. 2005. Global marine conservation policy versus site-level implementation: the mismatch of scale and its implications. Marine Ecology Progress Series 300:242–248.

Appeldoorn, R. S., A. Friedlander, J. Sladek Nowlis, P. Usseglio, and A. Mitchell-Chui. 2003. Habitat connectivity in reef fish communities and marine reserve design in Old Providence–Santa Catalina, Colombia. Gulf and Caribbean Research 14:61–78.

Ault, J. S., J. A. Bohnsack, and G. A. Meester. 1998. A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys. Fishery Bulletin 96(3):395–414.

Ault, J. S., J. A. Bohnsack, S. G. Smith, and J. Luo. 2005. Towards sustainable multispecies fisheries in the Florida, USA, coral reef ecosystem. Bulletin of Marine Science 76:595–622.

Babcock, E. A., E. K. Pikitch, M. K. McAllister, P. Apostolaki, and C. Santora. 2005. A perspective on the use of spatialized indicators for ecosystem-based fishery management through spatial zoning. ICES Journal of Marine Science 62:469–476.

Beets, J. 1997. Can coral reef fish assemblages be sustained as fishing intensity increases? Pages 2009–2014 in H. Lessios and I. G. Macintyre, editors. Proceedings of the Eighth International Coral Reef Symposium. Volume 2. Smithsonian Tropical Research Institute, Balboa, Republic of Panama.

Bellwood, D. R., T. P. Hughes, C. Folke, and M. Nystrom. 2004. Confronting the coral reef crisis. Nature 429:827–833.

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29:23–32.

Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Chapman and Hall, New York, New York, USA.

Bohnsack, J. A. 1998. Application of marine reserves to reef fisheries management. Australian Journal of Ecology 23:298–304.

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

Brock, R. E. 1982. A critique of the visual census method for assessing coral reef fish populations. Bulletin of Marine Science 32:269–276.

Brock, V. E. 1954. A preliminary report on a method of estimating reef fish populations. Journal of Wildlife Management 18:297–308.

Bros, W. E., and B. C. Cowell. 1987. A technique for optimizing sample size (replication). Journal of Experimental Marine Biology and Ecology 114:63–71.

Brown, E. K. 2004. Reef coral populations: spatial and temporal differences observed at six reefs off West Maui. Dissertation. University of Hawaii, Honolulu, Hawaii, USA.

Christensen, J. D., C. F. G. Jeffrey, C. Caldow, M. E. Monaco, M. S. Kendall, and R. S. Appeldoorn. 2003. Cross-shelf habitat utilization patterns of reef fishes in southwestern Puerto Rico. Gulf and Caribbean Research 14:9–28.

Clark, R. D., W. Morrison, J. D. Christensen, M. E. Monaco, and M. S. Coyne. 2003. Modeling the distribution and abundance of spotted seatrout: integration of ecology and GIS technology to support management needs. Pages 247–265 in S. A. Bortone, editor. Biology of the spotted seatrout. CRC Press, Boca Raton, Florida, USA.

Clarke, K, and R. Gorley. 2001. PRIMER v5: User manual/tutorial. Primer-E Ltd., Plymouth, UK.

Clarke, K., and R. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation. Second edition. Primer-E Ltd., Plymouth, UK.

Coleman, F. C., W. F. Figueira, J. S. Ueland, and L. B. Crowder. 2004. The impact of U.S. recreational fisheries on marine fish populations. Science 305:1958–1960.

Congalton, R., and K. Green. 1999. Assessing the accuracy of remotely sensed data: principles and practice. CRC Press, Boca Raton, Florida, USA.

Cowen, R. K. 2002. Larval dispersal and retention and their consequences for population connectivity. Pages 149–170 in P. F. Sale, editor. Coral reef fishes: dynamics and diversity in a complex ecosystems. Academic Press, San Diego, California, USA.

Coyne, M. S., M. E. Monaco, T. A. Battista, M. Anderson, J. Waddell, W. Smith, P. Jokiel, M. S. Kendall, and M. E. Monaco. 2003. Benthic habitats of the main Hawaiian Islands. NOAA Technical Memorandum NOS/NCCOS/CCMA 152. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Silver Spring, Maryland, USA.

