

**Faculty of Science and Engineering  
School of Molecular and Life Sciences**

**Spatial Predictive Modeling of Fish Distributions Incorporating  
Habitat Utilization and Behavior in the Context of Marine  
Protection**

**Kostantinos Stamoulis**

**This thesis is presented for the Degree of  
Doctor of Philosophy  
of  
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## **Declaration**

To the best of my knowledge and belief this thesis contains no material previously published by any other person except where due acknowledgment has been made.

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in compliance with the National Health and Medical Research Council Australian code for the care and use of animals for scientific purposes 8<sup>th</sup> edition (2013). The proposed research study received animal ethics approval from the Curtin University Animal Ethics Committee, Approval Number: AEC\_2014\_42

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## **Thesis Abstract**

Expanding anthropogenic impacts on coastal and marine areas reinforce the need to manage societal demands while preserving the marine environment. Marine spatial planning (MSP) has been recognized as a necessary framework for effective and ecosystem-based management of coastal and marine spaces. Chapter two of this thesis provides a review of the current literature to identify the available technological and methodological tools that are best suited for MSP and suggest areas for further research. Spatial ecological modeling is a component of the MSP process which combines and summarizes all available biological, ecological, and environmental information for a study area. It involves the characterization of seascapes and biological communities to identify ecologically important areas based on species-habitat associations. Species distribution models (SDMs) of fishes are an application of spatial ecological modeling which provides key inputs for MSP. While there are various ways in which SDMs can be improved, quantifying key drivers and understanding their effects on input/response data (fish assemblage metrics) is critically important, and the primary focus of this thesis.

In Chapter three, I demonstrate the utility of SDMs for fisheries management and MSP by developing models of targeted fish biomass and length across the main Hawaiian Islands using a comprehensive dataset of fish surveys, remotely sensed habitat layers, and estimated fishing pressure layers. Spatial patterns of fishing effort were shown to be highly variable and SDMs indicated a low threshold beyond which targeted fish assemblages were severely impacted. High targeted reef fish biomass and body length were found in areas not easily accessed by humans. When fishing effort was set to zero, model predictions showed these high values to be more widely dispersed among suitable habitats. Comparing current targeted fish distributions with those predicted when fishing effort was removed, revealed areas with high recovery potential on each island. On O‘ahu, the most heavily fished island, average biomass increased by 517% and mean body length increased by 59%. Spatial protection of these areas would aid recovery of nearshore coral reef fisheries.

Fish behavior in terms of diver avoidance has been shown to vary along gradients of fishing pressure, which can influence fish assemblage measures and SDMs based on

this data. Chapter four explores behavior differences for targeted reef fishes in Hawai‘i in areas with different levels of fishing pressure. I investigate the role of approach starting distance (SD) and a number of other variables then compare direct measures of diver avoidance behavior in a long-term marine reserve and heavily fished area. Relative effect sizes of SD and several other co-variables were large in comparison to site. After accounting for these co-variables, targeted fishes were found to maintain greater distances from divers in the fished area compared to the marine reserve. These results establish that measurable differences in targeted fish wariness in Hawai‘i are related to fishing pressure.

Building on these findings, I test whether incorporating fish behavior can improve SDMs in Chapter five. I use diver operated stereo-video to conduct fish assemblage surveys and record minimum approach distance (MAD) of targeted reef fishes inside and outside of two marine reserves. MAD is an indirect measure of fish wariness that has rarely been tested, compared with a direct measure used in Chapter four.

Distance from observed fishes was shown to be greater outside the marine reserves, compared to inside. Having established that MAD provides a proxy for fish wariness, I then use it as a predictor in SDMs and show that it improved models of targeted fish biomass compared to models with only habitat and management predictors. This work highlights the importance of fish behavior metrics in explaining patterns of observed fish assemblage characteristics and their utility as predictors in spatial predictive models.

Comprehensive and spatially explicit information on fishing patterns and marine species distributions is necessary to inform ecosystem-based management and MSP. Patterns of fishing pressure are critical inputs for modeling distributions of fishery resources and additional research should focus on mapping these patterns. Diver avoidance behavior provides a proxy for fishing effort that could be used to refine maps of fishing pressure. Measures of fish wariness hold promise for management applications such as measuring compliance in marine reserves and can greatly improve accuracy of SDMs when used as a predictor of targeted fish biomass. A more complete understanding of fish behavioral responses to human predation could be used to refine measures of fish assemblages and improve accuracy of SDMs, leading to improved ecosystem-based management of coastal fisheries.

