

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/authorsrights>



Contents lists available at SciVerse ScienceDirect

Fisheries Research

journal homepage: www.elsevier.com/locate/fishres

A seascape approach to investigating fish spillover across a marine protected area boundary in Hawai'i

Kostantinos A. Stamoulis^{a,b,*}, Alan M. Friedlander^c

^a Department of Geography, University of Hawai'i at Mānoa, 2424 Maile Way, Saunders Hall Room 445, Honolulu, HI 96822, USA

^b Hawai'i Cooperative Fishery Research Unit, University of Hawai'i at Mānoa, Department of Biology, 2450 Campus Road, Dean Hall Room 2, Honolulu, HI 96822, USA

^c US Geological Survey – Hawai'i Cooperative Fishery Research Unit, University of Hawai'i at Mānoa, Department of Biology, 2450 Campus Road, Dean Hall Room 2, Honolulu, HI 96822, USA

ARTICLE INFO

Article history:

Received 29 March 2012

Received in revised form 29 July 2012

Accepted 6 September 2012

Keywords:

Fishing
Management
Marine reserve
MPA
Seascape
Spillover

ABSTRACT

Marine protected areas (MPAs) can benefit fisheries through export of pelagic eggs and larvae and the net emigration of adults and juveniles (spillover). Spillover was investigated for a marine protected area on the north shore of Oahu, Hawai'i utilizing a seascape approach. This study incorporated habitat variables and underwater visual surveys of fishes and benthos measured at two distinct scales (125 m² and 1000 m²) inside and outside the protected area at varying distance from the boundary. The relationship between fish biomass from fine-scale surveys and key habitat variables was found to account for a large portion of the variability for both resource (targeted) fish species (15%) and non-resource fish (28%). The remaining variation in resource fish biomass was significantly correlated with distance from the MPA boundary showing a decreasing gradient from inside to outside ($r^2 = 0.46$, $p = 0.001$), indicating fish spillover at a local scale (<1 km). In contrast, non-resource fish biomass demonstrated no such relationship ($p = 0.45$). The evidence of spillover based on the fine-scale surveys was corroborated by results from broad-scale surveys, which also showed a significant relationship ($r^2 = 0.19$, $p < 0.01$) between resource fish biomass and distance from the MPA boundary. In addition, observed spatial distribution of fishing effort was consistent with predictions that fishers respond to biomass gradients across protected area boundaries. Fish spillover can help mitigate costs associated with the establishment of marine protected areas in terms of lost fishing area and therefore have a positive effect on the attitudes of fishers toward marine reserves and marine protected areas.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Marine protected areas (MPAs) are widely utilized as a management tool to conserve biodiversity and to protect or restore fish populations within their borders (Lester et al., 2009). Numerous field studies have documented how population numbers and biomass, species richness, size of organisms, reproductive potential, and/or community structure are positively affected by protection from fishing (Halpern and Warner, 2002; Gell and Roberts, 2003; Micheli et al., 2004). Another potential benefit of MPAs is that they supplement adjacent fisheries through two primary mechanisms: increased production and export of pelagic eggs and larvae, and net emigration of adults and juveniles ("spillover," Rowley, 1994). While density dependent emigration (hereafter spillover) can supplement fishery yields (McClanahan and Mangi,

2000), it is generally believed that the export of eggs and larvae provides greater overall fishery benefits (Palumbi, 2004; Sladek Nowlis and Friedlander, 2005). One effect of spillover of mature fishes could be to reduce potential for reproductive output from within the MPA with possible negative implications for stock enhancement (Sladek Nowlis and Roberts, 1999). From a fishers perspective; however, spillover of adult fish from MPAs may provide a more tangible benefit than larval export and serve to improve perceptions of marine protected areas (Russ and Alcala, 1996). Fisher attitudes toward MPAs and marine reserves have important implications for maintenance, enforcement, and designation of new protected areas (Suman et al., 1999).

Therefore, for a number of reasons, an understanding of the rate and extent of adult spillover from MPAs is essential for the evaluation of their effects on connected fisheries.

With higher densities and larger sizes of fished species inside of marine protected areas, considerations of spatial habitat use and behavior of fish (Lizaso et al., 2000; Abesamis and Russ, 2005) lead to predictions that population density and mean fish size will form gradients across protected area boundaries (Rakitin and Kramer, 1996). For this reason, gradients of fish abundance and

* Corresponding author at: Hawai'i Cooperative Fishery Research Unit, University of Hawai'i at Mānoa, Department of Biology, 2450 Campus Road, Dean Hall Room 2, Honolulu, HI 96822, USA. Tel.: +1 808 756 3947.

E-mail address: kostanti@hawaii.edu (K.A. Stamoulis).

biomass have been utilized as indicators of fish spillover across MPA boundaries and to assess the scale of influence of protection (McClanahan and Mangi, 2000; Ashworth and Ormond, 2005; Abesamis et al., 2006). The significance of gradients is further supported by Kellner et al. (2007) whose model shows that considering the effect of harvesting and the diffusion rate of species, the distribution of abundance or biomass with increasing distance from an MPA should produce a gradient with a steeper negative slope as diffusion process becomes more important or as fishing pressure increases. The existence of such a negative gradient could therefore be interpreted as evidence of spillover of adult fish. However, habitat variability is a primary factor driving the distribution of fish assemblages (Friedlander and Parrish, 1998; Friedlander et al., 2007a; Forcada et al., 2008) and can confound reserve effects. Therefore, the influence of habitat must first be resolved in order to show the effects of protection (Chapman and Kramer, 1999; Harmelin-Vivien et al., 2008). Additionally, information on fishing effort by gear type can provide important perspective for interpreting abundance and biomass gradients across the boundary and reveal linkages between fish spillover and fisher behavior (Russ et al., 2004; Russ and Alcala, 2004; Kellner et al., 2007).

Over the past four decades a series of MPAs known locally as Marine Life Conservation Districts (MLCDs) have been established in Hawai'i. Originally intended to provide areas for the public to interact with marine life, the MLCDs vary in size, habitat quality, and management regimes. Five of the eleven MLCDs (or portions of them) are true no-take marine reserves. All of the MLCDs have been shown to conserve fish populations within their boundaries to varying degrees (Friedlander et al., 2007a, 2007b, 2010). Friedlander et al. (2007b) showed that MLCD size is positively correlated with a number of fish assemblage characteristics, including species richness, density, and biomass and concluded that all of the MLCDs are likely too small to have any measurable influence on adjacent fished areas. Williams et al. (2009) investigated the effects of a marine protected area network in West Hawai'i on the distribution of yellow tang (*Zebrasoma flavescens*) a species important to the aquarium fishery (Walsh et al., 2003). After controlling for structural complexity, results indicated export of adults from protected areas, as shown by significantly higher densities at sites near protected area boundaries than at distant sites.

Given that MPAs in Hawai'i have higher levels of fish richness, abundance and biomass than adjacent fished areas (Friedlander et al., 2007a, 2007b, 2010) gradients of fish biomass across MPA boundaries should be detectable (Rakitin and Kramer, 1996). If these gradients exist as a result of protection, one would expect to see this pattern only for resource (targeted) species (Rakitin and Kramer, 1996; Williams et al., 2008). Furthermore, spatial patterns of fishing effort should correspond to resource fish biomass gradients (McClanahan and Mangi, 2000; Kellner et al., 2007). The goal of this study was to evaluate the spatial pattern of total biomass of resource fish species across an MPA boundary in order to determine if a negative gradient exists, and to determine if it is a function of fishing protection (i.e. spillover) by comparing it to the total biomass of non-resource fish species and spatial patterns of fishing effort. In order to accomplish this, several assumptions needed to be tested. First, that biomass (as well as species richness and abundance) of fishes was higher inside the MPA than outside (Friedlander et al., 2010). Second, that habitat variability is the primary driver of fish distributions and must be controlled for in order to test for protection effects (Friedlander and Parrish, 1998; Chapman and Kramer, 1999; Forcada et al., 2008). And finally, that fishing pressure is lower inside the MPA than outside. This study examined a marine protected area on the north shore of Oahu, Hawai'i using a seascape approach; controlling for habitat parameters, sampling at two distinct spatial scales, and measuring fishing effort in order to address

three main questions: (1) Does resource fish biomass form a negative gradient ("spillover") across the boundary of the MPA into the fished area? (2) If so, does non-resource fish biomass follow a similar pattern which contraindicates a response to fishing? and (3) How does this gradient of resource fish biomass (if detected) relate to fisher behavior in terms of spatial patterns of fishing effort?

2. Methods

2.1. Study area

To address our research questions we evaluated the Pupukea MLCD on the north shore of Oahu (Fig. 1). This MPA was established in 1983 (0.11 km²) and expanded in 2003 (0.71 km²) through a community-driven process (Friedlander et al., in review). The area is completely no-take except for collection of two species of seaweed throughout the MPA and in the Waimea Bay portion only; limited pole fishing from shore and seasonal net harvest of two coastal pelagic species (Fig. 2). Throughout the protected area, and extending out into the fished area to the north is a continuous stretch of hard bottom reef habitat (based on NOAA benthic habitat maps – Battista et al., 2007) (Fig. 2), which was the focus of the biological surveys.

