A SEASCAPE APPROACH TO INVESTIGATING FISH SPILLOVER
ACROSS A MARINE PROTECTED AREA BOUNDARY IN HAWAI'I

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE
UNIVERSITY OF HAWAI'I AT MĀNOA IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

IN

GEOGRAPHY

AUGUST 2012

By

Kostantinos Achilles Stamoulis

Thesis Committee:

Brian Szuster, Chairperson

Qi Chen

Alan Friedlander

Keywords: spillover, MPA, seascape, fishing, management

ACKNOWLEDGEMENTS

Committee members Brian Szuster, Qi Chen, and especially Alan Friedlander provided support and advice. Ivor Williams contributed valuable input during the writing phase. The Nature Conservancy (TNC) of Hawaii provided 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, Paolo Usseglio, Patrick Curry, Mary Donovan, Robert Hendrickson, 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 MLCD. This research was funded in part by an award from the Hawaii Geographic Information Coordinating Committee (HIGICC) and the Hawaii Cooperative Fishery Research Unit provided major logistic and administrative support.

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, Hawaii 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 small-scale surveys and key habitat variables was found to account for a large portion of the variability for both resource (targeted) fish species (17%) 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 ($r^2=0.34$, $p<0.01$), indicating fish spillover at a local scale (<1km). In contrast, non-resource fish biomass demonstrated no such relationship ($p=0.45$). The evidence of spillover based on the small-scale surveys was corroborated by results from large-scale surveys, which also showed a significant relationship ($r^2=0.30$, $p<0.01$) between resource fish biomass and distance from the MPA boundary. In addition, observed spatial distribution of fishing effort was consistent with fishers responding to biomass gradients across MPA 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 towards marine reserves and marine protected areas.

TABLE OF CONTENTS

Acknowledgements	ii
Abstract	iii
List of tables	v
List of figures	vi
Chapter 1. Introduction	1
1.1 Nature of the problem	1
1.2 Study area.....	3
1.3 Research questions.....	5
1.4 Outline of thesis	6
Chapter 2. Literature Review	7
2.1 Marine protected areas and marine reserves	7
2.2 Marine reserve effectiveness.....	8
2.3 Spillover.....	9
2.4 Conclusions.....	14
Chapter 3. Methods	17
3.1 Experimental Design	17
3.2 Data Collection	17
3.2.1 Fish surveys	17
3.2.2 Small-scale habitat variables	18
3.2.3 Large-scale habitat variables	19
3.2.4 Fishing effort data	19
3.3 Data Analysis	20
3.3.1 Fish data	20
3.3.2 Reserve effect	21
3.3.3 Habitat effects	21
3.3.4 Biomass gradients	22
3.3.5 Fishing effort data	23
3.3.6 Fishing effort spatial analysis	24
Chapter 4. Results	25
4.1 Fish data	25
4.2 Reserve effect	25
4.3 Habitat effects	25
4.4 Biomass gradients	30
4.5 Fishing effort	30
Chapter 5. Discussion and conclusions	36
5.1 Research implications	37
5.2 Management implications.....	40
5.3 Opportunities for further research.....	41
Appendix I. Supplementary Tables	43
Appendix II. Supplementary Figures	44
References – Literature cited	48

LIST OF TABLES

1. List of top ten species by total biomass in each study category	26
2. Comparisons of fish assemblage characteristics between management strata for small-scale surveys	27
3. Comparison of fish assemblage characteristics between management strata for large-scale surveys	27
4. Distance-based linear models of habitat variable effects on reduced fish biomass in each study category	28
5. Distance-based linear models of habitat variable effects - excluding distance from MPA boundary - on reduced fish biomass in each study category	29
6. Linear relationships between significant habitat variables and distance from MPA boundary	29

LIST OF FIGURES

1. Study location, Pupukea Marine Life Conservation District	4
2. Study design	18
3. Least-squares linear regression of small-scale survey reduced biomass vs. distance from MPA boundary	31
4. Least-squares linear regression of small-scale survey corrected biomass vs. distance from MPA boundary	31
5. Least-squares linear regressions of small-scale survey corrected biomass averaged in 100 m distance bins vs. distance from MPA boundary	32
6. Least-squares linear regression of large-scale survey reduced biomass and corrected biomass vs. distance from MPA boundary	32
7. Mean number of fishers per week in MPA and open zone by fishing gear type	33
8. Mean angler hours per week for each gear type by day strata	34
9. Spatial extent of observed spearfishing effort	35

CHAPTER 1. INTRODUCTION

1.1 Nature Of The Problem

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). 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 spillover can mitigate costs associated with marine protected areas, it is generally believed that the export of eggs and larvae typically provides greater fishery benefits (Nowlis and Friedlander, 2005). One effect of spillover of mature fishes would be to reduce scope for reproductive output from within the MPA. Hence, from a fisheries perspective, spillover may actually be detrimental to MPA larvae production (Nowlis and Roberts, 1999). From a fishers perspective however, spillover of adult fish from MPAs may provide a more tangible benefit than increased larval export and serve to improve perceptions of marine protected areas (Russ and Alcala, 1996). Therefore, for a number of reasons, an understanding of the extent of adult spillover from MPAs is essential for the evaluation of their effects on connected fisheries.

Fish assemblage dynamics are driven by habitat characteristics at a range of spatial scales (Ault and Johnson 1998; Anderson and Millar 2004; MacNeil et al. 2009). Consideration of these scale-dependent habitat factors is often overlooked in ecological studies of MPAs and their effects on fish population structure, which seek to standardize replicates by habitat type rather than control for associated variability. These eco-spatial relationships are the focus of the emerging field of seascape ecology (Bartlett and Carter 1991), and applying this approach can help to elucidate ecological patterns such as spillover. Seascapes ecology is the application of landscape ecology theory to the marine realm and focuses on the interaction between spatial pattern and ecological process (Pittman 2011). Various characteristics of the intricate mosaic of patches that characterize coral reef habitats have been shown to influence fish communities. Reef patch size as well as reef context (the spatial pattern of surrounding habitat patches) were strong

predictors of reef fish assemblage structure in the Caribbean (Grober-Dunsmore 2006, 2008). *In situ* measurements of three dimensional topographic complexity (rugosity) has long been linked with fish assemblage characteristics (Friedlander and Parrish 1998; Gratwicke and Speight 2005). More recently, metrics based on continuously varying 3D surfaces (eg. Lidar or multibeam bathymetry) at larger scales have shown significant relationships with fish assemblage variables (Wedding and Friedlander 2008; Pittman et al. 2009). These and other studies have shown that analysis of fish assemblages by functional or trophic group, in relationship to multi-scale habitat variables, can reveal ecologically relevant patterns of distribution across the seascape.

Gradients of fish abundance and biomass have been utilized as an indicator of fish spillover across MPA boundaries and to assess the scale of influence of the reserve (Rakitin and Kramer, 1996; 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 & 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 (Russ et al., 2003, 2004).

Over the past four decades a series of MPAs known locally as Marine Life Conservation Districts (MLCDs) have been established in Hawaii. 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 subsets thereof) 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).

A recent study showed that MLCD size is positively correlated with a number of fish assemblage characteristics, including species richness, density, and biomass, but also concluded that all of the MLCDs are likely too small to have any measurable influence on adjacent fished areas (Friedlander et al. 2007b). Williams et al. (2009) investigated the effects of a marine protected area network in West Hawaii on the distribution of a single 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.

This current study takes a seascape approach by measuring fishing effort, controlling for habitat parameters, and investigating multiple species, as well as sampling at two distinct spatial scales. The extent of sampling and the experimental design allows for a direct assessment of gradients of biomass as well as comparative tests of effect of protection from fishing. Gradients of fish biomass indicative of spillover would be a consequence of increased population size inside the protected area due to reduced fishing mortality. Therefore, if this is a protection effect, one would expect to see this pattern only for species targeted by fishers. By controlling for habitat differences and comparing patterns of biomass for resource species (targeted by fishers) and non-resource species (not targeted by fishers) (Williams et al., 2008), this study provides a robust assessment of fish spillover from a marine protected area in Hawaii.

1.2 Study Area

The site selected for this research project was the Pupukea MLCD on the north shore of Oahu (Figure 1). This marine protected area was established in 1983 (0.11 km²) and expanded in 2003 (0.71 km²) through a community-driven process (Friedlander et al. in review). Along with the increase in area, the perimeter to area ratio decreased and the average slope and rugosity both increased slightly between the 1983 and 2003 boundary configurations. According to the NOAA Biogeography branch benthic habitat maps (Battista et al., 2007), the geomorphic structure within the expanded MLCD consists of a mix of pavement (37%), sand (33%), and rock/boulder (26%). Biological cover consists

Figure 1. Study Location, Pupukea Marine Life Conservation District*

*Located on the north shore of Oahu, Hawai'i. Red outline in main frame delineates protected area boundary.

of a mixture of uncolonized hard bottom (33%), macroalgae (63%), turf algae (25%) and coral (12%) (Friedlander et al., 2010).

According to Friedlander et al. (2010), apex predators accounted for 1.8% of the total biomass in Pupukea MLCD and 3.1% in the open area yet they comprised more than twice as much total biomass in the MLCD compared to the open area. Benthic carnivores made up 24% of the biomass in the MLCD and 43% in the open area with total biomass nearly twice as high in the MLCD then the open area. Planktivores accounted for 5% of the total biomass in the MLCD and 6% in the open area although biomass was nearly three times higher in the MLCD. Finally, herbivores accounted for 70% of total biomass in the MLCD and had five times greater biomass than in the open area where herbivores accounted for 48% of the biomass (Friedlander et. al, 2010). These the results indicate that herbivores are the largest component of the fish assemblage in Pupukea MLCD and also show the greatest decline in adjacent open areas, possibly due to high fishing pressure.