Crowder, L. B., et al. 2006. Resolving mismatches in U.S. ocean governance. Science 313:617–618.

Daniel, W. W. 1990. Applied nonparametric statistics. Second edition. PWS-KENT Publishing Company, Boston, Massachusetts, USA.

DeMartini, E. D. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fishery Bulletin 91:414–427.

DeMartini, E. E., A. M. Friedlander, and S. Holzwarth. 2005. Size at sex change in protogynous labroids, prey size distributions, and apex predator densities at NW Hawaiian atolls. Marine Ecology Progress Series 297:259–271.

Dulvy, N. K., R. P. Freckleton, and N. V. C. Polunin. 2004. Coral reef cascades and indirect effects of predator removal by exploitation. Ecology Letters 7:410–416.

Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003a. 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., E. K. Brown, M. E. Monaco, and A. Clark. 2006. Fish habitat utilization patterns and evaluation of the efficacy of marine protected areas in Hawaii: integration of NOAA digital benthic habitat mapping and coral reef ecological studies. NOAA Technical Memorandum NOS NCCOS 23. National Oceanic and Atmospheric Administration, Silver Spring, Maryland, USA.

Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: the effects of fishing down apex predators. Marine Ecology Progress Series 230:253–264.

Friedlander, A. M., and J. D. Parrish. 1997. Fisheries harvest and standing stock in a Hawaiian Bay. Fisheries Research 32:33–50.

Friedlander, A. M., and J. D. Parrish. 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. Journal of Experimental Marine Biology and Ecology 224:1–30.

Friedlander, A., J. Sladek Nowlis, J. A. Sanchez, R. Appeldoorn, P. Usseglio, C. McCormick, S. Bejarano, and A. Mitchell-Chui. 2003b. Designing effective marine protected areas in Seaflower Biosphere Reserve, Colombia, based on biological and sociological information. Conservation Biology 17:1769–1784.

Graham, N. A. J., N. K. Dulvy, S. Jennings, and N. V. C. Polunin. 2005. Size spectra as indicators of the effects of fishing on coral reef fish assemblages. Coral Reefs 24:118–124.

Graham, N. A. J., R. D. Evans, and G. R. Russ. 2003. The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. Environmental Conservation 30:200–208.

Green, E. P., P. J. Mumby, A. J. Edwards, and C. D. Clark. 2000. Remote sensing handbook for tropical coastal management. UNESCO, Paris, France.

Gulko, D., J. Maragos, A. Friedlander, C. Hunter, and R. Brainard. 2000. Status of coral reef in the Hawaiian Archipelago. Pages 219–238 in C. Wilkinson, editor. Status of coral reefs of the world: 2000. Australian Institute of Marine Science. Cape Ferguson, Queensland, and Dampier, Western Australia, Australia.

Hawaii Division of Aquatic Resources. 1992. Marine life conservation district plan. Department of Land and Natural Resources, Division of Aquatic Resources. Honolulu, Hawaii, USA.

Holland, K. N., C. G. Lowe, and B. M. Wetherbee. 1996. Movements and dispersal patterns of blue trevally (Cranx melampygus) in a fisheries conservation zone. Fisheries Research 25:279–292.

Hunter, C. L., and C. W. Evans. 1995. Coral reefs in Kaneohe Bay, Hawaii: two centuries of western influence and two decades of data. Bulletin of Marine Science 57:501–515.

Jackson, J. B. C., et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–638.

Jennings, S., and M. J. Kaiser. 1998. The effects of fishing on marine ecosystems. Advances in Marine Biology 34:201–352.

Jennings, S., and N. V. C. Polunin. 1996. Effects of fishing effort and catch rates upon the structure and biomass of Fijian reef fish communities. Journal of Applied Ecology 33: 400–412.

Jokiel, P. L., E. K. Brown, A. Friedlander, S. K. Rodgers, and W. R. Smith. 2004. Hawaii Coral Reef Assessment and Monitoring Program: spatial patterns and temporal dynamics in reef coral communities. Pacific Science 58:159–174.

Kendall, M. S., J. D. Christensen, and 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.