2.2. Experimental design

Survey stations were randomly located on hard-bottom habitats, with stations stratified by distance into 200 m long blocks in two study zones: 'MPA' and 'open'. To avoid overlap, stations were separated by a minimum distance of 30 m. Zones consisted of adjacent areas approximately 1000 m in length and a depth range corresponding to the Pupukea MLCD (0–15 m). The MPA zone was located inside the MLCD with the north boundary at one end and the open zone located adjacent to this boundary (Fig. 2). Therefore, survey stations were located a maximum of 1000 m from the boundary. A total of 80 independent fine-scale fish and benthic surveys and 40 broad-scale fish surveys in a variety of hard-bottom habitats were conducted between June and September 2010. Timing was in large part dictated by winter surf patterns on the north shore of Oahu where diving is nearly impossible between October and May. Fishing effort surveys took place the following summer during June–September 2011. To address habitat effects and biomass gradients, resource fishes and non-resource fishes were analyzed separately (Abesamis et al., 2006; Williams et al., 2008). These classifications were formed based on commercial catch data from the Hawai'i Division of Aquatic Resources (2009) where resource fishes were defined as those species with at least 1000 lbs/year landed.

2.3. Data collection

2.3.1. Fish surveys

Fine-scale (125 m²) fish surveys used belt transects oriented at 200° – roughly parallel to shore. A diver swam along a 25 m × 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. Survey duration varied from 10 to 15 min, depending on habitat complexity and fish abundance. Total length (TL) of fishes was estimated to the nearest centimeter (Bell et al., 1985; Friedlander and Parrish, 1998). The same diver surveyed fish on all transects.

Broad-scale (1000 m²) fish surveys were focused on resource fishes >15 cm only and used timed swims with a pair of divers each counting, sizing, and identifying fishes within adjacent 5 m wide belt transects. Survey duration was 5 min with one diver towing a surface float equipped with GPS to enable measurement of transect

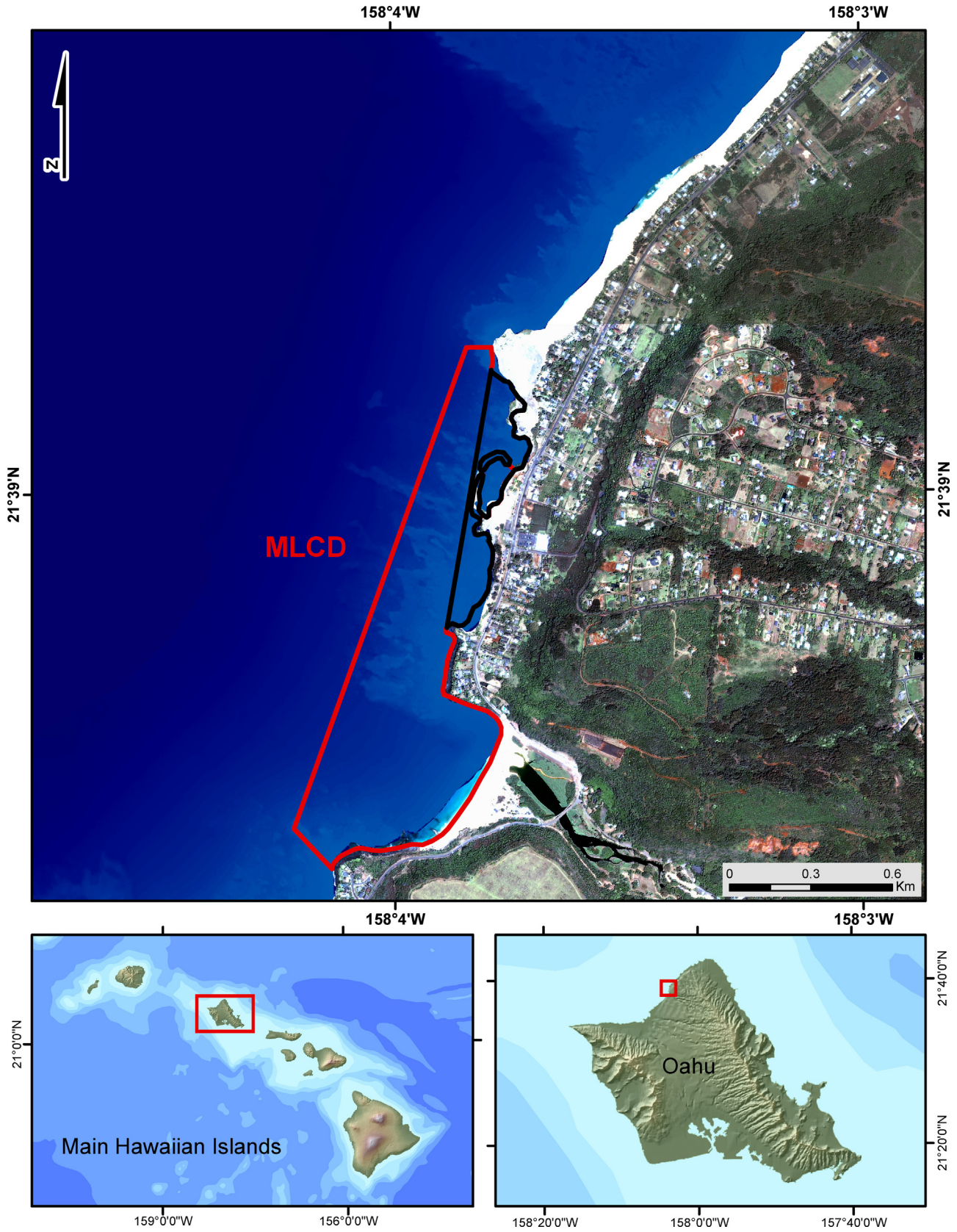


Fig. 1. Study location, Pupukea Marine Life Conservation District (MLCD) located on the north shore of Oahu, Hawaii. Grey outline in main frame delineates current (est. 2000) protected area boundary, black outline represents previous (est. 1983) boundary.

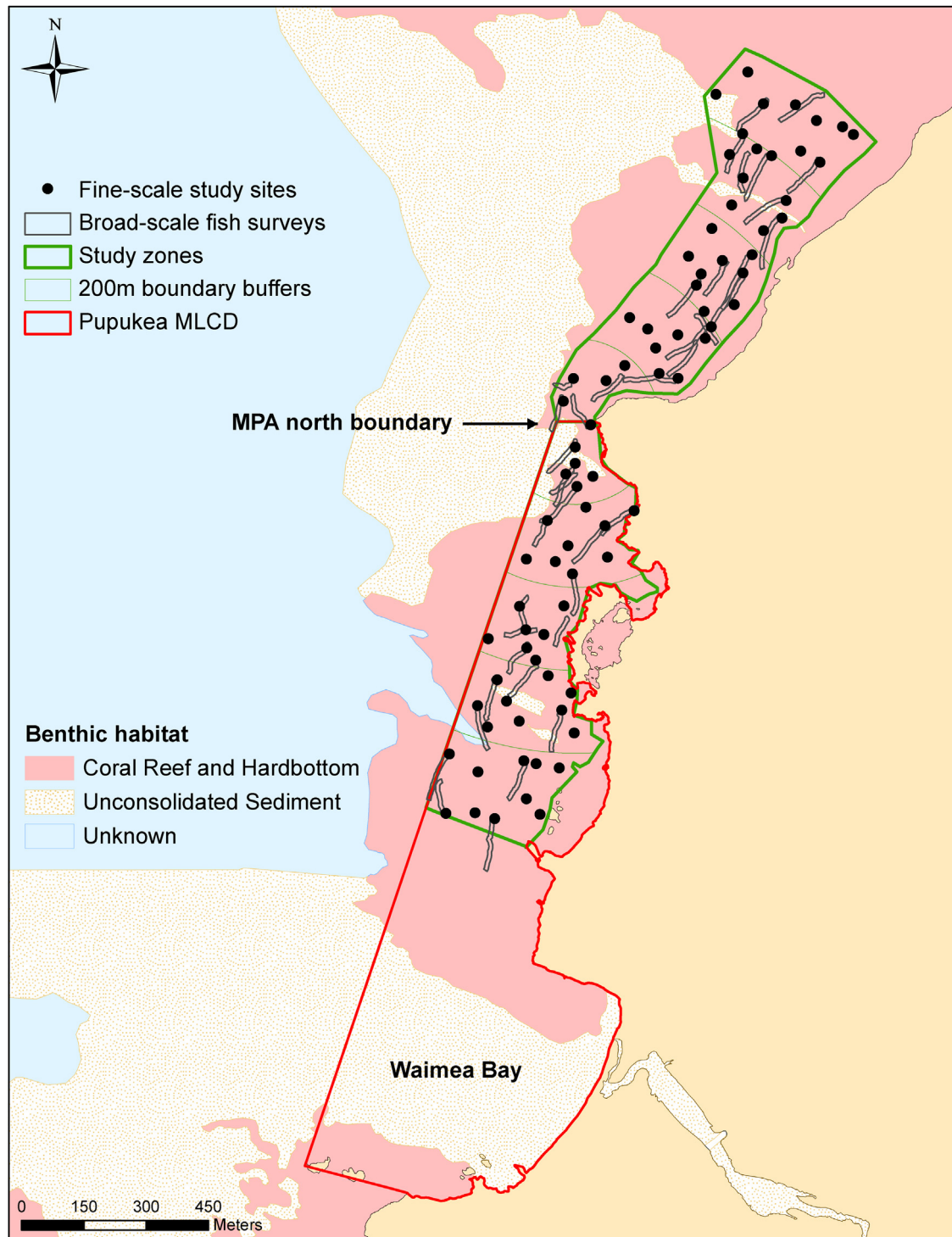


Fig. 2. Pupukea study design. Map elements indicated in legend. Black dots represent fine-scale survey stations; gray linear polygons represent broad-scale timed surveys; light gray, thick outline indicates the boundary of the MPA; and dark gray, thick outlines indicate study zones. Hard and soft bottom habitats are included for reference.

length, from which area was derived. Average transect length was 107 ± 20 m (SD, standard deviation).