Pupukea MLCD is a completely no-take area except for limited fishing from shore and seasonal harvest of a coastal pelagic species in Waimea Bay only (Figure 2). Therefore, the area of the MLCD north of Waimea Bay can be considered a marine reserve and is this part of the MLCD that was selected for this project. Throughout the fully protected area, and extending out into the fished area to the north is a continuous stretch of hard bottom reef habitat (Figure 2), which was the focus of the biological surveys (based on NOAA benthic habitat maps).

1.3 Research Questions

Questions addressed by this research are as follows:

1. Are fish assemblage characteristics - richness, density, and biomass - higher inside the MPA then outside?
2. After removing the variability in resource fish biomass that can be attributed to habitat, is there a decreasing gradient in “corrected” resource fish biomass across MPA boundaries due to the spillover effect?

3. Are tested reserve effects including spillover evident for target species, but not for non-target species (non-resource fish)?
4. Does the negative gradient of resource fish biomass outside the reserve coincide with a negative gradient of fishing effort?

1.4 Outline Of Thesis

This thesis is organized in the monograph style. Chapter one is the Introduction which describes the research topic and the nature of the problem, as well as introduces the study area, research questions, and provides an outline of the thesis. Chapter two is a Literature Review which provides a detailed summary of research findings in the field which are applicable to the current study. The literature review is organized so that the theoretical basis of spillover is discussed first, followed by a chronological overview of empirical research findings, finishing off in a local context with similar research conducted in Hawai'i. The conclusion of the literature review identifies how lessons learned from the current body of spillover research have informed the design of this project. Chapter three is Methods and provides a description of the experimental design, data-collection methodologies, and data analysis. Chapter four is the Results and Discussion section and provides a presentation of the results of the completed data analyses including data tables and figures as well as interpretation of the findings. Chapter five is Conclusions which is a summary of the research results, implications of the research findings, management implications, and opportunities for further study.

CHAPTER 2. LITERATURE REVIEW

2.1 Marine Protected Areas and Marine Reserves

Marine protected areas (MPAs) can be defined as ‘areas of the ocean designated to enhance conservation of marine resources.’ (Lubchenco et al., 2003) MPAs vary greatly in terms of their objectives and regulations, encompassing a range of protection levels, from full protection reserves to restriction of only particular activities, user groups, gear types, extraction periods, or target species. For this reason, their effectiveness for conservation will vary considerably based on the level of protection, which makes it difficult to generalize about the benefits of MPAs (Mora et al., 2006; Lester & Halpern, 2008).

Marine reserves are an important subset of MPAs and are defined here as ‘areas of the ocean completely protected from all extractive and destructive activities... except as necessary for monitoring or research’ (Lubchenco et al., 2003). Though MPAs with less restrictive regulations can be important management tools, no-take marine reserves offer the greatest protection for marine resources and ecosystems. By protecting geographical areas, including both resident species and their biophysical environments, marine reserves provide an ecosystem-based approach to conservation or fisheries management. This is distinct from the traditional focus on single species conservation or management (NMFS, 1999).

Marine reserves may provide multiple benefits including: conservation of biodiversity; protection of habitat; enhancement of ecosystem services; export of individuals to fished areas; recovery of depleted stocks of exploited species; insurance against environmental or management uncertainty; and sites for scientific investigation, baseline information, education, and recreation (Allison et al. 1998, NRC, 2000). Research is demonstrating that that marine reserves are powerful management and conservation tools, however they are not a cure-all. They cannot alleviate all threats to marine ecosystems, such as climate change, pollution, or overfishing, that originate outside reserve boundaries. Thus, marine reserves are emerging as a powerful tool, but one that should be accompanied by other approaches (Lubchenco et al., 2003).

2.2 Marine Reserve Effectiveness

A number of reviews of monitoring studies have documented how population numbers and biomass, species richness, size of organisms, reproductive potential, and/or community structure are positively affected by reserve protection (Halpern & Warner, 2002; Gell & Roberts, 2003; Micheli et al., 2004). This is particularly apparent when numerical density and biomass of exploited species are compared inside and outside reserves and/or before and after reserve protection (Côté et al., 2001; Gell & Roberts, 2003; Halpern, 2003). Interestingly, comparisons across reserves in different locations suggest that changes in biological metrics do not vary appreciably with reserve size (Côté et al., 2001; Micheli et al., 2004; Guidetti & Sala, 2007), though size has not been examined with respect to geographical differences among reserves (Lester et al., 2009).

Marine reserve protection is also likely to affect individual species differently, based on whether they are exploited or otherwise affected by activities outside the reserve area. Biological characteristics such as longevity, mobility, dispersal ability, and fecundity also determine how individual species respond to reserve protection (Mosqueira et al., 2000; Gaines et al., 2003; Gerber et al., 2005). Though different responses may be expected for different taxonomic groups, this issue has been primarily examined for fish species. However, there is a growing body of data not only for fishes, but also for invertebrates and algae from a range of geographic locations which shows variability in reserve response within, rather than among, taxonomic groups based on biological characteristics as well as reserve characteristics and context. However, despite considerable variability, positive responses are far more common than no difference or negative reserve responses (Lester et al. 2009).

Marine reserves are believed to cause changes outside the reserve as well as inside. They may augment nearby fisheries through two primary mechanisms: ‘spillover’ of individuals across reserve borders and ‘larval export’ to fished areas (Rowley, 1994). Both of these processes are difficult to measure and direct evidence has been limited, though increases in catches adjacent to reserves have been well documented. Roberts et al. (2001) investigated the effects of marine reserves on adjacent fisheries in St. Lucia and found catch per unit effort (CPUE) of fish traps increased by 46-90% after five years of protection. In Nabq, Egypt, the CPUE from the trammel net fishery increased by 66%

after five years protection from a series of reserves (Galal et al., 2002). A similar effect was reported from the Philippines, where the CPUE of the line fishery around Apo Island Reserve increased tenfold over 20 years of protection (Maypa et al., 2002).

The efficacy of the system of 12 marine protected areas known locally as Marine Life Conservation Districts (MLCDs) in Hawaii as was evaluated by Friedlander et al. (2007a, 2007b). These MLCDs vary in size, habitat quality, and management regimes and were initially established to provide opportunities for public interaction with the marine environment. Only four of these MPAs are complete no-take areas. Despite varying levels of protection from fishing and small average size (0.55 km²), overall fish biomass was 2.6 times greater in 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 MPAs in conserving fish populations within their boundaries (Friedlander, 2007a).

2.3 Spillover

A frequent expectation of the use of marine reserves in management of coral reef fisheries is maintenance or enhancement of yields in adjacent areas through adult movements (Russ and Alcala, 1996). The use of the term ‘spillover’ to describe density dependent emigration of marine organisms from marine reserves was first coined by Rowley (1994). This mechanism has been described with theoretical models and investigated through empirical studies in various locations around the world. The theoretical basis for spillover will be discussed first, then key empirical studies addressing this mechanism will be discussed in chronological order to outline the development of this research topic.

As described in the previous section, marine reserves support higher densities and larger sizes of heavily fished species than are found outside of reserves. As population density increases inside the reserve, increased local competition for resources or interference between conspecifics may cause fish to move to areas of lower density (Travis et al., 1999; Lizaso et al., 2000; Abesamis & Russ, 2005). This mechanism is known as density dependent dispersal or movement, and when it occurs across the boundaries of an MPA or marine reserve, density dependent emigration or spillover.

Models describing spillover show that the rate and extent are variable between species and depend primarily on mobility as well as growth rate and natural mortality (DeMartini, 1993; Kramer & Chapman, 1999; Gerber, 2005). Reserves can protect fish species only if individuals restrict their movements to a localized home range during at least part of their life cycle. For this reason highly vagile species are not likely to show a high rate of spillover because they will be exposed to fishing throughout their life cycle keeping densities low within reserves. In contrast, despite high density inside of reserves, highly sedentary species will show low rates of spillover due to limited movements. Therefore, species with moderate mobility should show the highest rates of spillover (DeMartini, 1993; Kramer & Chapman, 1999; Gerber, 2005).

Considerations of spatial habitat use and behavior of fish lead to predictions that population density and mean fish size will form gradients across reserve boundaries (Rakitin & Kramer, 1996); will increase rapidly in newly established reserves, only later providing spillover to adjacent fisheries; and will be higher in reserves with greater area to edge ratios, more habitat types, natural barriers between reserve and non-reserve areas, and higher habitat quality inside than outside the reserve (Chapman & Kramer, 1999). Reserves intended strictly for conservation should be designed to minimize adult spillover, thereby maximizing spawning stock inside the reserve. Reserves designed for fishery enhancement however, should be designed to allow spillover with smaller area to edge ratios and continuous habitat across reserve boundaries facilitating movement (Roberts, 2000).

Some of the first empirical evidence of adult fish spillover comes from the Apo Island marine reserve in the Philippines. Russ and Alcala (1996) performed underwater visual censuses of large predatory coral reef fishes inside and adjacent to the small marine reserve at Apo Island over a ten year period. They documented a significantly higher density of these fishes in the area closest to the marine reserve after 9 years of protection, compared to the first 8 years of reserve protection. This result coincided with interview data collected from local fishers who were unanimous that their yields had increased since the reserve was implemented. This evidence was not conclusive however, because as the authors themselves point out, quantification of the effect of reserve

protection on reef fish communities should incorporate controls for both spatial and temporal variation in fish distribution (Russ and Alcala, 1996).