Kulbicki, M. 1998. How acquired behaviour of commercial reef fish may influence results obtained from visual censuses. Journal of Experimental Marine Biology and Ecology 222: 11–30.

Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8: S72–S78.

Ludwig, J. A., and J. F. Reynolds. 1988. Statistical ecology. Wiley, New York, New York, USA.

Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. Ecology Letters 1:87–90.

Manly, B. F. J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, New York, New York, USA.

McClanahan, T. R., and B. Kaunda-Arara. 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. Conservation Biology 10:1187–1199.

Meyer, C. G., K. N. Holland, B. M. Wetherbee, and C. G. Lowe. 2001. Diet, resource partitioning and gear vulnerability of Hawaiian jacks captured in fishing tournaments. Fisheries Research 53:105–113.

Monaco, M., M. Kendall, J. Higgins, C. Alexander, and M. Tartt. 2005. Biogeographic assessments of NOAA national marine sanctuaries: the integration of ecology and GIS to aid in marine management boundary delineation and assessment. Pages 2–13 *in* D. J. Wright and D. J. Scholz, editors. Place matters: geospatial tools for marine science, conservation, and management in the Pacific Northwest. Oregon State University Press, Corvallis, Oregon, USA.

Monaco, M. E., S. B. Weisberg, and T. A. Lowery. 1998. Summer habitat affinities of estuarine fish in US mid-Atlantic coastal systems. Fisheries Management and Ecology 5:161–171.

Mumby, P., and E. Green. 2000. Field survey: building the link between image and reality. Pages 57–65 *in* A. J. Edwards, editor. Remote sensing handbook for tropical coastal management. UNESCO, Paris, France.

Mumby, P. J., E. P. Green, A. J. Edwards, and C. D. Clark. 1997. Coral reef habitat mapping: how much detail can remote sensing provide? Marine Biology 130:193–202.

Mumby, P. J., J. D. Hedley, J. R. M. Chisholm, C. D. Clark, and J. Jaubert. 2004. The cover of living and dead corals using airborne remote sensing. Coral Reefs 23:171–183.

Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. Nature 423:280–283.

Myers, R. A., and B. Worm. 2005. Extinction, survival or recovery of large predatory fishes. Philosophical Transactions of the Royal Society B 360:13–20.

Naesset, E. 1996. Conditional tau coefficient for assessment of producer's accuracy of classified remotely sensed data. ISPRS Journal of Photogrammetry and Remote Sensing 51:91–98.

National Research Council. 2001. Marine protected areas: tools for sustaining ocean ecosystems. National Academy Press, Washington, D.C., USA.

Ogden, J. C. 1988. The influence of adjacent systems on the structure and function of coral reefs. Pages 123–129 *in* J. H. Choat, et al., editors. Proceedings of the 6th International Coral Reef Symposium. Volume 1. Executive Committee, Townsville, Australia.

Palumbi, S. R. 2003. Population genetics, demographic connectivity and the design of marine protected areas. Ecological Applications 13:S146–S158.

Pandolfi, J., 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 US coral reefs on the slippery slope to slime? Science 307:1725–1726.

Parrish, J. D. 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Marine Ecology Progress Series 58:143–160.

Pauly, D., V. Christensen, J. Dalsgaaard, R. Froese, and F. Torres, Jr. 1998. Fishing down marine food webs. Science 279:860–863.

Pauly, D., M. L. Palomares, R. Froese, P. Sala, M. Vakily, D. Preikshot, and S. Wallace. 2001. Fishing down Canadian aquatic food webs. Canadian Journal of Fisheries and Aquatic Science 58:51–62.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 *in* G. E. Likens, editor. Long-term studies in ecology: approaches and alternatives. Springer–Verlag, New York, New York, USA.

Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. Science 305:346–347.

Polacheck, T. 1990. Year around closed areas as a management tool. Natural Resource Modeling 4:327–353.

Reed, J. K. 2002. Deep-water *Oculina* coral reefs of Florida: biology, impacts, and management. Hydrobiologia 471:43–55.

Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. Atoll Research Bulletin 193:1–6.