2.3.2. Fine-scale habitat variables

Rugosity was measured on each of the fine-scale transects using the chain and tape method whereby a fiberglass measuring tape was carefully contoured along the reef surface directly beneath the transect, with rugosity calculated as tape

length/transect length (Risk, 1972). Photo quadrats were collected every 2 m for a total of 12 per transect using a 0.5 m rod connected to the camera housing to standardize distance from the substrate and thus quadrat size. Benthic cover was estimated for each transect using the CPCe image analysis software (Kohler and Gill, 2006), using 15 random points per photo. Cover was identified under each point for a total of 180 points per transect.

2.3.3. Broad-scale habitat variables

The SHOALS (Scanning Hydrographic Operational Airborne LiDAR Survey) system developed by the US Army Corp of Engineers uses light detection and ranging (LiDAR) technology to remotely measure bathymetry in the coastal zone (Irish and Lillycrop, 1999). LiDAR data for the coastal areas of Hawai'i were collected in 1999 and 2000. Habitat metrics were quantified using LiDAR point data interpolated to a 2 m grid cell size. Average depth and slope-of-slope (a measurement of structural complexity) were quantified for each of the study sites using ArcGIS 10 (ESRI). Slope-of-slope was chosen to quantify benthic complexity because Pittman et al. (2009) showed a strong relationship between slope-of-slope and fish biomass, and because analysis showed a higher concordance with field-measured rugosity than other LiDAR-derived metrics. Polygons representing all fine and broad scale fish transects were used to sample grid cell values from the bathymetric raster layers, which were averaged to create a representative metric for each transect. Major benthic cover categories for the broad-scale transects were derived from NOAA Benthic habitat maps (Battista et al., 2007). These included coral, macroalgae, and turf algae dominated habitats.

2.3.4. Fishing effort data

Surveys of fishing effort were conducted in the open zone during daylight hours, with each survey consisting of 4 h of observation. Survey units were stratified by time of day (morning: 7–11, mid-day: 11–3, afternoon: 3–7) and by weekday and weekend/holiday. Sampling days and times were randomized within each stratum to minimize bias and weekdays were randomized without replacement in order to obtain better coverage (Friedlander and Parrish, 1997). When fishing activity was observed, the start time and end times were recorded along with type of fishing gear, number of gear, and number of fishers. The precise location of each fishing activity along the shoreline was noted using a GPS unit. Locations of fishing activities taking place off-shore were recorded in relation to shoreline landmarks with distance from shore estimated visually. Location updates were recorded every 15 min. A total of 22 fishing effort surveys were conducted comprising 88 total hours of observation.

A community organization, Malama Pupukeya-Waimea (MPW), conducts education and outreach activities at the marine protected area. As part of their program they conduct human use surveys and maintain a database of fishing violations within the MPA. During the summer months they record activity at least twice a week. This dataset provided a comparison for fishing effort data collected in the open area.

2.4. Data analysis

2.4.1. Fish data

Length estimates of fishes from visual censuses were converted to weight using the following length–weight relationship: $W = a(SL)^b$, where a and b are constants for the allometric growth equation, SL is standard length in millimeters, and W is weight in grams. Where necessary, size in total length was converted to fork length or standard length using length-fitting parameters obtained from FishBase (Froese and Pauly, 2011). Length–weight fitting parameters were available for 150 species commonly observed on visual fish transects in Hawai'i (Hawai'i Cooperative Fishery Research Unit, unpublished data) and supplemented with information from other published and web-based sources. In the cases where length–weight information did not exist for a given species, the parameters from similar bodied congeners were used. Biomass estimates were converted to grams per square meter (g/m^2) and abundance was converted to density (num/m^2), to enable

comparisons between broad and fine-scale surveys as well as other studies in Hawai'i and worldwide.

In addition to grouping fish species into resource and non-resource fishes, they were further categorized into trophic and mobility guilds (Friedlander and Parrish, 1998). Trophic guilds included herbivores, planktivores, piscivores, obligate corallivores, feeders on mobile benthic invertebrates (e.g., crustaceans), and feeders on sessile invertebrates (e.g., sedentary polychaetes). Mobility guilds included (in order of increasing mobility); residents, semi-vagile type I, semi-vagile type II, and transients. Residents were defined as those species with limited movement (<10 m) and well defined home ranges (e.g., squirrelfishes, eels, hawkfishes, and some damselfishes). Species with intermediate degrees of mobility were classified into semi-vagile groups. Semi-vagile type I included species such as butterflyfishes and small wrasses with daily movement patterns on the order of tens of meters. Semi-vagile type II species made daily movements on the order of hundreds of meters and included groups such as large surgeonfishes and parrotfishes. Transients were those species that moved rapidly over relatively large distances (>1 km) including jacks and some snappers species.

2.4.2. Reserve effect

In order to test the reserve effect of greater biomass, density, or richness within the MPA, which is a pre-requisite for fish spillover, a Student's t -test was used to compare analogous values between the MPA and the open area where $p < 0.05$ was considered statistically significant. Data from the fine-scale surveys was transformed to meet assumptions of normality. Richness data were square root transformed, density data were $\ln(x)$ transformed, and biomass was $\ln(x+1)$ transformed. In addition to testing all species together, resource and non-resource fish values were also tested separately. Fish assemblage data from the broad-scale resource fish surveys did not meet the assumptions for parametric statistics despite transformation, therefore a Wilcoxon rank sum test was used to compare MPA and open area transects.

2.4.3. Habitat effects

Pearson's correlation coefficients were calculated to evaluate associations between habitat variables. Multivariate habitat effects on patterns of average total reduced fish biomass were modeled using distance-based linear models (Legendre and Anderson, 1999; McArdle and Anderson, 2001). This technique provides nonparametric analysis and modeling of the relationship between a multivariate data cloud, as described by a resemblance matrix, and one or more predictor variables. Analyses were conducted using biomass with planktivorous species excluded, hereby referred to as "reduced" biomass. These species are often abundant with very patchy distribution, so typically high variability for this group may mask the effects of protection or habitat (Harmelin-Vivien et al., 2008). Habitat association was modeled separately for resource and non-resource fish data from the fine-scale surveys and resource fish data from broad-scale surveys. The Bray–Curtis similarity measure was used to construct a resemblance matrix of untransformed, reduced biomass for each of these groups forming the basis for subsequent analysis. A zero-adjusted Bray–Curtis was used for resource fish reduced biomass data at both scales to account for transects where no resource fish were observed using a constant equal to the lowest recorded value in each case (Clarke and Gorley, 2006). Environmental variables were ranked to reduce the impact of outliers and highly correlated variables ($\rho > 0.5$) were removed from consideration in the models. A step-wise procedure was utilized to select variables for the models based on the AIC_c value, which is a modification of the Akaike Information Criterion (Akaike, 1973) developed to handle situations where the number of samples

is small relative to the number of predictor variables (Burnham and Anderson, 2002).

2.4.4. Biomass gradients

Gradients of fish biomass across reserve boundaries were evaluated using standard least-squares linear regressions. Average total reduced biomass for each group (fine-scale survey resource fish, fine-scale survey non-resource fish, and broad-scale survey resource fish) were tested vs. distance from the MPA boundary. Fine-scale survey fish biomass data were $\ln(x+1)$ transformed and broad-scale survey biomass data were square-root transformed to meet assumptions of normality and homoscedasticity. F -tests were performed in order to determine if the relationships were statistically significant.