## Statement of Contributors

### Published chapters

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**Author contribution:** KS, JD, and ID designed the study. KS, JD, MP, and JL contributed to predictor generation. JD and MP adapted the computer code. KS conceived and executed the data analyses and wrote and edited the manuscript. BC, MK, and AM secured funding and provided guidance. All co-authors reviewed and commented on the manuscript.

**Chapter 4:** Stamoulis, K. A., E. S. Harvey, A. M. Friedlander, I. D. Williams, K. C. Weng, C. Wiggins, G. W. Wagner, and E. J. Conklin. 2018. Flight behavior of targeted fishes depends on variables other than fishing. *Ecological Indicators*. <https://doi.org/10.1016/j.ecolind.2018.09.006>

**Author contribution:** KS designed the study, collected the data, executed the data analyses, and wrote the manuscript. EH, AF, and ID provided guidance. EC, KW, and CW contributed to data collection. GW assisted with video analysis. All co-authors reviewed and commented on the manuscript.

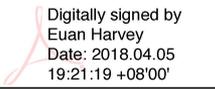
Chapters in Preparation

**Chapter 5:** Incorporating fish behavior improves accuracy of species distribution models

**Author contribution:** KS designed the study, collected the data, executed the data analysis, and wrote the manuscript. EH, IW, and JD provided guidance and reviewed and commented on the manuscript.

Signature of candidate: 

Date: 4 April, 2018

Signature of supervisor:  Euan  
Harvey

Date: 5-Apr-2018

## **Acknowledgements**

I grew up far away from coral reefs on a small island in the Puget Sound in Washington State. There was always saltwater nearby, but it was dark and cold. My father was a ferry boat captain and a fisherman. He kindled an early interest in boats and fishes, though I never really had the patience for fishing in those days. In grade school, a friend of mine would go on vacation to Hawai‘i and bring back stories and pictures of his adventures SCUBA diving there. That began the dream which I did not realize until many years later when my mother moved to the Big Island of Hawai‘i giving me the opportunity to join her and begin a life focused around the ocean and coral reefs. I never really planned to pursue a PhD in marine ecology but just kept doing what I loved and eventually arrived here.

There are many people that have provided encouragement, inspiration, and motivation throughout this process of becoming a doctor in philosophy. First of all, I’d like to thank Jade Delevaux for being a constant source of light during this period of my life and for helping to shape who I am today. These last four years I’ve learned at least as much about life as I have about science. I’d like to thank my PhD supervisor, Euan Harvey for giving me this opportunity and for his support along the way. We met over beers and I took him surfing in Hawai‘i, when I started my PhD he returned the favor and took me surfing in West Oz. He has been as much of a friend as a supervisor and I’m grateful for that and look forward to more surf sessions together.

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## Abbreviations

BRT	boosted regression trees
CCR	closed circuit rebreather
CV	coefficient of variation
CV PDE	cross-validated percent deviance explained
CV SE	cross-validated standard error
DistLM	distance based linear model
dMAD	direct minimum approach distance
DSS	decision support systems
FID	flight initiation distance
GIS	geographic information system
GISc	geographic information science
GPS	global positioning system
LiDAR	light detection and ranging
MAD	minimum approach distance
MAD <sub>10</sub>	mean minimum approach distance by transect with the maximum possible value (10m) substituted for transects with no targeted fishes
MHI	main Hawaiian Islands
MPA	marine protected area
MSP	marine spatial planning
NOAA	national oceanic and atmospheric association
NWHI	northwestern Hawaiian Islands
SCUBA	self-contained underwater breathing apparatus
SD	approach starting distance
SDMs	species distribution models
Stereo-DOV	diver operated stereo-video system
PDE	percent deviance explained
UVC	underwater visual census

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**Note to readers:** Every effort has been made to facilitate navigation of this electronic document. The Table of Contents and Lists of Figures, Tables, and Supplementary Material all contain active links and each section is bookmarked. Figures and tables are placed in the text as close as possible to where they are referenced. Supplementary material is located at the end of each chapter and in-text references to this material are active links to each item.

# CHAPTER 1 – General Introduction

## Background and rationale

### Marine spatial planning

For centuries, vast ocean spaces have provided challenges to movement of the human species and ocean resources have historically been viewed as being limitless (Dalzell 1998). In modern times, human impacts are increasing as a result of growing populations and the advancement of technologies that allow for rapid transportation across oceans as well as the ability to exploit their resources (Pauly et al. 2002). As a result, marine spatial planning (MSP) is a concept that has gained momentum due to the increased necessity of managing marine spaces. According to the United Nations, “marine spatial planning is a public process of analyzing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic, and social objectives” (Ehler and Douvère 2009).