Rakitin and Kramer (1996) hypothesized 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. To test this hypothesis, abundance and size of fishes were estimated by trapping and visual census on reefs inside the Barbados Marine Reserve (BMR) and outside within four kilometers 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. Chapman and Kramer (1999) built upon this work recognizing that such gradients may be affected by other factors, primarily differences in habitat quality between reserve and non-reserve areas and the movement of fish across reserve boundaries. They measured spatial patterns of fish density and size (using visual surveys) near the boundary of the Barbados Marine Reserve and statistically controlled for habitat correlates. They found a significant difference in total density between reserve and non-reserve sites, though did not find a relationship between mobility of each species and relative difference between reserve and non-reserve sites. Though they were not specifically testing the spillover effect, elements of their approach were incorporated into subsequent studies addressing this mechanism.

McClanahan and Mangi (2000) investigated the spillover effect from the Mombasa Marine Park in Kenya using baited fish traps finding the total wet mass of catches per trap, mean size of trapped fish, and the number of species caught per trap declined as a function of distance away from the park edge. Habitat was not found to be a significant factor. They found that spillover was greatest for species of moderate mobility which were also the dominant fishery species.

On the Great Barrier Reef, gradients of fish densities were observed across experimental boundaries where manipulated by removal through spearfishing in contrast to non-manipulated control sites (Zeller et al., 2003). There was no evidence of experimentally induced directional movements, likely due to the short post-manipulation time-frame of the study (~3 mo.) and the response to the threat of diver spearing. Also, habitat differences were not taken into consideration.

Russ et al. (2003) showed a three-fold increase in the biomass of a targeted surgeonfish in a reserve at Apo Island, Philippines. Over time the biomass of this species increased by a factor of 40 outside but close to reserve boundaries (200 - 250m) but not at greater distances. CPUE for this species was 45 times higher within 200m of the reserve boundary than for all other fishing grounds combined. The combination of fishery and fishery independent data provides strong evidence of fishery replenishment through spillover and their estimate of the spatial extent of this process is one of the first in the literature.

Ashworth and Ormond (2005) investigated the spillover effect in a marine reserve in the Red Sea. The existence of gradients of abundance of both targeted and non-targeted fish species were tested with visual censuses at different depths. Varying effects of spillover were observed for different trophic groups and at different depths. At 1 m depth six families showed significant declines in abundance moving away from the center of the reserve, whereas at 10 m depth the only two families (which were lightly fished) showed significant gradients in abundance which increased with distance from the reserve center. The authors speculate that this positive gradient in abundance for the lightly fished species may be due to competitive release resulting from the lower density of fishery target species outside of the reserve. These results indicate that spillover may occur to an extent and in a direction depending on trophic group and fishing intensity.

Spillover of commercially valuable reef fishes from three marine protected areas in Guam, Micronesia was investigated through mark-recapture experiments, in which fishes were tagged both inside and outside of three MPAs (Tupper, 2007). Study sites for each MPA were located at the center of the protected area with a control (fished) site located at the same distance from the boundary outside the MPA. Four out of five species investigated showed little or no net movement out of MPAs, while one species showed a net spillover of biomass from all three MPAs. Patterns of spillover were strongly influenced by physical habitat barriers, such as channels, headlands, or other topographic features. The author concluded that MPA's which are physically connected by contiguous reef structures will likely provide more spillover to adjacent fished areas than those separated by habitat barriers (Tupper, 2007).

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 (100s of meters).

At Tabarca Marine Reserve in Italy, Forcada et al. (2008) investigated if the patchy nature of the marine environment might act as a barrier for fish export. They used visual censuses and showed significant decreasing gradients in total fish biomass indicating spillover, on the two dominant substrate types, independently of their continuity through the reserve boundaries. A year later Forcada et al. (2009) used experimental fishing to test if catches were higher near MPA boundaries in three Mediterranean MPAs, and arrived at a different conclusion. They showed significantly higher catches for some species near MPA borders on seagrass habitat but not on sandy bottoms, leading to the conclusion that spillover does appear to be limited by a lack of continuous habitat through protected area boundaries.

The most recently published empirical study addressing spillover took place at the Jardines de la Reina Marine Reserve in Cuba. Amargos et al. (2010) followed the approach of Zeller et al. (2003) using visual census and tagging methods in order to quantify distance and movement direction due to a manufactured density gradient. Before experimental manipulation, fish density was similar on both sides of the reserve boundary. After manipulation, fish density on the unprotected side declined dramatically forming a strong gradient through the boundary. After a month the gradient disappeared, an effect the authors attribute to spillover. This conclusion is corroborated by the tagging data which shows a 1.5x increase in mean distance traveled, a 2x increase in emigration rate and a decrease in immigration rate.

Williams et al. (2009) investigated the impacts of an MPA network in Hawaii on abundance and fishery sustainability for a species important for the aquarium fishery. After controlling for the effect of reef structural complexity they showed significantly higher densities of adults in boundary areas (< 1 km from MPA boundaries) compared to

open areas far from MPA boundaries, which was indicative of spillover at that scale. This is the only published study which addresses the spillover effect in the Hawaiian Islands.

In general, the studies discussed have not fully incorporated environmental variables which affect the process of spillover. An ecosystem-based approach can help to address this problem. In Hawai'i, research has demonstrated MPA effectiveness (e.g. Friedlander et al. 2007a), a pre-requisite for fish spillover, and spillover was investigated for one species important to the aquarium fishery (Williams et al., 2009). This fishery is unlike traditional food fisheries in that it targets juvenile individuals as opposed to large adults. Thus, spillover of exploited food fishes has not been investigated in Hawai'i though the groundwork for this research has been laid. This research project directly addresses this gap in scientific knowledge of spillover in Hawai'i while incorporating lessons learned from related research worldwide.

2.4 Conclusions

Marine protected areas, particularly no-take reserves, positively influence fish assemblage characteristics within their boundaries (Lester et al., 2009). These include abundance and biomass, species richness, size of organisms, and reproductive potential. MPAs are also thought to benefit surrounding fished areas through larval export and adult spillover. Enhancement of fisheries quantified by increases in catch per unit effort near marine reserves has been documented in various locations around the world (Roberts et al., 2001; Galal et al., 2002; Maypa et al., 2002), though direct evidence for the export of larval and adult fish is sparse.

As population density increases inside marine reserves, increased competition for resources, space, and mates may cause fish to move to areas of lower density outside of reserve boundaries resulting in fish spillover (Travis et al., 1999; Lizaso et al., 2000; Abesamis & Russ, 2005). The rate and extent of spillover is variable between species and dependent on mobility and level of fishing pressure (DeMartini, 1993; Kramer & Chapman, 1999; Gerber, 2005). Spillover is also influenced by the spatial characteristics of the protected area and habitat configuration as well as spatial and temporal patterns of fishing effort (Chapman and Kramer, 1999; Russ, 2002). Spillover should be highest for species of moderate mobility that experience high fishing pressure, across reserve

boundaries with continuous habitat and no major barriers to fish movement (DeMartini, 1993; Kramer & Chapman, 1999; Gerber, 2005).

Studies investigating spillover have tested for higher fish abundance, mean size and/or biomass near reserve boundaries using visual census, fishing methods or a combination of both. Movement across boundaries was investigated using mark-recapture experiments. Study designs were highly variable and many did not properly account for habitat characteristics or spatial patterns of fishing effort. Results were inconsistent but supported several key elements of spillover theory. Gradients of abundance, biomass, or mean size across reserve boundaries were demonstrated; spillover was shown to be greatest for moderate mobility species; and habitat was shown to be an important factor, especially across protected area boundaries. Spillover was shown to be a common phenomenon for species that respond positively to reserve protection but at relatively small scales, typically less than one kilometer from reserve boundaries (see Halpern, 2009).

Conclusions can be drawn on how to improve experimental designs to test spillover based on difficulties encountered in the published research. Rakitin and Kramer (1996) incorporated both trapping and visual censuses to measure fish abundance patterns and found conflicting results between the methods. Traps allow nondestructive measurement and identification of specimens, but their selectivity depends on complex and poorly understood behavioral traits of fishes (Munro, 1974). Furthermore, the marine habitats in which traps can be used are limited. McClanahan and Mangi's (2000) finding of no habitat effect is suspect due to their use of baited fish traps. Though visual census incorporates its own biases, it is non-selective, allows for quantification and measurement of fishes in a variety of habitats, and facilitates simultaneous habitat characterization. When an experiment incorporates manipulations of density patterns through spearing however (Zeller et al., 2003; Amargos et al., 2010), subsequent visual census results may be confounded due to diver avoidance.

While some studies attempted to control for habitat, few considered potential barriers to movement (such as sand patches) in the selection of their sites. Habitat effects may have been a confounding factor for several of the studies described. Habitat characterization should be as rigorous as possible in order to separate the effects of

habitat from the effects of fishing protection. Spatial patterns of fishing effort was another factor neglected by many of the studies. The production and maintenance of negative gradients of abundance and biomass across reserve boundaries which indicate spillover are dependent on higher fishing pressure outside the boundaries, though very high fishing pressure near the boundary has the potential to truncate this pattern (Kellner et al., 2007).