In order to measure the spatial variation in fish biomass after removing the influence of habitat, habitat variables found to be significant ($p < 0.05$) in the distance-based linear models were used as explanatory variables in standard least-squares multiple linear regressions with reduced biomass. Residuals from the multiple linear regression models (defined as corrected biomass) were then used as response variables in linear regressions with distance from boundary. This was to ensure that tests of gradients were related to protection level and not differences in habitat (García-Charton et al., 2004; Harmelin-Vivien et al., 2008). The significance of these relationships was evaluated using an F -test. This procedure is more conservative than including distance from boundary in the multiple regression model, since it may attribute a reserve effect to habitat variables, but will not attribute an effect of habitat to reserve protection (Chapman and Kramer, 1999). In addition to testing all transects separately for fine-scale resource and non-resource corrected biomass, transects were also grouped into 100 m bins in order to decrease variability and clarify patterns for the purpose of comparison.

2.4.5. Fishing effort data

To compare fishing effort between the MPA and open areas, values were standardized to number of fishers per week. This is because the fishing violation dataset provided by MPW did not record time spent fishing, although there were records of number of fishers and gear type. For the purpose of comparison, the MPW dataset and our dataset were analyzed in the same manner and records corresponding to the period June–September 2011 were selected for analysis. Values for each gear type were calculated separately. Records were divided into weekdays and weekends/holidays and number of fishers summed in each of these strata. Summed values were then divided by total hours of observation in each stratum and multiplied by 12 (daylight hours) to produce an average number of fishers per day. This was expanded to a weekly average by multiplying by number of weekdays/weekend days per week and adding the result.

$$F_{wk} = 2\bar{f}_{we} + 5\bar{f}_{wd}$$

where

$$\bar{f} = \frac{f}{h}$$

f is the fishers observed per stratum (weekday or weekend); h is the hours observed per stratum (weekday or weekend).

Fishing effort in the open area by gear type was further quantified as total effort, E , per week adapting the methods of Friedlander and Parrish (1997). The mean daily effort by all fishers in each sub-stratum (weekend/weekday, time of day) combined was calculated,

summed across time periods for each day stratum, then expanded by the number of days in a week.

$$E = \bar{E} \times D = \frac{\sum_{i=1}^{td} \sum_{j=1}^{N_i} E_{ij}}{td} \times D$$

where E is the total effort; \bar{E} the mean daily effort; D the total number of days; td the time/day strata; N_i the number of fishers observed on day i ; E_{ij} the observed effort of fisher j on day i , where $i = 1, \dots, d, j = 1, \dots, N_i$.

2.4.6. Fishing effort spatial analysis

A unique polygon was created from spatial information recorded for each fishing effort observation using ArcGIS 10. Attributes for each polygon included type of gear, number of gears used, number of fishers, and time spent fishing. Angler hours for each polygon were calculated by multiplying number of gear by fishing time. Multiple, overlapping polygons were combined and angler hours summed for each. The summed polygon layer was then converted to a raster surface representing total observed angler hours for each cell. A 10 m grid cell size was selected to match the resolution of the data collected. This resulted in a relative fishing effort measure that could be compared across space. Total observed spearfishing hours were averaged for each study block representing intervals of 200 m from the MPA boundary. The significance of the relationship between average spearfishing effort and distance from boundary was evaluated with an F -test. Spatial patterns of spearfishing effort were investigated because this gear in Hawai'i is known to have high catch rates (Everson and Friedlander, 2004), occurs primarily in the depth range represented by the study zones, and selects for larger individual fish including herbivores which are not targeted by pole and line.

3. Results

3.1. Fish data

The mean number of species observed per transect was 16 ± 7 (SD), with considerable variation among transects. In total, 122 fish species from 30 families were counted, with 50 of these defined as resource species. The top five resource species by total biomass for both fine and broad scale surveys were all semi-vagile type II herbivores (Appendix I, Table A). Redlip parrotfish, *Scarus rubroviolaceus*, accounted for the highest biomass followed by four surgeonfishes: *Acanthurus olivaceus*, *A. leucopareius*, *Naso unicornis*, and *N. lituratus*. Three of the top five non-resource species by total biomass on fine-scale surveys were semi-vagile type I invertivores, one was a semi-vagile type I herbivore, and the fifth was semi-vagile type II invertivore (Appendix I, Table A). Non-resource species represented diverse families and include (in order of total biomass) *Acanthurus nigrofuscus*, *Sufflamen bursa*, *Thalassoma duperrey*, *Rhinecanthus rectangulus*, and *Sufflamen fraenatus*.

3.2. Reserve effect

Fish assemblage characteristics (e.g., species richness, numerical density, and biomass) varied by survey type and between resource and non-resource fish, although all were significantly higher inside the reserve than in the open area (Appendix I, Tables B and C). MPA-open differences in assemblage characteristics for resource fishes were all greater than for non-resource fishes, biomass in particular was 2.5 times greater in the reserve vs. the open area for resource species, compared to 1.4 times greater for non-resource species (Appendix I, Table B). These differences were most extreme for the broad-scale resource fish surveys, with density of fishes three

Table 1
Distance-based linear models of effects of habitat variables on reduced fish biomass in each study category. Variable selection was stepwise with the first term explaining the most variability and model selection was based on the modified Akaike Information Criterion (AIC_c). SS: sum of squares; pseudo-F: test statistic; df: degrees of freedom.

Variable	Effect	AIC _c	SS (trace)	Pseudo-F	P	r ²	r ² cumulative	Res. df
Resource fish biomass								
<i>Fine-scale (125 m²)</i>								
Slope-of-slope	+	621.72	24,904	10.78	0.001	0.12	0.12	78
%Coral	+	621.09	6188	2.74	0.024	0.03	0.15	77
<i>Broad-scale (1000 m²)</i>								
Turf cover	-	302.99	20,903	11.36	0.001	0.23	0.23	38
Slope-of-slope	+	301.7	6074	3.52	0.014	0.07	0.30	37
Non-resource fish biomass								
<i>Fine-scale (125 m²)</i>								
Rugosity	+	539.81	15,032	18.12	0.001	0.19	0.19	78
Depth	+	537.39	3605	4.54	0.014	0.05	0.23	77
%CCA	+	534.58	3725	4.93	0.017	0.05	0.28	76

times greater in the MPA and biomass nearly four times greater, compared to the open area (Appendix I, Table C).

3.3. Habitat effects

Some fine-scale habitat variables were correlated, with the strongest relationship occurring between rugosity and slope-of-slope ($\rho=0.67$). These are both measures of benthic complexity and after single factor distance-based linear models were run, the variable with the strongest relationship was kept for multi-factor model selection while the other was excluded. The strongest correlation between broad-scale habitat variables was between broad-scale coral cover and depth ($\rho=-0.76$). For this reason and due to correlation values (ρ) > 0.5 between broad-scale cover types, coral and macroalgae cover were excluded from broad-scale habitat effect models. Correlation tables for all habitat variables tested at each scale are provided in Appendix I, Tables D and E. Some fine-scale habitat variables that were significant factors in the distance-based linear models also had significant negative relationships with distance from boundary. These were coralline algae cover, rugosity, and slope-of-slope (Table 2). All broad-scale habitat variables had significant negative relationships with distance from boundary except for turf algae cover, which had a significant positive relationship, and macroalgae cover, which was not significant (Table 2).

Habitat effects on fish biomass varied between resource and non-resource fishes and between fine and broad scales. For resource fish biomass on fine-scale surveys, slope-of-slope explained the most variability (12%) followed by percent coral cover for a total of 15% explained variation (Table 1). Resource fish biomass from broad-scale surveys was heavily influenced by turf cover (23%), followed by slope-of-slope, resulting in a total

Table 2
Linear relationships between significant habitat variables and distance from boundary. Standard least-squares linear regressions with distance from boundary as the explanatory (x) variable.

Variable	Effect	r ²	p
Fine-scale			
%Coral	-	0.05	0.056
%CCA	-	0.23	<0.001
Rugosity	-	0.23	<0.001
Depth	-	0.01	0.482
Slope-of-slope	-	0.15	<0.001
Broad-scale			
Depth	-	0.10	0.046
Slope of slope	-	0.16	0.011
Coral	-	0.21	0.003
Macroalgae	-	0.04	0.213
Turf	+	0.39	<0.001

of 30% explained variation (Table 1). Variation in non-resource fish biomass from the fine-scale surveys was explained largely by rugosity (19%), followed by depth and coralline algae cover with 28% total variation explained by the model (Table 1).

3.4. Biomass gradients

For fine-scale survey data, both resource (Fig. 3a) and non-resource fish (Fig. 3b) reduced biomass showed a significant negative relationship with distance from boundary. After controlling for habitat, resource fish corrected biomass (Fig. 4a) still showed a significant relationship with distance from boundary whereas non-resource fish corrected biomass did not (Fig. 4b). Fit was improved for resource fish corrected biomass when sites were averaged by 100 m bins (Fig. 5a), although the relationship between distance to boundary and non-resource fish corrected biomass remained non-significant (Fig. 5b). Broad-scale resource fish reduced biomass showed a very strong relationship with distance from reserve boundary (Fig. 6a). After correcting for habitat the relationship was not as strong, although still highly significant (Fig. 6b).