Key steps in the MSP process include defining existing conditions through data collection, analyzing existing conditions and projecting future conditions (Ehler and Douvère 2009). These steps are made possible by the use of data, software tools, and other well-defined spatially explicit methodologies (Papathanasiou and Kenward 2014, Shucksmith and Kelly 2014). Information gathered and generated through this process informs the preparation of a spatial management plan. A primary objective of MSP is to support current and future uses of ocean ecosystems and sustain the availability of ecosystem services for future generations (Douvère 2008).

MSP can be data intensive and is facilitated by the increasing availability of spatial data (Collie et al. 2013). The types of spatial data required are administrative, ecological, environmental and human use (Shucksmith and Kelly 2014).

Administrative data includes government regulations and jurisdictional boundaries. Ecological data is comprised of biodiversity, species distributions, connectivity, and habitat information (Crowder and Norse 2008, Foley et al. 2010). Environmental data deals with ocean and near shore physical parameters such as sea level change, temperature, ocean winds, circulation, currents, waves, and water chemistry (Mellin et al. 2010). Human uses of ocean and coastal areas encompass a broad range of

activities including fishing, marine transportation and shipping, offshore renewable energy and a range of recreational activities (Katsanevakis et al. 2011).

Spatial ecological modeling is a type of analysis that compiles and summarizes all ecological and environmental information for a study area to represent existing conditions. When applied to species distributions, it is often referred to as species distribution modeling and involves the characterization of seascapes and biological communities to identify ecologically important areas (Kendall et al. 2004, Pittman et al. 2007b, Mellin et al. 2009). Seascape ecologists apply species distribution models (SDMs) to geographically extrapolate *in-situ* data on the distribution, diversity, and abundance of species based on seascape properties (Franklin 2010, Boström et al. 2011). Thus, species distribution modelling provides spatial ecological information of the scope and scale necessary for MSP. This thesis focuses on the application of SDMs for predictive mapping of the distribution of targeted fishes.

#### Species distribution models of targeted fishes

SDMs are analytical tools that combine observations of species occurrence or abundance with environmental and habitat variables, and more recently human uses and other socio-economic attributes. They are used to gain ecological and evolutionary insights and to predict distributions across land and seascapes, sometimes requiring extrapolation in space and time (Elith and Leathwick 2009). The development of SDMs begins with observations of species distributions and the identification of environmental and other variables thought to influence habitat suitability and, therefore, the distributions of the species being modeled (Mellin et al. 2006, Franklin 2010, Schmiing et al. 2013). Modeling techniques can be rule-based or quantitative, and can include multivariate ordination, generalized linear models (Guisan et al. 2002, Knudby et al. 2010a), classification and tree ensemble techniques (Pittman et al. 2009, Knudby et al. 2010b) and artificial neural networks (Guisan and Zimmermann 2000, Pittman et al. 2007b).

A number of studies have used remotely sensed environmental and habitat variables as predictors in SDMs of fishes (Sundblad et al. 2009, Moore et al. 2009, Mellin et al. 2010). Seascape variables such as seafloor topography, benthic cover and wave exposure, at a range of spatial scales, have been shown to be important predictors of

fish assemblages (Friedlander et al. 2003, Bouchet et al. 2015, Galaiduk et al. 2017). Human activities also drive patterns of species distributions. Fishing has direct impacts on fish communities and removes fish biomass, alters the trophic and size structure, and distorts community composition resulting in the loss of ecological functions (Jackson et al. 2001). Therefore, SDMs of targeted fishes should be more accurate when data on fishing patterns are incorporated.

Fish assemblage metrics are response variables for SDMs and are critical to model accuracy. Monk et al. (Monk et al. 2012) compared modeling approaches and input datasets derived from two underwater video methods (i.e. baited and towed video) to create spatial predictive models of temperate marine fishes in southeastern Australia. They found larger differences in model outputs between input (fish occurrence) datasets compared to differences between modeling approaches for the same input data. Previous work has established a positive relationship between fishing pressure and diver avoidance behavior of targeted fishes (Kulbicki 1998, Gotanda et al. 2009, Feary et al. 2010). Area-based UVC methods are the most widely used methods to survey reef fish assemblages worldwide (Caldwell et al. 2016). In locations with high fishing pressure, area-based UVC methods may underestimate fish abundance for species targeted by spear fishers (Kulbicki 1998, Feary et al. 2010). This behavioral bias in the response data for SDMs may have implications for model accuracy.