Lessons learned from the published body of research addressing the spillover effect have informed the design of this research project. A seascape approach has helped address many of the shortcomings of previous studies. Spillover has been shown to occur at relatively small scales (< 1 km), therefore the scale of investigation should match. Multi-scale habitat variables need to be incorporated in order to understand and control for habitat effects which may confound patterns produced by fish spillover. Habitat features such as large sand patches have been shown to act as barriers to movement. An area for study should be selected that excludes such barriers and has continuous hard-bottom habitat across protected area boundaries. Ideally, spatial patterns of fishing effort should be quantified and compared with spatial patterns of fish distribution. These key considerations were incorporated into the design of the current study and the methodologies selected were based on previous research experience and the MPA/marine reserve, spillover, and seascape ecology literature.

CHAPTER 3. METHODS

3.1 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 25 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 (Figure 2). Therefore, survey stations were located a maximum of 1000 m from the boundary. Fish and benthic surveys were conducted during June-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 (Williams et al., 2008). These classifications were formed based on commercial catch data from the Hawaii Division of Aquatic Resources (2009) where resource fishes are defined as those species with at least 1,000 lbs / year landed.

3.2 Data Collection

The data collected for this study falls into four categories and the methodologies for each are described below:

3.2.1 Fish Surveys

Small-scale (125 m^2) fish surveys ($N=80$) were conducted using belt transect methodology with transects oriented at 200° , which is roughly parallel to shore. A diver swam along a $25 \times 5 \text{ m}$ 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). Survey duration varied from 10-15 min, depending on habitat complexity and fish abundance. Total length (TL) of fishes was estimated to the nearest centimeter.

Figure 2. Study Design*

*Map elements indicated in legend. Note that unlike figure 1, this map is orientated so that north is to the left of the frame. Black dots represent small-scale survey stations; grey polygons represent large-scale timed surveys; red shape indicates the boundary of the MPA; green shapes indicate study zones; and sand habitat is shown by light, speckled areas.

Large-scale (1000 m²) fish surveys (N=40) were focused on resource fishes > 15 cm only and used timed swims conducted with a pair of divers each counting, sizing, and identifying fishes within adjacent 5 m wide belt transects. Survey duration was five minutes with one diver towing a surface float equipped with GPS to enable measurement of transect length, from which area was derived. Average transect length was 107 ± 20 m (SD, standard deviation).

3.2.2 Small-Scale Habitat Variables

Rugosity was measured on each of the small-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.

3.2.3 Large-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 Hawaii 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 benthic complexity) were quantified for each of the study sites using ArcGIS 10 (ESRI). Slope of slope was chosen to quantify structural complexity because Pittman et al. (2009) showed a strong relationship between slope of slope and fish biomass, and because previous analysis showed a higher concordance with field-measured rugosity than other Lidar-derived metrics. Polygons representing all small and large 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 large-scale transects were derived from NOAA Benthic habitat maps (Battista et al., 2007).

3.2.4 Fishing Effort Data

Surveys of fishing effort were conducted in the open zone during daylight hours, with each survey consisting of four hours 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 & Parrish, 1997). When fishing activity was observed, the start time was 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 and distance from shore was visually estimated. Location updates were recorded every 15 minutes. A total of 22 fishing effort surveys were conducted comprising 88 total hours of observation.

A community organization, Malama Pupukea-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.

3.3 Data Analysis

Data analysis was split into six categories and the methods for each is described as follows:

3.3.1 Fish Data

Length estimates of fishes from visual censuses were converted to weight using the following length–weight relationship: $W = aSL^b$, 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 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-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, or number per square meter (num/m^2), to enable comparisons between large and small-scale surveys as well as other studies in Hawaii 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 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 including jacks and some snappers species.

3.3.2 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 two sample Student's t- test was used to compare values for these fish assemblage characteristics inside the MPA to the open area. Data from the small-scale surveys was transformed to conform to test assumptions of parametric statistics; 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 large-scale resource fish survey 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.

3.3.3 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 small-scale surveys and resource fish data from large-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 in order to reduce the impact of outliers and a step-wise procedure was utilized to select variables for the model based on the Akaike Information Criterion (Akaike, 1973). In order to more fully explore habitat effects independent of distance from MPA boundary, in models where distance from boundary was found to be a significant term, it was subsequently excluded as a possible variable and the procedure repeated to find the next best fitting model.

3.3.4 Biomass Gradients

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

In order to measure the spatial variation after removing the influence of habitat, habitat variables (excluding distance from boundary) found to be significant in the distance-based linear models were used as explanatory variables in standard least-squares linear regressions with reduced biomass. Residuals from the standard linear regression models (defined as corrected biomass) were then used as response variables in linear

regressions with distance from boundary. This was done 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 each tested using an ANOVA. 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 small-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.

3.3.5 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, though 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.

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

$$\bar{f}_x = f_x/h_x$$

f_x = fishers observed per stratum x

h_x = hours observed per stratum x

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.

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

E = Total effort

$\bar{E}$ = Mean daily effort

D = Total number of days

td = time/day strata

N_i = Number of fishers observed on day i

E_{ij} = Observed effort of fisher j on day i , where $i = 1 \dots d, j = 1 \dots N_i$

3.3.6 Fishing Effort Spatial Analysis

A 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. This polygon layer was then converted to a raster surface representing total observed angler hours for each 10 m grid cell, thereby creating a relative fishing effort measure that could be compared across space. Total observed angler hours were also averaged for each study zone segment representing intervals of 200 m from the MPA boundary. Spatial patterns of spearfishing effort in particular were investigated because this gear in Hawaii 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.

CHAPTER 4. RESULTS

4.1 Fish Data

A total of 80 independent small-scale fish surveys and 40 large-scale surveys in a wide variety of hard-bottom habitats were conducted between June and September, 2010. The average 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 small and large scale surveys were semi-vagile type II herbivores (Table 1). Redlip parrotfish, *Scarus rubroviolaceus*, accounted for the highest biomass followed by four surgeonfishes; *Acanthurus olivaceus*, *A. leucopareius*, *Naso unicornis*, and *N. lituratus*. The top five non-resource species by total biomass on small-scale surveys were nearly all semi-vagile type I invertivores with the exception of one herbivore and one semi-vagile type II species (Table 1). These fishes represent a variety of families and include (in order of total biomass) *Acanthurus nigrofusus*, *Sufflamen bursa*, *Thalassoma duperrey*, *Rhinecanthus rectangulus*, and *Sufflamen fraenatus*.

4.2 Reserve Effect

Fish assemblage characteristics (e.g., species richness, numerical density, and biomass) varied by survey type and between resource and non-resource fish, though all were significantly higher inside the reserve than in the open area (Tables 2 & 3). 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 (Table 2). Management strata differences were most extreme however for the large-scale resource fish surveys, with density of fishes three times greater in the reserve and biomass nearly four times greater, compared to the open area (Table 3).

4.3 Habitat Effects

For resource fish biomass on small-scale surveys, slope of slope explained the most variability (12%) followed by distance from boundary, and coral cover for a total of

Table 1. List Of Top Ten Species By Total Biomass In Each Study Category*

Fish species	Family	Total biomass (kg)	Trophic Group	Mobility Guild
Large-scale survey resource species				
<i>Scarus rubroviolaceus</i>	Scaridae	217.8	H	S2
<i>Acanthurus olivaceus</i>	Acanthuridae	117.5	H	S2
<i>Acanthurus leucopareius</i>	Acanthuridae	71.7	H	S2
<i>Naso unicornis</i>	Acanthuridae	64.0	H	S2
<i>Naso lituratus</i>	Acanthuridae	57.9	H	S2
<i>Acanthurus dussumieri</i>	Acanthuridae	38.6	H	S2
<i>Parupeneus multifasciatus</i>	Mullidae	26.9	MI	S1
<i>Monotaxis grandoculis</i>	Lethrinidae	16.4	MI	S2
<i>Cephalopholis argus</i>	Serranidae	15.8	P	S1
<i>Kyphosus spp.</i>	Kyphosidae	15.8	H	S2
Small-scale survey resource species				
<i>Scarus rubroviolaceus</i>	Scaridae	128.1	H	S2
<i>Acanthurus olivaceus</i>	Acanthuridae	46.0	H	S2
<i>Acanthurus leucopareius</i>	Acanthuridae	33.2	H	S2
<i>Naso unicornis</i>	Acanthuridae	16.8	H	S2
<i>Naso lituratus</i>	Acanthuridae	16.4	H	S2
<i>Parupeneus multifasciatus</i>	Mullidae	16.3	MI	S1
<i>Cephalopholis argus</i>	Serranidae	14.8	P	S1
<i>Kyphosus sp.</i>	Kyphosidae	14.2	H	S2
<i>Acanthurus triostegus</i>	Acanthuridae	11.8	H	S2
<i>Acanthurus dussumieri</i>	Acanthuridae	7.2	H	S2
Small-scale survey non-resource species				
<i>Acanthurus nigrofusus</i>	Acanthuridae	22.4	H	S1
<i>Sufflamen bursa</i>	Balistidae	21.4	MI	S1
<i>Thalassoma duperrey</i>	Labridae	20.3	MI	S1
<i>Rhinecanthus rectangulus</i>	Balistidae	11.1	MI	S1
<i>Sufflamen fraenatus</i>	Balistidae	7.1	MI	S2
<i>Coris venusta</i>	Labridae	5.8	MI	S1
<i>Paracirrhites arcatus</i>	Cirrhitidae	4.7	MI	R
<i>Stegastes marginatus</i>	Pomacentridae	3.6	H	R
<i>Gymnothorax flavimarginatus</i>	Muraenidae	1.9	P	R
<i>Zanclus cornutus</i>	Zanclidae	1.9	SI	S1

*Trophic groupings include herbivores (H), piscivores (P), feeders on mobile benthic invertebrates (MI), and feeders on sessile invertebrates (SI). Mobility guilds include resident (R), semi-vagile type I (S1) and II (S2), and transient (T) (defined in text).