3.5. Fishing effort

Average number of fishers per week was 26.5 in the reserve and 194.7 in the open area during the study period. Pole fishing was the dominant gear, used by 65% of fishers in the MPA and 54% of fishers in the open area, followed by spear (22%, 24%), trolling (5%, 15%), and netting (8%, 1%) (Appendix I, Figure A). Relative proportions of gear use were similar between MPA and open areas although netting formed a larger proportion in the reserve due to hand-net activity in tidepools, which were less common in the open area. Trolling was more frequent in the open area, likely because of boating restrictions in the MPA. Total mean angler hours per week in the open area was 241.2. Fishing effort of all gear types per week was greater during the weekdays with the exception of whipping (repeated casting with small pole) and netting which were observed more often on weekends (Appendix I, Figure B).

Spearfishing effort occurred widely throughout the open zone and was somewhat associated with beach access. Movements parallel to shore are evident, presumably along a depth gradient. Some hotspots of activity further offshore could represent underwater features of interest such as areas of high complexity. There is an obvious predominance of effort near and directly adjacent to the MPA boundary, as well as crossing over into the MPA (Fig. 7A). When spearfishing effort was averaged in study blocks (200 m increments) it ranged from 4.5 h near the boundary (0–200 m) to 0.8 h at the far end of the study area (800–1000 m) (Fig. 7B). The

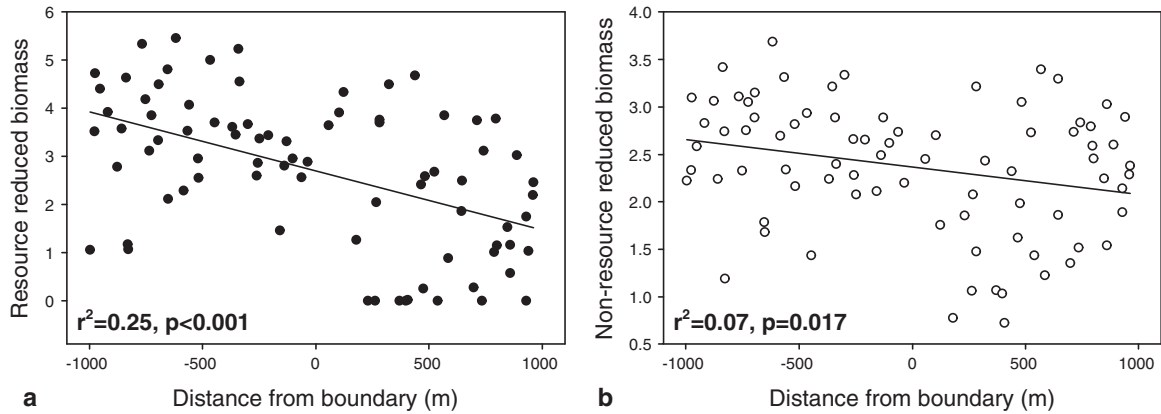


Fig. 3. Least-squares linear regression of fine-scale survey reduced biomass ($\ln(x+1)$ transformed) vs. distance from MPA boundary for resource fish ● (a) and non-resource fish ○ (b). For x-axis, negative distance values are inside MPA, positive values are outside, zero distance represents MPA boundary.

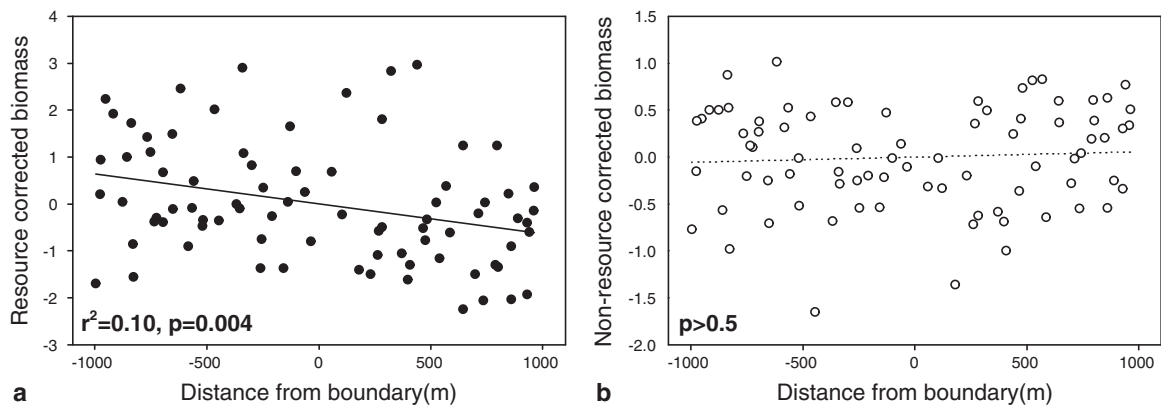


Fig. 4. Least-squares linear regression of fine-scale survey corrected biomass (residuals) vs. distance from MPA boundary for resource fish ● (a) and non-resource fish ○ (b). x-axis same as preceding figure.

relationship between mean spearfishing effort and distance from boundary in the open area ($N=5$) was highly significant ($r^2 = 0.98$, $p = 0.002$).

4. Discussion

4.1. Reserve effect and multi-scale fish data

The Pupukeya MLCD shows a strong reserve effect as indicated by comparisons of fish assemblage metrics inside and outside the

fished area. This effect was significant for non-resource fish as well as resource fish at both scales of measurement, although the magnitude of these differences are likely due to differences in habitat quality. Many habitat variables at both fine and broad scales correlated significantly with distance from boundary (Table 2), thus controlling for these habitat variables was critical to testing the spillover hypothesis.

The density and biomass of resource fishes were greater on small-scale (125 m^2) vs. large-scale (1000 m^2) transects although the latter were focused on resource fishes $>15\text{ cm}$ only. One reason for this is that more time (10–15 min) is spent in a smaller

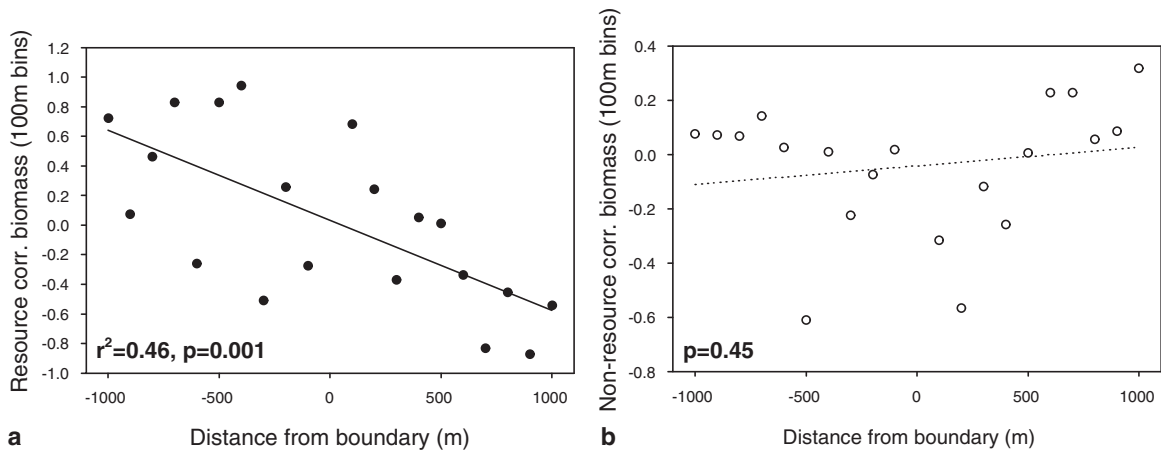


Fig. 5. Least-squares linear regressions of fine-scale survey corrected biomass (residuals) averaged in 100 m distance bins vs. distance from MPA boundary for resource fish ● (a) and non-resource fish ○ (b). x-axis same as preceding figures.

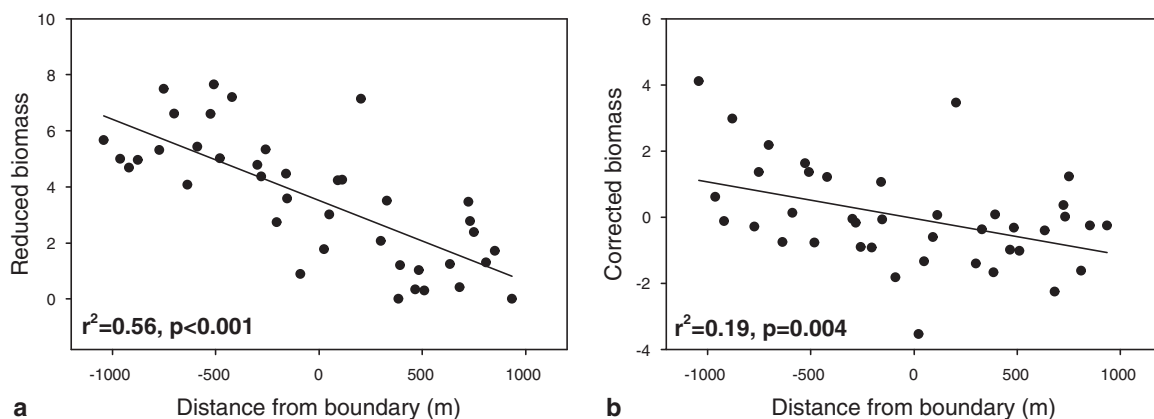


Fig. 6. Least-squares linear regression of broad-scale survey reduced biomass (square root transformed) (a) and corrected biomass (residuals) (b) vs. distance from MPA boundary. *x*-axis same as preceding figures.

area for the fine-scale surveys compared to broad-scale surveys (5 min) and these metrics are scaled by area (num/m^2 , g/m^2). Another reason is that the broad-scale surveys did not record resource species <15 cm. However, the broad-scale surveys did record higher species richness of resource species, which indicates that they are more effective in recording these fishes which tend to be more mobile and therefore less likely to be encountered on smaller transects. Also notable is that the broad-scale surveys showed greater differences between the reserve and open area for all three resource fish assemblage characteristics (e.g., species richness, density, and biomass). This was true for biomass in particular which suggests that while the broad-scale surveys may underestimate total biomass of resource species across all size classes, they provide a more accurate measurement of the portion of the assemblage that is subject to the greatest fishing pressure. Hence, the larger apparent effect size could be due to measuring only larger size resource fishes, rather than all sizes of resource fish.