#### Diver avoidance behavior

Fleeing from predators involves costs in time, energy and lost opportunities for other activities that enhance fitness. When animals detect predators that are too far away to be a threat, they should not necessarily flee immediately. Instead, the timing of flight should be optimized according to the costs and benefits of fleeing and remaining in place (Ydenberg and Dill 1986, Cooper Jr. and Frederick 2007). For this reason, flight initiation distance (FID, the distance between prey and potential predator at which the prey starts to flee) provides a measure of the animal's perception of danger in a given situation and the risks it is willing to take (Gotanda et al. 2009).

FID should increase with the risk posed by an approaching predator. This perceived threat, however, may be influenced by prior experience (Brown, 2003). Therefore, FID is expected to vary in space and time (Gotanda et al. 2009). Marine reserves

protect fish from spearfishing (among other types of fishing) and are often used for ecotourism and recreational diving (Bhat 2003, Stevenson and Tissot 2013). A few studies have investigated the extent to which this protection and/or exposure to human predators influences FID (Gotanda et al. 2009, Feary et al. 2010, Januchowski-Hartley et al. 2013). More research is necessary to understand the relationship between fishing pressure and fish behavior for different management and habitat regimes, and for different species and places.

Other factors may also influence measures of fish wariness. Starting distance (the distance at which the observer begins the trial approach) has been shown to have a strong relationship with FID in terrestrial species (Samia et al. 2013), although this has not been incorporated into studies of flight distance of harvested fishes. In addition, factors such as fish body size have been recognized as important predictors of fish wariness related to increased reproductive value (Clark 1994). There is a need to explore additional variables that may explain variation in flight distance besides fishing pressure. More recently, minimum approach distance (MAD) which is an alternative metric of fish wariness has also been linked to fishing pressure (Lindfield et al. 2014a, Goetze et al. 2017). Measures of targeted fish wariness may have utility as predictors in SDMs and lead to methods to incorporate fish behavior in measures of fish assemblage characteristics.