Table 2. Comparisons Of Fish Assemblage Characteristics Between Management Strata For Small-Scale Surveys*

Assemblage metric	MLCD	Open	Diff. factor	t	p
25m transects all fish					
Richness	19.02 (6.05)	13.22 (7.39)	1.4	3.85	< 0.001
Density (no. m-2)	1.17 (0.71)	0.76 (0.62)	1.5	2.78	0.007
Biomass (g m-2)	69.78 (65.91)	29.89 (30.38)	2.3	3.45	< 0.001
25m transects non-resource fish					
Richness	12.92 (4.08)	10.17 (5.16)	1.3	2.65	0.010
Density (no. m-2)	0.98 (0.68)	0.68 (0.58)	1.4	2.11	0.038
Biomass (g m-2)	15.52 (8.29)	10.78 (8.17)	1.4	2.57	0.012
25m transects resource fish					
Richness	6.11 (2.95)	3.50 (2.62)	1.7	4.01	< 0.001
Density (no. m-2)	0.19 (0.24)	0.09 (0.10)	2.1	2.48	0.015
Biomass (g m-2)	54.27 (61.3)	21.92 (28.01)	2.5	2.84	0.006

*Values are means ($\pm$ SD) for all transects in each stratum. Difference (Diff.) factor is MPA value/Open value. t: statistical results of 2-sample Student's t- test.

Table 3. Comparison Of Fish Assemblage Characteristics Between Management Strata For Large-Scale Surveys*

Assemblage metric	MLCD	Open	Diff. factor	Z	p
Resource fish 5 min. swims					
Richness	10.35 (2.89)	4.39 (2.83)	2.6	4.76	< 0.001
Density (no. m-2)	0.03 (0.02)	0.01 (0.02)	3.0	2.88	0.004
Biomass(g m-2)	28.68 (15.49)	8.36 (12.17)	3.7	4.23	< 0.001

*Values are means ($\pm$ SD) for all transects in each stratum. Difference (Diff.) factor is MPA value/ open value. Z: statistical results of Wilcoxon rank-sum test.

19% explained variation (Table 4). After excluding distance from boundary, rugosity was included in the model for a total of 17% explained variation (Table 5). Resource fish biomass from large scale surveys was heavily influenced by distance from boundary (31%), followed by slope of slope, and depth resulting in a total of 42% explained variation (Table 4). When distance from boundary was excluded, broad-scale benthic cover became the most influential variable (24%) for a total of 35% of variation explained (Table 5). Variation in non-resource fish biomass from the small-scale surveys

was explained largely by rugosity (19%), followed by coralline algae cover, and depth (Table 4). It is important to note that in the first run models, which included distance from boundary, this factor was found to be a significant variable for resource fish at both scales, but not for non-resource fish.

Table 4. Distance-Based Linear Models Of Habitat Variable Effects On Reduced Fish Biomass In Each Study Category*

Habitat variable	Effect	AIC	SS	Pseudo-F	p	r ²	R ² cum.	df
Resource Fish Biomass								
<i>Small-scale (125 m²)</i>								
Slope of Slope	+	621.57	24904	10.78	0.001	0.12	0.12	78
Distance from boundary	–	619.65	8613.4	3.87	0.005	0.04	0.16	77
% Coral	+	619.08	5421.9	2.48	0.044	0.03	0.19	76
<i>Large-scale (1000 m²)</i>								
Distance from boundary	–	298.35	28065	16.98	0.001	0.31	0.31	38
Slope of slope	+	296.42	5877.7	3.82	0.008	0.06	0.37	37
Depth	+	295.36	4185.2	2.86	0.044	0.05	0.42	36
Non-Resource Fish Biomass								
<i>Small-scale (125 m²)</i>								
Rugosity	+	539.66	15032	18.12	0.001	0.19	0.19	78
%CCA	+	537.07	3605.2	4.54	0.03	0.05	0.23	77
Depth	+	534.04	3725.2	4.93	0.016	0.05	0.28	76

*Fish biomass excluding planktivores. Variable selection was stepwise with the first term explaining the most variability and model selection was based on the Akaike Information Criterion (AIC). SS: sum of squares; Pseudo-F: test statistic; df: degrees of freedom.

Some small-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 however are not correlated strongly enough to justify excluding one from the model. The strongest correlation between large scale habitat variables was between broad-scale coral cover and depth ($\rho = -0.76$). Correlation tables for all habitat variables tested at each scale are provided in Appendix I. Some small-scale habitat

Table 5. Distance-based Linear Models Of Habitat Variable Effects - Excluding Distance From Boundary - On Reduced Fish Biomass In Each Study Category*

Variable	Effect	AIC	SS	Pseudo-F	p	r ²	R ² cum.	df
Resource Fish Biomass								
<i>Small-scale (125 m²)</i>								
Slope of Slope	+	621.57	24904	10.78	0.001	0.12	0.12	78
% Coral	+	620.77	6188.3	2.74	0.028	0.03	0.15	77
Rugosity	+	620.72	4401.8	1.97	0.101	0.02	0.17	76
<i>Large-scale (1000 m²)</i>								
Benthic cover	–	304.41	21355	5.68	0.001	0.24	0.24	37
Slope of slope	+	302.75	6073	3.45	0.016	0.07	0.30	36
Depth	+	301.83	4473.7	2.66	0.043	0.05	0.35	35

*Fish biomass excluding planktivores. Variable selection was stepwise with the first term explaining the most variability and model selection was based on the Akaike Information Criterion (AIC). SS: sum of squares; Pseudo-F: test statistic; df: degrees of freedom.

Table 6. Linear Relationships Between Significant Habitat Variables And Distance From MPA Boundary*

Variable	Effect	r ²	p
Small-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
Large 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

*Standard least-squares linear regressions with distance from boundary as the explanatory (X) variable.

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 6). All large-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 6).

4.4 Biomass Gradients

Least-squares linear regressions were performed with distance from boundary first against reduced biomass (raw), then on corrected biomass (residuals of standard multiple linear regressions with significant habitat factors). For small-scale survey data, both resource and non-resource fish reduced biomass showed a significant negative relationship with distance from boundary (Figure 3). After controlling for habitat, resource fish corrected biomass still showed a significant relationship with distance from boundary ($r^2=0.07$, $p=0.021$) whereas non-resource fish corrected biomass did not ($r^2=0.00$, $p=0.568$) (Figure 4). Fit was improved for resource fish corrected biomass when sites were averaged by 100 m bins ($r^2=0.34$, $p=0.007$), though the relationship between distance to boundary and non-resource fish corrected biomass remained non-significant ($r^2=0.03$, $p=0.453$) (Figure 5). Large-scale resource fish reduced biomass showed a very strong relationship with distance from reserve boundary ($r^2=0.56$, $p<0.001$). After correcting for habitat the relationship was not as strong, although still highly significant ($r^2=0.18$, $p=0.006$) (Figure 6).

4.5 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 (Figure 7). 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%). Relative proportions of gear use were similar between MPA and open areas though netting formed a larger proportion in the reserve due to hand-net activity in tidepools, which were less common in the open areas. Trolling was relatively more common than other fishing 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

Figure 3. Least-Squares Linear Regression Of Small-Scale Survey Reduced Biomass vs. Distance From MPA Boundary*

*Small-scale survey reduced biomass was $\ln(x+1)$ transformed. Resource fish (●) on left and non-resource fish (○) on right. Negative distance values are inside MPA, positive values are outside, zero distance represents MPA boundary.

Figure 4. Least-Squares Linear Regression Of Small-Scale Survey Corrected Biomass vs. Distance From MPA Boundary.*

*Corrected biomass = residuals from distance-based linear model. Resource fish (●) on left and non-resource fish (○) on right. X-axis same as preceding figure.

the exception of whipping (repeated casting with small pole) and netting which were observed more often on weekends (Figure 8). Spearing effort occurred widely throughout the open zone and was somewhat associated with beach access, though it was highest near the boundary and decreased with distance from it (Figure 9A, 9B).

Figure 5. Least-Squares Linear Regressions Of Small-scale Survey Corrected Biomass Averaged In 100 m Distance Bins vs. Distance From MPA Boundary.

*Corrected biomass = residuals from distance-based linear models. Resource fish (●) on left and non-resource fish (○) on right. X-axis same as preceding figures.

Figure 6. Least-Squares Linear Regression of Large-Scale Survey Reduced Biomass and Corrected Biomass vs. Distance From MPA Boundary.

*Corrected biomass = residuals from distance-based linear models. Large-scale survey reduced biomass was square root transformed. X-axis same as preceding figures.

Figure 7. Mean Number Of Fishers Per Week In MPA And Open Zone By Fishing Gear Type

Figure 8. Mean Angler Hours Per Week For Each Gear Type By Day Strata*

*Weekdays (WD) and weekends/holidays (WE).

Figure 9. Spatial Extent Of Observed Spearfishing Effort*

*A - Spatial extent of total observed spearfishing effort. Black arrows represent beach access locations.
B - Total spearfishing effort hours averaged in each study unit a - f. Red dotted line represents MPA boundary.