4.2. Habitat effects on fish biomass

Rugosity was the most important habitat variable tested for non-resource fish biomass (fine-scale surveys) and slope-of-slope was the most important habitat variable for resource fish biomass measured at both fine and broad scales. This has an ecological basis, as structurally complex habitats provide more surface area for food production as well as opportunities for shelter (McCoy and Bell, 1991; García-Charton et al., 2004). Both rugosity and slope-of-slope are measures of structural complexity; however, they differ in scale. Rugosity represents linear fine-scale complexity and is measured in situ, slope-of-slope represents planar complexity averaged over the transect area and is based on a LiDAR-derived model (2 m cell size) of the substrate. Because non-resource fish biomass was dominated by lower mobility species, it was not surprising that that this group would respond to the more fine-scale measure of complexity, compared to resource fishes where higher mobility species comprise the majority of total biomass. These findings support previous research by Wedding et al. (2008) and Pittman et al. (2009) which showed that structural complexity measured at fine spatial resolutions is a strong predictor of fish abundance and biomass. While these studies tested the relationships of complexity metrics calculated using different window sizes, this study quantified fish populations at different scales to use as the basis for comparisons.

4.3. Fishing effort

Fishing effort inside the MPA (poaching) was not negligible; however, fishing effort outside was over seven times higher. Levels of fishing effort were also likely underestimated, especially within the MPA. Anecdotal evidence points to some amount of fishing occurring during the nighttime hours, when we did not survey. Fishers may likely use the reserve at night in order to avoid detection. The work of the MPW community group helps to discourage poaching in the reserve and they are instrumental in achieving higher levels of resource enforcement than is typical in Hawai'i by notifying enforcement officers when they observe violations. According to MPW records, enforcement officers responded in person to 24 out of 75 total calls between January 2010 and October 2011 or 32% of calls.

A catch consisting of two very large (55 and 65 cm) terminal redlip parrotfish (*S. rubroviolaceus*) and one large (45 cm) peacock grouper (*Cephalopholus argus*) was observed from a spear fisher that emerged from the MPA area. This further validated the decision to focus on spatial patterns of spearing effort because these species rank as the first and seventh highest for total resource fish biomass observed on the fine-scale surveys, and first and tenth highest for the broad-scale surveys (Appendix I, Table A). The ability to compare spatial patterns of fishing effort with fish biomass was very informative. The methodology for conducting spatially explicit surveys and representing them on a map was developed for this study and if conducted on a broader scale would have great utility for ecosystem based management and marine spatial planning. Spatial analysis of spearfishing effort showed effort was highest near the reserve boundary and decreased with distance, which is consistent with adult fish spillover (McClanahan and Mangi, 2000; Kellner et al., 2007). Because costs of fishing in this area are low and equal across the area (based on entry from shore), the fishing effort most likely reflects the spatial pattern of catch rates (Abesamis et al., 2006). The observed pattern suggests that fishers are responding to gradients in resource fish biomass.

The average level of observed spearfishing in the boundary unit ("b" in Fig. 7) was less than 5 h over the study period. This translates to a maximum of 0.7 h per day on average. Catch per unit effort for spear fishing is relatively high, estimates elsewhere in Hawai'i are about 0.9 kg/h (Friedlander and Parrish, 1997; Everson and Friedlander, 2004). Assuming a CPUE of 1 kg/h, the observed level spearfishing effort would produce a yield of 0.7 kg per day, and because high winter surf allows for a maximum of six months of fishing per year, this translates to around 126 kg per year. Average observed resource fish biomass in this boundary unit ("b" in Fig. 7) was 0.05 kg/m² so if we extrapolate to the

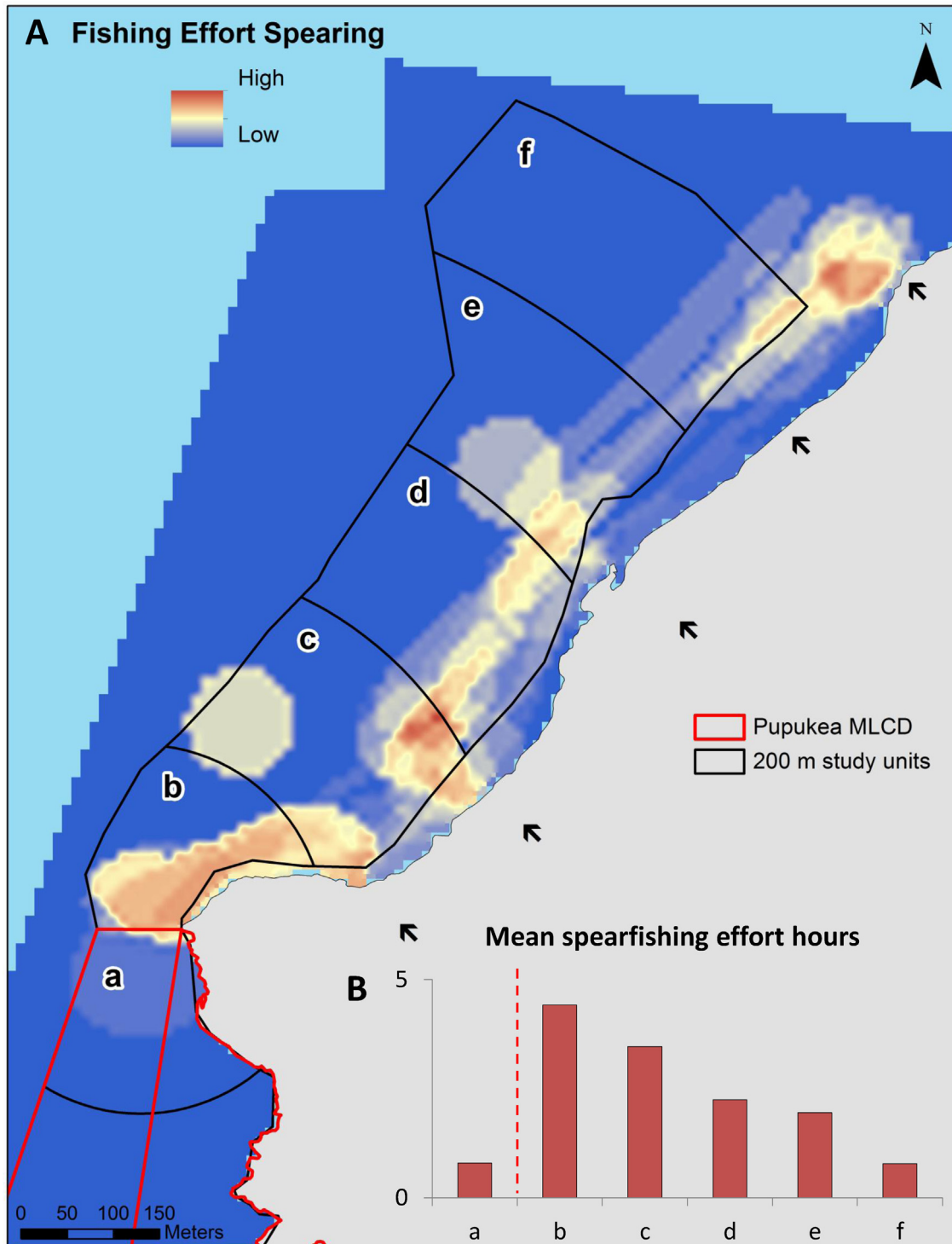


Fig. 7. (A) Spatial extent of total observed spearfishing effort. Relative effort is represented on a gradient where white: low effort and black: high effort. Black arrows represent beach access locations. (B) Total spearfishing effort hours averaged in study units a–f. Dotted line represents MPA boundary.

total boundary unit area (28,379 m²), the estimated total biomass is 1391 kg. Therefore, the observed (daylight) spear fishing effort in the MPA boundary unit (“b” in Fig. 7) has the potential to remove as much as 9% of the standing stock biomass there in a year. Although pole fishing effort is also relatively high near the MPA boundary, CPUE is low and herbivores are not targeted. It appears then, that this rate of removal is not large enough to obscure the gradient of resource fish biomass produced by spillover.