Roberts, C. M. 2005. Marine protected areas and biodiversity conservation. Pages 265–279 *in* E. Norse and L. Crowder, editors. Marine conservation biology: the science of maintaining the sea's biodiversity. Island Press, Washington, D.C., USA.

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., G. Branch, R. Bustamente, J. C. Castilla, J. Dugan, B. Halpern, K. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, M. Ruckleshaus, and R. Warner. 2003. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecological Applications 13: S199–S214.

Roberts, C. M., and N. V. C. Polunin. 1993. Marine reserves: simple solutions to managing complex fisheries? Ambio 22: 363–368.

Rosenberg, A. A., and K. L. McLeod. 2005. Implementing ecosystem-based approaches to management for the conservation of ecosystem services. Marine Ecology Progress Series 300:270–274.

Rubec, P. J., J. C. W. Bexley, H. Norris, M. S. Coyne, M. E. Monaco, S. G. Smith, and J. S. Ault. 1999. Suitability modeling to delineate habitat essential to sustainable fisheries. American Fisheries Society Symposium 22:108–133.

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., A. C. Alcala, A. P. Maypa, H. P. Calumpong, and A. T. White. 2004. Marine reserves benefits local fisheries. Ecological Applications 14:597–606.

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., R. K. Cowen, B. S. Danilowicz, G. P. Jones, J. P. Kritzer, K. C. Lindeman, S. Planes, N. V. C. Polunin, G. R. Russ, Y. J. Sadovy, and R. S. Steneck. 2005. Critical science gaps impede use of no-take fishery reserves. Trends in Ecology and Evolution 20:74–80.

Shanks, A. L., B. Grantham, and M. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:S159–S169.

Shomura, R. 1987. Hawaii's marine fishery resources: yesterday (1900) and today (1986). Administrative Report H-87-21. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California, USA.

Siegel, S., and J. J. Castellan, Jr. 1988. Nonparametric statistics for the behavioral sciences. Second edition. McGraw-Hill, New York, New York, USA.

Sladek Nowlis, J., and B. Bollerman. 2002. Methods for increasing the likelihood of restoring and maintaining productive fisheries. Bulletin of Marine Science 70:715–731.

Sladek Nowles, J., and A. M. Friedlander. 2004. Marine reserve design and designation process. Pages 128–163 in J. Sobel

and C. Dahlgren, editors. Marine reserves; their science, design and use. Island Press, Washington, D.C., USA.

Sladek Nowles, J., and A. M. Friedlander. 2005. Marine reserve design and function for fisheries management. Pages 280–301 in E. A. Norse and L. B. Crowder, editors. Marine conservation biology: the science of maintaining the sea's biodiversity. Island Press, Washington, D.C., USA.

Sladek Nowlis, J., and C. M. Roberts. 1999. Fisheries benefits and optimal design of marine reserves. Fishery Bulletin 97: 604–616.

Smith, J. E., C. M. Hunter, and C. M. Smith. 2002. Distribution and reproductive characteristics of nonindigenous and invasive marine algae in the Hawaiian Islands. Pacific Science 53:299–315.

Stehman, S. V. 1997. Selecting and interpreting measures of thematic classification accuracy. Remote Sensing of Environment 62:77–89.

Swearer, S. E., J. S. Shima, M. E. Hellberg, S. R. Thorrold, G. P. Jones, D. R. Robertson, S. G. Morgan, K. A. Selkoe, G. M. Ruiz, and R. R. Warner. 2002. Evidence of self-recruitment in demersal marine populations. Bulletin of Marine Science 70:251–271.

Tissot, B. N., and L. E. Hallacher. 2003. Effects of aquarium collectors on coral reef fishes in Kona, Hawaii. Conservation Biology 17:1759–1768.

Wallace, S. S. 1999. Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. Conservation Biology 13:882–887.

Williams, I. D., W. J. Walsh, A. Miyasaka, and A. M. Friedlander. 2006. Effects of rotational closure on coral reef fishes in the Waikiki-Diamond Head Fishery Management Area, Oahu, Hawaii. Marine Ecology Progress Series 310: 139–149.

Zar, J. H. 1999. Biostatistical analysis. Fourth edition. Prentice Hall, New Jersey, USA.