CHAPTER 5. DISCUSSION AND CONCLUSIONS

The Pupukea 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 large-scale surveys. Fish assemblage characteristics varied by survey type and between resource and non-resource fish, though all were significantly higher inside the reserve than in the open area. 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. Management strata differences were most extreme however for the large-scale resource fish surveys, with density of fishes three times greater in the reserve and biomass nearly four times greater, compared to the open area.

Structural complexity explained much of the variability in fish biomass for both resource and non-resource species. For resource fish biomass on small-scale surveys, slope of slope explained the most variability followed by distance from boundary, and coral cover. After excluding distance from boundary, rugosity was included in the model. Resource fish biomass from large scale surveys was heavily influenced by distance from boundary, followed by slope of slope, and depth. When distance from boundary was excluded, broad-scale benthic cover became the most influential variable. Variation in non-resource fish biomass from the small-scale surveys was explained largely by rugosity, followed by coralline algae cover, and depth. It is important to note that in the first run models, which included distance from boundary, this factor was found to be a significant variable for resource fish at both scales, but not for non-resource fish.

For small-scale survey data, both resource and non-resource fish reduced biomass showed a significant negative relationship with distance from boundary. After controlling for habitat, resource fish corrected biomass still showed a significant relationship with distance from boundary whereas non-resource fish corrected biomass did not. Fit was improved for resource fish corrected biomass when sites were averaged by 100 m bins, though the relationship between distance to boundary and non-resource fish corrected biomass remained non-significant. Large-scale resource fish reduced biomass showed a

very strong relationship with distance from reserve boundary. After correcting for habitat the relationship was not as strong, although still highly significant.

Average number of fishers per week was over seven times greater in the open area than in the reserve area during the study period. Pole fishing was the dominant gear, followed by spear, trolling, and netting. Relative proportions of gear use were similar between MPA and open areas though netting formed a larger proportion in the reserve due to hand-net activity in tidepools, which were less common in the open areas. Trolling was relatively more common than other fishing 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. Spearing effort occurred widely throughout the open zone and was somewhat associated with beach access, though it was highest near the boundary and decreased with distance from it.

Based on these results, Pupukea MLCD shows a strong reserve effect and spillover of resource fishes likely occurs across the north boundary of the MPA, indicated by a significant negative gradient of resource fish biomass from inside to outside the protected area. This effect was not observed for non-targeted fish species. This pattern in fish biomass coincided with a decline in spear fishing effort from the MPA boundary towards the open area. These results provide some of the best evidence to date in support of adult fish spillover and are consistent with the findings of studies in the Mediterranean (Forcada et al., 2008), Caribbean (Chapman and Kramer, 1999), and the Philippines (Abesamis et al., 2006).

5.1 Research Implications

The strong reserve effect as indicated by comparisons of fish assemblage metrics inside and outside the fished area was significant for non-resource fish as well as resource fish at both scales of measurement, but the magnitude of these differences are likely due to differences in habitat quality. The MLCD has relatively high levels of habitat variables that correlate significantly with fish biomass (Table 6), thus controlling for these habitat variables was important in order to test the spillover hypothesis.

The small-scale (125 m^2) transects recorded higher density and biomass of resource fishes than the large-scale ($\sim 1,000 \text{ m}^2$) transects which 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 area for the small-scale surveys compared to large scale surveys (5 min) and these metrics are scaled by area (num/m^2 , g/m^2). Another reason is that the large-scale surveys did not record resource species $< 15 \text{ cm}$. However the large-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 than non-resource species. Also notable is that the large-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 large-scale surveys may underestimate total biomass of resource species across all size classes, it provides 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.

Rugosity was the most important habitat variable tested for non-resource fish biomass (small-scale surveys) and slope of slope was the most important habitat variable (excluding distance from boundary) for resource fish biomass measured at both small and large 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; Garcia-Charton, 2008). Both rugosity and slope of slope are measurements 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) who showed that structural complexity measured at fine spatial resolutions is a strong predictor of fish abundance and biomass. While those

studies tested the relationship of complexity metrics calculated from different bathymetric grid resolutions and window sizes, this study is the first to quantify fish populations at different scales to use as the basis for comparisons.

Levels of fishing effort were 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 Hawaii 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 Jan 2010 and October 2011 or 32% of calls.

A catch consisting of two very large (55 & 65 cm) terminal redlip parrotfish (*S. rubroviolaceus*) and one large (45cm) peacock grouper (*Cephalopholus argus*) was observed from a spear fisher that emerged from the MPA area. This further validates 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 small-scale surveys, and first and tenth highest for the large-scale surveys. 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 project and if conducted on a larger scale would have great utility for ecosystem based management and marine spatial planning. Spatial analysis of spear fishing effort showed effort was highest near the reserve boundary and decreased with distance, which is somewhat consistent with adult fish spillover (McClanahan and Mangi, 2000). 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 average level of observed spearfishing in the boundary unit (“b” in Figure 9) was less than 5 hours total over the study period. This translates to a maximum of 0.7 hours per day on average. Catch per unit effort for spear fishing is relatively high, estimates elsewhere in Hawaii are about 0.9 kg/hr (Friedlander and Parrish, 1997; Everson and Friedlander, 2004). Assuming a CPUE of 1 kg/hr, the observed spearfishing

effort would only 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 Figure 9) is 0.05 kg/m² so if we extrapolate to the boundary unit area (28,379 m²), the estimated total biomass is 1,391 kg. Therefore, the observed (daylight) spear fishing effort in the MPA boundary unit has the potential to remove as much as 9% of the standing stock biomass there in a year. Though 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.

5.2 Management Implications

The establishment of marine protected areas and marine reserves almost always requires the support of local people living in and around the area in question (White et al., 1994; Christie & White, 2007). In many cases, promises of ‘stock wide’ (i.e. recruitment) rather than local (i.e. spillover) benefits can appear rather tenuous. It is a common assumption that fish populations will increase inside the reserve and procreate, thus providing direct benefits for fished areas nearby because both adults and their offspring will move out from the reserve. This belief is not only restricted to local people, but also the community-based managers who encourage the establishment of marine reserves. Convincing a community that a marine reserve may benefit the fisheries 10 to 100km away (based on larval export) is inevitably difficult. Therefore, any demonstration that marine reserves may positively affect nearby fisheries, even on a minor scale, may be critical to the successful establishment of community-based marine protected areas or marine reserves (Russ & Alcala, 1996).

While this and previous research provides evidence supporting spillover, it appears to occur at relatively small scales of 100 – 1,000 m (Roberts & Polunin, 1991; Russ, 2002). 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; Nowlis and

Friedlander, 2005). This is a reasonable expectation, provided that there is a greater larval production per unit area in protected areas compared to fished areas, the scale of dispersal of larvae is much larger than the dispersal scale of the individual reserves, and that protected areas are located in areas where larvae are likely to disperse (i.e., ‘source’ areas) (Russ, 2002). Unfortunately, evidence for the “recruitment effect”, wherein populations of target species in marine protected areas replenish target species outside of protected areas, is largely nonexistent due to the difficulties inherent in measuring movement patterns of eggs/larvae. Research on this topic is a complex integration of oceanography, larval biology, and computer modeling. It is these theoretical models (often enhanced with empirical measurements) that provide some of the best evidence of the recruitment effect (e.g. Cudney-Bueno et al., 2009; Pelc et al., 2010). Recently, studies using a new genetic technique called DNA parentage analysis have also provided support for the recruitment effect by identifying offspring outside of protected areas (e.g. Planes et al., 2009; Christie et al., 2010).

Based on the scientific consensus that larval export provides greater overall fishery benefits than adult spillover, MPAs 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 & Reed, 1993). While there is potential for larval export from Pūpūkea 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 in Hawai’i and worldwide.

5.3 Opportunities For Further Research

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, measuring both to what extent MPAs are self-recruiting, and to what degree they can replenish fished areas through larval export. In addition to modeling approaches, these questions can be addressed through new techniques such as mass-marking based on maternal transmission of stable isotopes (Almany et al., 2007) and genetic parentage analysis (Christie et al., 2010).

Though evidence for adult spillover continues to mount, unequivocal proof is still lacking. Russ (2002) outlines a statistical design robust enough to provide such proof. The first requirement is a Before-After-Control-Impact-Pairs (BACIP) design (Underwood, 1994). In this design, you have control-impact pairs (fished and reserve locations) monitored through time, starting before the reserves are established and continuing after they are established. Confounding variables such as benthic habitat should be measured, monitored and controlled for where possible with multiple regression techniques (such as was done in this study). In addition, replicate sampling units should be monitored at replicate sites, nested within reserve and fished locations along a gradient of distance. Fished should be tagged with either visual or radio tags at each distance interval. These fishes could be recaptured over time, either by underwater visual census, fishing, or acoustic receivers (in the case of radio tags). Initial tagging and subsequent recapture effort should be allocated as evenly as possible across all portions of the distance gradient. Spatial patterns of fishing effort should also be measured for the duration of the experiment. Such a design could then measure the dispersion of post settlement fishes, before and after the establishment of reserves, to test the idea of net export of biomass from reserves.

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 idealized experimental design were incorporated into the design of the current study. Probability is high that new marine reserves will be established in Hawai'i in the coming years, and the execution of an experiment using the design outlined above would be the gold-standard in spillover research.