4.4. Context of research

This study builds upon previous spillover research conducted around the world. Rakitin and Kramer (1996) tested the hypothesis that high population densities of larger fish within reserves could result in emigration to non-reserve areas, producing a gradient of abundance and mean size across reserve boundaries, by estimating abundance and size of fishes with trapping and visual census on reefs inside the Barbados Marine Reserve (BMR) and

outside within 4 km of the reserve boundary. Trap catches decreased gradually with distance from the BMR center, but this gradient of abundance was less evident in visual census counts. Failure to account for habitat differences may have masked a stronger pattern. *Abesamis et al. (2006)* found significant spatial gradients of decreasing abundance of target fishes across a reserve boundary in the Philippines and no significant decline in the abundance of non-target fishes. Habitat factors could not account for these results for target fishes, but did influence patterns of non-target fishes. *Harmelin-Vivien et al. (2008)* assessed the existence of gradients of fish abundance and biomass across marine reserve boundaries in six Mediterranean MPAs using underwater visual censuses performed at various distances from the core of the MPA. Linear correlations revealed significant negative gradients in mean fish biomass in all reserves studied after the effect of habitat had been removed. They estimated that fish spillover beneficial to local fisheries occurred mostly at a small spatial scale (100 s of meters).

The results of this study are consistent with these previous findings and add to the body of spillover research evidence from a geographically distinct coral reef ecosystem. This research also goes further than previous studies in its application of a seascape approach to comprehensively model and control for habitat variables and conduct investigations at multiple scales in addition to measuring spatially explicit fishing effort patterns. This study provides strong evidence in support of spillover and upholds published results with respect to contrasting patterns between resource and non-resource species (*Abesamis et al., 2006*), spatial scales of fish spillover (*Russ, 2002; Harmelin-Vivien et al., 2008*) and response of fishers in terms of spatial distribution of fishing effort (*Rakitin and Kramer, 1996; McClanahan and Mangi, 2000*).

4.5. Further research and implications for management

This project is the first to address the spillover effect for food fish in Hawai'i. An obvious next step is to undertake similar research at other MPAs in Hawai'i to see if they also support the spillover effect, and how differences between marine protected areas may affect this process. Also needed is a better understanding of larval dispersal relative to marine protected areas in Hawai'i, measuring both to what extent they are self-recruiting, and to what degree the MPAs can replenish fished areas through larval export. Although evidence for adult spillover continues to mount, unequivocal proof is still lacking. *Russ (2002)* outlined a statistical design robust enough to provide such proof using a Before-After-Control-Impact-Pairs (BACIP) design (*Underwood, 1994*). Such a study should control for habitat variables, use tagging methods to quantify fish movements, incorporate fish surveys and measure fishing effort. This proposed experimental design, while ambitious, could be achievable in Hawai'i given the establishment of a new marine reserve and effective enforcement of the reserve (at least during the study period). Many of the attributes of this design were incorporated into the current study. There is a high probability that new marine reserves will be established in Hawai'i in the coming years, and the execution of such an experiment would be the gold-standard in spillover research.

Information on the behavior of fishers in response to marine protected areas is critical to management and can vary based upon cultural and local practices. Nevertheless, some generalizations can be made and this study upheld predictions based on previous research that fishers would concentrate effort near the reserve boundary in response to real or perceived spillover (*Kellner et al., 2007*). In this case, enhanced levels of fishing effort near the boundary were not high enough to remove biomass levels attributable to spillover, although monitoring is needed to see if this situation persists through time. Nevertheless, these results show that fish spillover from Pupukeya MLCD is enhancing stocks of species

targeted by spearfishers in the adjacent open area and current estimated levels of removal are sustainable.

While this and other findings provide evidence supporting spillover, it appears to occur at relatively small scales of 100–1000 m (*Roberts and Polunin, 1991; Russ et al., 2003; Harmelin-Vivien et al., 2008*). This range is affected by the mobility of fished species and the distribution and level of fishing intensity or fishing effort. Partly due to this limited range of influence, there seems to be a consensus that increased reproductive output and subsequent larval export will generally be the more important MPA effect since it has the capability to enhance fisheries on much larger scales (*Russ, 2002; Sladek Nowlis and Friedlander, 2005*). Unfortunately, evidence for the “recruitment effect” is sparse due to the difficulties inherent in measuring movement patterns of eggs/larvae. Theoretical models (often enhanced with empirical measurements) have provided some of the best support for the recruitment effect (e.g., *Cudney-Bueno et al., 2009; Pelc et al., 2010*) and recently, studies using DNA parentage analysis have provided evidence by identifying offspring outside of protected areas (e.g., *Planes et al., 2009; Christie et al., 2010*).

Marine protected areas aimed to benefit fisheries should be designed to minimize spillover, thereby maximizing the production of pelagic eggs and larvae. MPAs can be designed to incorporate natural barriers to movement such as sand areas to limit spillover across boundaries. However, as long as the perimeter to area ratio is not overly high, MPAs with favorable habitats should be able to maintain sufficient larval production for self-recruitment and larval export (*Carr and Reed, 1993*). While there is potential for larval export from Pupukeya MLCD due to a large spawning stock within the protected area, the direction, magnitude, and scale of fishery replenishment via this mechanism is unknown. This research has shown the ability of a small MPA to provide local fishery enhancement through adult spillover. This evidence of a tangible fishery benefit can be used to promote the maintenance of this and similar MPAs and the establishment of additional marine protected areas.

5. Conclusions

The Pupukeya MLCD on the north shore of Oahu shows a strong reserve effect with significantly higher species richness, numerical density, and biomass compared to the adjacent open area, including a nearly four-fold difference in resource fish biomass estimated by broad-scale surveys. Structural complexity explained much of the variability in fish biomass for both resource and non-resource species. Spillover of resource fishes across the north boundary of the reserve is indicated by a significant negative gradient of resource fish corrected biomass from inside to outside the protected area. This effect was not observed for non-targeted fish species. Results from this research are consistent with similar studies in the Mediterranean (*Harmelin-Vivien et al., 2008*), Caribbean (*Rakitin and Kramer, 1996*), and the Philippines (*Abesamis et al., 2006*).

Fish spillover can help mitigate costs associated with the establishment of MPAs in terms of lost fishing area. Yields from spillover, while small, may play a critical role in convincing fishers to support establishment and maintenance of reserves (*Russ and Alcala, 1996*). For some fishers, spillover of adult fish from marine reserves, especially larger fishes, will appear to be a more direct and tangible benefit than increased recruitment to potentially distant fishing grounds (*Abesamis et al., 2006*). Thus, spillover may have a substantial positive effect on the attitudes of fishers toward marine reserves and serve to encourage the establishment and maintenance of MPAs in Hawai'i and worldwide.

Acknowledgements

This work constitutes the lead authors master's thesis. Committee members Brian Szuster and Qi Chen both provided support and advice. Ivor Williams contributed valuable input during preparation of the manuscript, which was further improved by comments from three anonymous reviewers. The Nature Conservancy (TNC) of Hawai'i supplied vital field support thanks to Marine Science Advisor Eric Conklin and members of the TNC marine team; Kydd Pollock, Russell Amimoto, and Zachary Caldwell. Subsequent fieldwork would have been very difficult without the use of a boat belonging to Dewolf Miller. Able field assistance was provided by (in order of involvement) Leilani Pena, Ily Iglesias, Nyssa Silbiger, Alec Nordschow, Mary Donovan, Paolo Usseglio, Patrick Curry, Robert Henderson, Christina Comfort, James Anderson, and Maui Scanlon-Givens. Special thanks to the good people of Malama Pupukea-Waimea for sharing their data and for providing education and supporting enforcement in Pupukea MLC. This research was funded in part by an award from the Hawai'i Geographic Information Coordinating Committee (HIGICC) and the Hawai'i Cooperative Fishery Research Unit provided major logistic and administrative support.

The use of trade names or products does not constitute endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2012.09.016>.