APPENDIX I. SUPPLEMENTARY TABLES

Table A. Correlations Between Small-Scale Habitat Variables.*

	%Coral	%CCA	%Algae	%Sand	%Turf	Rugosity	Distance	Depth
%CCA	0.43							
%Algae	0.28	0.32						
%Sand	-0.37	-0.47	-0.06					
%Turf	-0.41	-0.58	-0.37	-0.2				
Rugosity	0.32	0.35	0.19	-0.02	-0.32			
Distance	-0.21	-0.48	-0.31	0.17	0.38	-0.48		
Depth	0.33	-0.23	0.17	0.31	-0.14	0.33	-0.08	
Slope of slope	0.23	0.43	0.28	-0.04	-0.38	0.67	-0.38	0.22

*Values Are Pearsons Rho (ρ) Correlation coefficients.

Table B. Correlations Between Large-Scale Habitat Variables.*

	Depth	Slope of slope	Distance	Coral	MA
Slope of slope	0.37				
Distance	-0.32	-0.4			
Coral	-0.76	-0.09	-0.45		
MA	0.26	-0.34	-0.2	-0.45	
Turf	0.46	0.41	0.62	-0.51	-0.54

*Values are Pearsons rho (ρ) correlation coefficients.

APPENDIX II. SUPPLEMENTARY FIGURES

Figure A. Pupukea MLCD Historical Boundary Comparison*

*1983 boundary in yellow – 10.6 ha. 2003 boundary in red – 71.0 ha.

Figure B. Three-Dimensional Representation Of Study Site*

*Red area denotes MPA zone, green area shows open zone. Benthic surface is Lidar bathymetry used for analysis of selected habitat metrics.

Figure C. Example of NOAA Benthic Habitat Maps*

*Used for large-scale benthic cover classifications. Black outline shows study zones.

Figure D. Example of Lidar-Derived Slope-Of-Slope Layer*

*Used for measuring habitat complexity.

Figure E. Spatial Extent Of Observed Fishing Effort*

*A - Spatial extent of total observed fishing effort. Black arrows represent beach access locations.
B - Total fishing effort hours averaged in each study unit a - f. Red dotted line represents MPA boundary.

REFERENCES – LITERATURE CITED

- Abesamis, R. A., G. R. Russ & A. C. Alcala (2006) Gradients of abundance of fish across no-take marine reserve boundaries: evidence from Philippine coral reefs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 16, 349-371.
- Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. In *2nd International Symposium on Information Theory*, eds. B. Petroa & F. Csake, 267-281.
- Allison, G. W., S. D. Gaines, J. Lubchenco & H. P. Possingham (2003) Ensuring Persistence of Marine Reserves: Catastrophes Require Adopting an Insurance Factor. *Ecological Applications*, 13, S8-S24.
- Allison, G. W., J. Lubchenco & M. H. Carr (1998) Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications*, 8, 79-92.
- Amargós, F., G. Sansón, A. del Castillo, A. Fernández, F. Blanco & W. de la Red (2010) An experiment of fish spillover from a marine reserve in Cuba. *Environmental Biology of Fishes*, 87, 363-372.
- Anderson, M. J. & R. B. Millar (2004) Spatial variation and effects of habitat on temperate reef fish assemblages in northeastern New Zealand. *Journal of Experimental Marine Biology and Ecology*, 305, 191-221.
<http://www.sciencedirect.com/science/article/pii/S0022098104000139>.
- Anonymous. 2009. Commercial Marine Landings Summary Trend Report - Calendar Year 2009. Hawaii Division of Aquatic Resources.
- Ashworth, J. S. & R. F. G. Ormond (2005) Effects of fishing pressure and trophic group on abundance and spillover across boundaries of a no-take zone. *Biological Conservation*, 121, 333-344.
- Ault, T. R. & C. R. Johnson (1998) SPATIALLY AND TEMPORALLY PREDICTABLE FISHCOMMUNITIES ON CORAL REEFS. *Ecological Monographs*, 68, 25-50.
- Bartlett, D. & R. W. G. Carter (1991) Seascape ecology: The landscape ecology of the coastal zone. *EKOLOGIA(CSFR)/ECOLOGY(CSFR)*. 10, 43-53.
- Battista, T. A., B. M. Costa & S. M. Anderson. 2007. Shallow-Water Benthic Habitats of the Main Eight Hawaiian Islands (DVD). Silver Spring, MD: Biogeography Branch.
- Chapman, M. R. & D. L. Kramer (1999) Gradients in coral reef fish density and size across the Barbados Marine Reserve boundary: effects of reserve protection and habitat characteristics. *Marine ecology. Progress series(Halstenbek)*, 181, 81-96.
- Christie, P. & A. T. White. 2007. BEST PRACTICES IN GOVERNANCE AND ENFORCEMENT OF MARINE PROTECTED AREAS: AN OVERVIEW1. In *EXPERT WORKSHOP ON MARINE PROTECTED AREAS AND FISHERIES MANAGEMENT: REVIEW OF ISSUES AND CONSIDERATIONS*, 183.
- Clarke, K. R. & R. N. Gorley. 2006. PRIMER v6: User Manual/Tutorial. Plymouth: PRIMER-E.
- Côté, I. M., I. Mosqueira & J. D. Reynolds (2001) Effects of marine reserve characteristics on the protection of fish populations: a meta-analysis. *Journal of Fish Biology*, 59, 178-189.

- DeMartini, E. E. (1993) Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fishery Bulletin*, 91, 414-427.
- Everson, A. & A. M. Friedlander (2004) Catch, effort, and yields for coral reef fisheries in Kane 'ohe Bay, O 'ahu and Hanalei Bay, Kaua 'i: Comparisons between a large urban and a small rural embayment. *Status of Hawai 'i's Coastal Fisheries in the New Millennium*, 110-131.
- Forcada, A., J. T. Bayle-Sempere, C. Valle & P. Sánchez-Jerez (2008) Habitat continuity effects on gradients of fish biomass across marine protected area boundaries. *Marine Environmental Research*, 66, 536-547.
- Forcada, A., C. Valle, P. Bonhomme, G. Criquet, G. Cadiou, P. Lenfant, J. L. Sánchez-Lizaso & others (2009) Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Marine Ecology Progress Series*, 379.
- Friedlander, A. M., E. Brown & M. E. Monaco (2007a) Defining reef fish habitat utilization patterns in Hawaii: comparisons between marine protected areas and areas open to fishing. *Marine Ecology Progress Series*, 351, 221-233.
- Friedlander, A. M., E. K. Brown & M. E. Monaco (2007b) Coupling ecology and GIS to evaluate efficacy of marine protected areas in Hawaii. *Ecological Applications*, 17, 715-730.
- Friedlander, A. M. & J. D. Parrish (1997) Fisheries harvest and standing stock in a Hawaiian Bay. *Fisheries Research*, 32, 33-50.
- Friedlander, A. M. & 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. M., L. M. Wedding & M. E. Monaco. 2010. Monitoring Hawaii's Marine Protected Areas: Examining Spatial and Temporal Trends using a Seascape Approach. 130. Silver Spring, MD: NCCOS Center for Coastal Monitoring and Assessment Biogeography Branch.
- Froese, R. & D. Pauly. 2011. FishBase. In *World Wide Web electronic publication*.
- Gaines, S. D., B. Gaylord & J. L. Largier (2003) AVOIDING CURRENT OVERSIGHTS IN MARINE RESERVE DESIGN. *Ecological Applications*, 13, 32-46.
- Galal, N., R. F. G. Ormond & O. Hassan (2002) Effect of a network of no-take reserves in increasing catch per unit effort and stocks of exploited reef fish at Nabq, South Sinai, Egypt. *Mar. Freshwater Res.*, 53, 199-205.
- García-Charton, J. A., Á. Pérez-Ruzafa, P. Sánchez-Jerez, J. T. Bayle-Sempere, O. Reñones & D. Moreno (2004) Multi-scale spatial heterogeneity, habitat structure, and the effect of marine reserves on Western Mediterranean rocky reef fish assemblages. *Marine Biology*, 144, 161-182.
- Gell, F. R. & C. M. Roberts (2003) Benefits beyond boundaries: the fishery effects of marine reserves. *Trends in Ecology & Evolution*, 18, 448-455.
- Gerber, L. R., S. S. Heppell, F. Ballantyne & E. Sala (2005) The role of dispersal and demography in determining the efficacy of marine reserves. *Canadian Journal of Fisheries and Aquatic Sciences*, 62, 863-871.
- Gratwicke, B. & M. R. Speight (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology*, 66, 650-667.

- Grober-Dunsmore, R., T. K. Frazer, J. P. Beets, W. J. Lindberg, P. Zwick & N. A. Funicelli (2008) Influence of landscape structure on reef fish assemblages. *Landscape Ecology*, 23, 37-53.
<http://www.springerlink.com.eres.library.manoa.hawaii.edu/content/e97702142r4vm808/>.
- Grober-Dunsmore, R., T. K. Frazer, W. J. Lindberg & J. Beets (2006) Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. *Coral Reefs*, 26, 201-216.
- Guidetti & E. Sala (2007) Community-wide effects of marine reserves in the Mediterranean Sea. *Marine Ecology Progress Series*, 335, 43-56.
- Halpern, B. S. (2003) The impact of marine reserves: do reserves work and does reserve size matter? . *Ecological Applications*, 13, 117-137.
- Halpern, B. S. & R. R. Warner (2002) Marine reserves have rapid and lasting effects. *Ecology Letters*, 5, 361-366.
- Halpern, B. S. & R. R. Warner (2003) Review Paper. Matching marine reserve design to reserve objectives. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 270, 1871-1878.
- Harmelin-Vivien, M., L. Le Diréach, J. Bayle-Sempere, E. Charbonnel, J. A. García-Charton, D. Ody, A. Pérez-Ruzafa, O. Reñones, P. Sánchez-Jerez & C. Valle (2008) Gradients of abundance and biomass across reserve boundaries in six Mediterranean marine protected areas: Evidence of fish spillover? *Biological Conservation*, 141, 1829-1839.
- Irish, J. L. & W. J. Lillycrop (1999) Scanning laser mapping of the coastal zone: the SHOALS system. *ISPRS Journal of Photogrammetry and Remote Sensing*, 54, 123-129.
- Kellner, J. B., I. Tetreault, S. D. Gaines & R. M. Nisbet (2007) Fishing the line near marine reserves in single and multispecies fisheries. *Ecological Applications*, 17, 1039-1054.
- Kohler, K. E. & S. M. Gill (2006) Coral Point Count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers & Geosciences*, 32, 1259-1269.
- Kramer, D. L. & M. R. Chapman (1999) Implications of fish home range size and relocation for marine reserve function. *Environmental Biology of Fishes*, 55, 65-79.
- Legendre, P. & M. J. Anderson (1999) Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological Monographs*, 69, 1-24.
- Lester, S. E. & B. S. Halpern (2008) Biological responses in marine no-take reserves versus partially protected areas. *Marine Ecology Progress Series*, 367, 49-56.
- Lester, S. E., B. S. Halpern, K. Grorud-Colvert, J. Lubchenco, B. I. Ruttenberg, S. D. Gaines, S. Airamé & R. R. Warner (2009) Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series*, 384, 33-46.
- Lizaso, J. L. S., R. Goni, O. Renones, J. A. G. Charton, R. Galzin, J. T. Bayle, P. S. Jerez, A. P. Ruzafa & A. A. Ramos (2000) Density dependence in marine protected populations: a review. *Environmental Conservation*, 27, 144-158.
- Lubchenco, J., S. R. Palumbi, S. D. Gaines & S. Andelman (2003) PLUGGING A HOLE IN THE OCEAN: THE EMERGING SCIENCE OF MARINE RESERVES¹. *Ecological Applications*, 13, 3-7.

- MacNeil, M. A., N. A. J. Graham, N. V. C. Polunin, M. Kulbicki, R. Galzin, M. Harmelin-Vivien & S. P. Rushton (2009) Hierarchical drivers of reef-fish metacommunity structure. *Ecology*, 90, 252-264.
- Maypa, A. P., G. R. Russ, A. C. Alcala & H. P. Calumpong (2002) Long-term trends in yield and catch rates of the coral reef fishery at Apo Island, central Philippines. *Mar. Freshwater Res.*, 53, 207-213.
- McArdle, B. H. & M. J. Anderson (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82, 290-297.
- McClanahan, T. R. & S. Mangi (2000) Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications*, 10, 1792-1805.
- McCook, L. J., T. Ayling, M. Cappel, J. H. Choat, R. D. Evans, D. M. De Freitas, M. Heupel, T. P. Hughes, G. P. Jones, B. Mapstone, H. Marsh, M. Mills, F. J. Molloy, C. R. Pitcher, R. L. Pressey, G. R. Russ, S. Sutton, H. Sweatman, R. Tobin, D. R. Wachenfeld & D. H. Williamson (2010) Marine Reserves Special Feature: Adaptive management of the Great Barrier Reef: A globally significant demonstration of the benefits of networks of marine reserves.
- McCoy, E. D. & S. S. Bell. 1991. Habitat structure: the evolution and diversification of a complex topic. In *Habitat Structure: the Physical Arrangement of Objects in Space*, eds. S. S. Bell, E. D. McCoy & H. R. Mushinsky, 3-27. New York: Chapman and Hall.
- Micheli, F., B. S. Halpern, L. W. Botsford & R. R. Warner (2004) Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications*, 14, 1709-1723.
- Mora, C., S. Andréfouët, M. J. Costello, C. Kranenburg, A. Rollo, J. Veron, K. J. Gaston & R. A. Myers (2006) Coral reefs and the global network of marine protected areas. *Science(Washington)*, 312, 1750-1751.
- Mosquera, I., I. M. Côté, S. Jennings & J. D. Reynolds (2000) Conservation benefits of marine reserves for fish populations. *Animal Conservation*, 3, 321-332.
- Munro, J. L. (1974) The Mode of Operation of Antillean Fish Traps and the Relationships Between Ingress, Escapement, Catch and Soak. *Journal du Conseil*, 35, 337-350.
- Nmfs. 1999. Ecosystem-based fishery management: a report to congress by the ecosystem principles advisory panel. 54. Washington, D.C.: Department of Commerce, National Oceanic and Atmospheric Administration.
- Nowlis, J. S. & A. Friedlander. 2005. Marine reserve function and design for fisheries management. In *Marine conservation biology: the science of maintaining the sea's biodiversity*, eds. E. A. Norse & L. B. Crowder, 280-301. Island Press.
- Nowlis, J. S. & C. M. Roberts (1999) Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin*, 97, 604-616.
- Nrc. 2000. Marine protected areas: tools for sustaining ocean ecosystems. Washington, D.C.: National Academy Press.
- Pelc, R. A., R. R. Warner, S. D. Gaines & C. B. Paris (2010) Detecting Larval Export from Marine Reserves. *Proceedings of the National Academy of Sciences*, 107, 18266-18271.
- Pittman, S. J., B. M. Costa & T. A. Battista (2009) Using Lidar Bathymetry and Boosted Regression Trees to Predict the Diversity and Abundance of Fish and Corals. *Journal of Coastal Research*, 27-38.

- Pittman, S. J., R. T. Kneib & C. A. Simenstad (2011) Practicing coastal seascape ecology. *Marine Ecology Progress Series*, 427, 187-190.
- Planes, S., G. P. Jones & S. R. Thorrold (2009) Larval Dispersal Connects Fish Populations in a Network of Marine Protected Areas. *Proceedings of the National Academy of Sciences*, 106, 5693-5697.
- Rakitin, A. & D. Kramer (1996) Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Marine Ecology Progress Series*, 131, 97-113.
- Risk, M. J. (1972) Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin*, 153, 1-6.
- Roberts, C. M. & N. V. C. Polunin (1991) Are marine reserves effective in management of reef fisheries? *Reviews in Fish Biology and Fisheries*, 1, 65-91.
- Rowley, R. J. (1994) Marine reserves in fisheries management. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 4, 233-254.
- Russ, G. R. 2002. Yet another review of marine reserves as reef fishery management tools. In *Coral reef fishes: dynamics and diversity in a complex ecosystem*, ed. P. F. Sale, 421-443. San Diego, CA: Academic Press Inc.
- Russ, G. R. & 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 (2004) Marine reserves: long-term protection is required for full recovery of predatory fish populations. *Oecologia*, 138, 622-627.
- Russ, G. R., A. C. Alcala & A. P. Maypa (2003) Spillover from marine reserves: the case of *Naso vlamingii* at Apo Island, the Philippines. *Marine Ecology Progress Series*, 264, 15-20.
- Travis, J. M. J., D. J. Murrell & C. Dytham (1999) The Evolution of Density-dependent Dispersal. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 266, 1837-1842.
- Tupper, M. (2007) Spillover of commercially valuable reef fishes from marine protected areas in Guam, Micronesia. *Fishery Bulletin*, 105, 527-537.
- Underwood, A. J. (1994) On Beyond BACI: Sampling Designs that Might Reliably Detect Environmental Disturbances. *Ecological Applications*, 4, 3-15.
- Walsh, W. J., S. S. P. Cotton, J. Dierking & I. D. Williams. 2003. The commercial marine aquarium fishery in Hawai'i. In *Status of Hawai'i's Coastal Fisheries in the New Millennium: Proceedings of the 2001 Fisheries Symposium*, ed. A. M. Friedlander, 132-159. Honolulu: American Fisheries Society, Hawai'i Chapter.
- Wedding, L. M., A. M. Friedlander, M. McGranaghan, R. S. Yost & M. E. Monaco (2008) Using bathymetric lidar to define nearshore benthic habitat complexity: Implications for management of reef fish assemblages in Hawaii. *Remote Sensing of Environment*, 112, 4159-4165.
- White, A. T. 1988. *Marine parks and reserves: Management for coastal environments in Southeast Asia*. Manila, Philippines: ICLARM.
- White, A. T., L. Z. Hale, Y. Renard & L. Cortesi (1994) Collaborative and community-based management of coral reefs: lessons from experience.

- Williams, I. D., W. J. Walsh, J. T. Claisse, B. N. Tissot & K. A. Stamoulis (2009) Impacts of a Hawaiian marine protected area network on the abundance and fishery sustainability of the yellow tang, *Zebrasoma flavescens*. *Biological Conservation*, 142, 1066-1073.
- Williams, I. D., W. J. Walsh, R. E. Schroeder, A. M. Friedlander, B. L. Richards & K. A. Stamoulis (2008) Assessing the Importance of Fishing Impacts on Hawaiian Coral Reef Fish Assemblages Along Regional-Scale Human Population Gradients. *Environmental Conservation*, 35, 261-272.
- Zeller, D., S. L. Stoute & G. R. Russ (2003) Movements of reef fishes across marine reserve boundaries: effects of manipulating a density gradient. *Marine Ecology Progress Series*, 254, 269–280.