References

- Abesamis, R.A., Russ, G.R., 2005. Density-dependent spillover from a marine reserve: long-term evidence. *Ecol. Appl.* 15, 1798–1812.
- Abesamis, R.A., Russ, G.R., Alcala, A.C., 2006. Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 16, 349–371.
- Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. In: Petroa, B., Csake, F. (Eds.), 2nd International Symposium on Information Theory.
- Anonymous, 2009. Commercial Marine Landings Summary Trend Report – Calendar Year 2009. Hawaii Division of Aquatic Resources.
- Ashworth, J.S., Ormond, R.F.G., 2005. Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biol. Conserv.* 121, 333–344.
- Battista, T.A., Costa, B.M., Anderson, S.M., 2007. Shallow-Water Benthic Habitats of the Main Eight Hawaiian Islands (DVD). Biogeography Branch, Silver Spring, MD.
- Bell, J.D., Craik, G.J.S., Pollard, D.A., Russell, B.C., 1985. Estimating length frequency distributions of large reef fish underwater. *Coral Reefs* 4, 41–44.
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer Verlag.
- Carr, M.H., Reed, D.C., 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* 50, 2019–2028.
- Chapman, M.R., Kramer, D.L., 1999. Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Mar. Ecol. Progr. Ser.* 181, 81–96.
- Christie, M.R., Tissot, B.N., Albins, M.A., Beets, J.P., Jia, Y., Ortiz, D.M., Thompson, S.E., Hixon, M.A., 2010. Larval connectivity in an effective network of marine protected areas. *PLoS One* 5, 12.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Cudney-Bueno, R., Lavín, M.F., Marinone, S.G., Raimondi, P.T., Shaw, W.W., 2009. Rapid effects of marine reserves via larval dispersal. *PLoS One* 4, 1.
- Everson, A., Friedlander, A.M., 2004. Catch, effort, and yields for coral reef fisheries in Kane 'ohē Bay, O 'ahu and Hanalei Bay, Kaua 'i: Comparisons between a large urban and a small rural embayment. In: Friedlander, A.M. (Ed.), Status of Hawai 'i's Coastal Fisheries in the New Millennium, Honolulu, HI, Proceedings of the 2001 Fisheries Symposium sponsored by The American Fisheries Society Hawai 'i Chapter.
- Forcada, A., Bayle-Sempere, J.T., Valle, C., Sánchez-Jerez, P., 2008. Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Mar. Environ. Res.* 66, 536–547.
- Friedlander, A.M., Parrish, J.D., 1997. Fisheries harvest and standing stock in a Hawaiian Bay. *Fish. Res.* 32, 33–50.
- Friedlander, A.M., Parrish, J.D., 1998. Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. *J. Exp. Mar. Biol. Ecol.* 224, 1–30.
- Friedlander, A.M., Brown, E., Monaco, M.E., 2007a. Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Mar. Ecol. Progr. Ser.* 351, 221–233.
- Friedlander, A.M., Brown, E.K., Monaco, M.E., 2007b. Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. *Ecol. Appl.* 17, 715–730.
- Friedlander, A.M., Wedding, L.M., Brown, E., Monaco, M.E., 2010. Monitoring Hawaii's Marine Protected Areas: Examining Spatial and Temporal Trends Using a Seascape Approach. Silver Spring, NCCOS Center for Coastal Monitoring and Assessment Biogeography Branch, MD.
- Friedlander, A.M., Wedding, L.M., Monaco, M.E., Brown, E.K., Clark, A.C., Antoline, D., In Review. Evaluating the expansion of a marine protected area using a seascape ecology approach. *Ecol. Appl.*
- Froese, R., Pauly, D., 2011. FishBase. World Wide Web electronic publication.
- García-Charton, J.A., Pérez-Ruzafa, Á., Sánchez-Jerez, P., Bayle-Sempere, J.T., Reñones, O., Moreno, D., 2004. Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Mar. Biol.* 144, 161–182.
- Gell, F.R., Roberts, C.M., 2003. Benefits beyond boundaries: the fishery effects of marine reserves. *Trends Ecol. Evol.* 18, 448–455.
- Halpern, B.S., Warner, R.R., 2002. Marine reserves have rapid and lasting effects. *Ecol. Lett.* 5, 361–366.
- Harmelin-Vivien, M., Le Diréach, L., Bayle-Sempere, J., Charbonnel, E., García-Charton, J.A., Ody, D., Pérez-Ruzafa, Á., Reñones, O., Sánchez-Jerez, P., Valle, C., 2008. Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: evidence of fish spillover? *Biol. Conserv.* 141, 1829–1839.
- Irish, J.L., Lillycrop, W.J., 1999. Scanning laser mapping of the coastal zone: the SHOALS system. *ISPRS J. Photogram. Rem. Sens.* 54, 123–129.
- Kellner, J.B., Tetreault, I., Gaines, S.D., Nisbet, R.M., 2007. Fishing the line near marine reserves in single and multispecies fisheries. *Ecol. Appl.* 17, 1039–1054.
- Kohler, K.E., Gill, S.M., 2006. Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Comp. Geosci.* 32, 1259–1269.
- Legendre, P., Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecol. Monogr.* 69, 1–24.
- Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S., Warner, R.R., 2009. Biological effects within no-take marine reserves: a global synthesis. *Mar. Ecol. Progr. Ser.* 384, 33–46.
- Lizaso, J.L.S., Goni, R., Renones, O., Charton, J.A.G., Galzin, R., Bayle, J.T., Jerez, P.S., Ruzafa, A.P., Ramos, A.A., 2000. Density dependence in marine protected populations: a review. *Environ. Conserv.* 27, 144–158.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82, 290–297.
- McClanahan, T.R., Mangi, S., 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecol. Appl.* 10, 1792–1805.
- McCoy, E.D., Bell, S.S., 1991. Habitat structure: the evolution and diversification of a complex topic. In: Bell, S.S., McCoy, E.D., Mushinsky, H.R. (Eds.), *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman and Hall, New York, pp. 3–27.
- Micheli, F., Halpern, B.S., Botsford, L.W., Warner, R.R., 2004. Trajectories and correlates of community change in no-take marine reserves. *Ecol. Appl.* 14, 1709–1723.
- Palumbi, S.R., 2004. Fisheries science: why mothers matter. *Nature* 430, 621–622.
- Pelc, R.A., Warner, R.R., Gaines, S.D., Paris, C.B., 2010. Detecting larval export from marine reserves. *PNAS* 107, 18266–18271.
- Pittman, S.J., Costa, B.M., Battista, T.A., 2009. Using Lidar Bathymetry and boosted regression trees to predict the diversity and abundance of fish and corals. *J. Coast. Res.* 27–38.
- Planes, S., Jones, G.P., Thorrold, S.R., 2009. Larval dispersal connects fish populations in a network of marine protected areas. *PNAS* 106, 5693–5697.
- Rakitin, A., Kramer, D., 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Mar. Ecol. Progr. Ser.* 131, 97–113.
- Risk, M.J., 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.* 153, 1–6.
- Roberts, C.M., Polunin, N.V.C., 1991. Are marine reserves effective in management of reef fisheries? *Rev. Fish Biol. Fish.* 1, 65–91.
- Rowley, R.J., 1994. Marine reserves in fisheries management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 4, 233–254.
- Russ, G.R., Alcala, A.C., 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Mar. Ecol. Progr. Ser.* 132, 1–9.
- Russ, G.R., 2002. Yet another review of marine reserves as reef fishery management tools. In: Sale, P.F. (Ed.), *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. Academic Press Inc., San Diego, CA, pp. 421–443.
- Russ, G.R., Alcala, A.C., Maypa, A.P., 2003. Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. *Mar. Ecol. Progr. Ser.* 264, 15–20.
- Russ, G.R., Alcala, A.C., 2004. Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia* 138, 622–627.
- Russ, G.R., Alcala, A.C., Maypa, A.P., Calumpong, H.P., White, A.T., 2004. Marine reserve benefits local fisheries. *Ecol. Appl.* 14, 597–606.
- Sladek Nowlis, J.S., Roberts, C.M., 1999. Fisheries benefits and optimal design of marine reserves. *Fish. Bull.* 97, 604–616.
- Sladek Nowlis, J.S., Friedlander, A., 2005. Marine reserve function and design for fisheries management. In: Norse, E.A., Crowder, L.B. (Eds.), *Marine*

- Conservation Biology: The Science of Maintaining The Sea's Biodiversity. Island Press, pp. 280–301.
- Suman, D., Shrivani, M., Walter Milon, J., 1999. Perceptions and attitudes regarding marine reserves: a comparison of stakeholder groups in the Florida Keys National Marine Sanctuary. *Ocean Coast. Manage.* 42, 1019–1040.
- Underwood, A.J., 1994. On Beyond BACI: Sampling Designs that Might Reliably Detect Environmental Disturbances. *Ecol. Appl.* 4, 3–15.
- Walsh, W.J., Cotton, S.S.P., Dierking, J., Williams, I.D., 2003. The commercial marine aquarium fishery in Hawai'i. In: Friedlander, A.M. (Ed.), Status of Hawai'i's Coastal Fisheries in the New Millennium: Proceedings of the 2001 Fisheries Symposium. American Fisheries Society, Hawai'i Chapter, Honolulu, pp. 132–159.
- Wedding, L.M., Friedlander, A.M., McGranaghan, M., Yost, R.S., Monaco, M.E., 2008. Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Rem. Sens. Environ.* 112, 4159–4165.
- Williams, I.D., Walsh, W.J., Schroeder, R.E., Friedlander, A.M., Richards, B.L., Stamoulis, K.A., 2008. Assessing the importance of fishing impacts on Hawaiian coral reef fish assemblages along regional-scale human population gradients. *Environ. Conserv.* 35, 261–272.
- Williams, I.D., Walsh, W.J., Claisse, J.T., Tissot, B.N., Stamoulis, K.A., 2009. Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. *Biol. Conserv.* 142, 1066–1073.