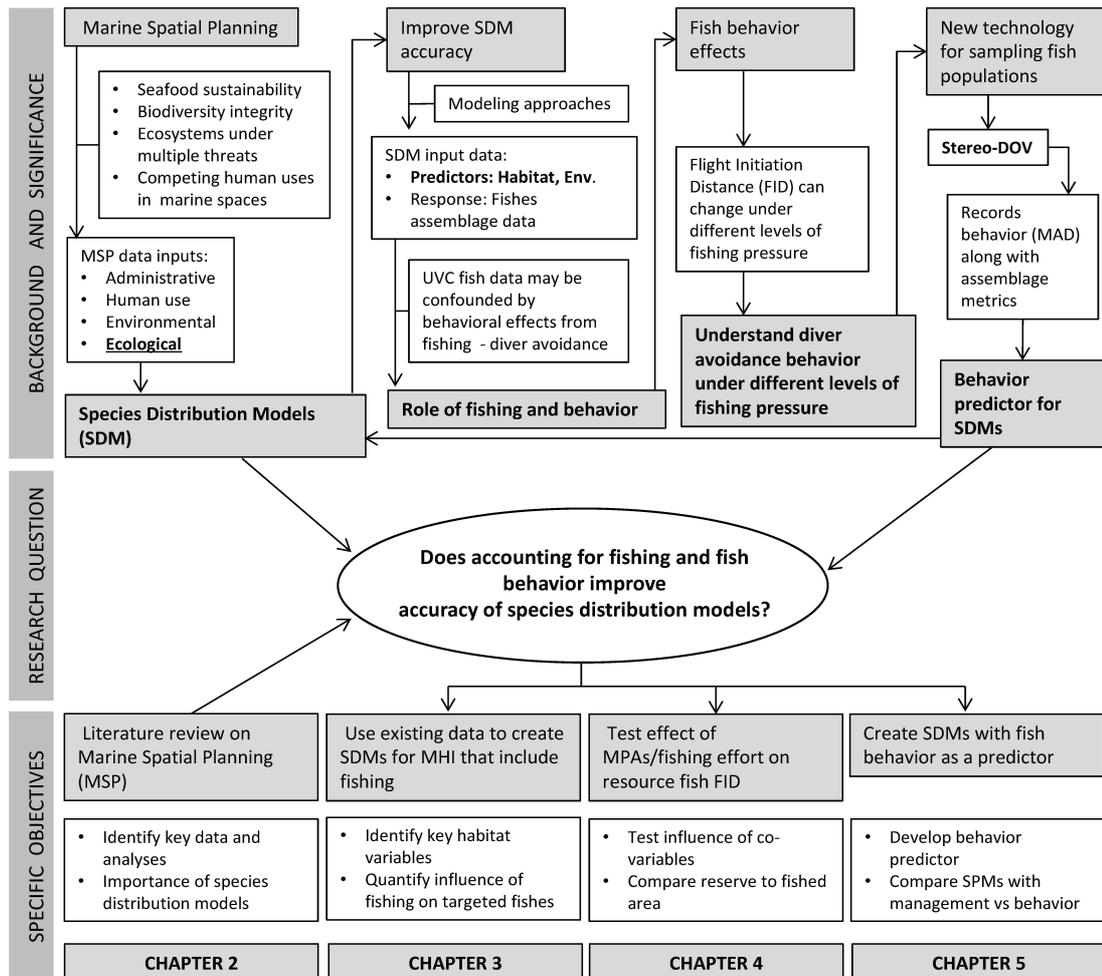
## **Research question**

The overall goal of this research project is to improve the science of spatial predictive modeling of targeted reef fishes by evaluating the role of fishing pressure and resulting behavioral shifts on explanatory power and accuracy (Figure 1.1). Additional aims are to 1) identify key habitat variables important for targeted reef fishes, 2) use spatial predictions to prioritize reef areas for management, 3) investigate the role of other variables in measuring fish wariness, 4) compare measures of fish wariness and assess the influence of fishing pressure, and 5) evaluate MAD as a proxy for fishing pressure (Figure 1.1).

## **Analytical methods**

A variety of analytical methods were employed to address the research questions. Boosted regression trees (BRTs) were chosen for species distribution modeling in

Chapters three and five based on a review of the literature. Chapter four incorporates a number of analyses; distance-based linear models (DistLM), quantile regression, OLS linear regression, one-way ANOVAs, linear mixed models, and a Chi-squared test. These statistical methods were selected based on relevance to the data and research questions as part of the analytical learning process. Chapter five builds upon the methods and results of Chapters three and four and utilizes linear mixed models and BRTs.



**Figure 1.1** Flow diagram outlining the background, significance, and structure of the thesis.

## Thesis structure

The chapters in this thesis have been written and formatted as four manuscripts. Each chapter has its own formatting style based on the formatting requirement of the targeted journals. Chapters two and three have been published, chapter four has been submitted to a journal for review and chapter five is being prepared for submission. Chapter six is a discussion of thesis outcomes. There is an appendix at the end of

each chapter with supplementary material specific to that chapter. The references for all chapters are combined into one section located at the end of the thesis.

## **Specific aims**

### Data and tools for Marine Spatial Planning (Chapter 2)

Chapter two is a literature review focused on data and tools for MSP in the United States. Following earlier efforts in Europe, the U.S. is adopting an MSP approach to address the sometimes conflicting objectives of resource development and conservation in marine spaces. Expanding anthropogenic impacts on coastal and marine areas reinforce the need to adopt a MSP approach in order to manage societal demands while preserving the marine environment and resources (Douvere 2008). I review the current literature to reveal the available technological and methodological tools that are best suited for MSP, as well as suggest areas for further research in order to better inform this process. I identify spatial ecological modeling and more specifically, species distribution modelling as a critical component of MSP and thus the primary focus of chapters three and five and the thesis as a whole.

### Species distribution models of targeted fishes based on existing data and estimated fishing pressure (Chapter 3)

Chapter three demonstrates the application of SDMs of targeted fishes using existing data and estimated fishing pressure layers. I develop a set of fishing effort and habitat layers at high resolution and employ machine learning techniques to create regional-scale SDMs and predictive maps of biomass and body length of targeted fishes. I use a large and geographically comprehensive database of reef fish surveys and of predictor variables that includes measures of two-dimensional and three-dimensional spatial patterning of the seafloor and the distribution of wave energy. The specific aims of this chapter are to quantify and map fishing effort and habitat patterns, identify and characterize key habitat variables which promote high targeted reef fish biomass and body length, model and quantify the recovery potential of targeted fish assemblages in the absence of fishing pressure, and identify areas with the highest recovery potential to prioritize for management actions.

#### Effect of fishing on targeted fish wariness (Chapter 4)

In chapter four, I investigate the effect of fishing on targeted fish diver avoidance behavior or wariness. A number of studies have identified a positive relationship between fishing pressure and FID of targeted fishes (Gotanda et al. 2009, Januchowski-Hartley et al. 2011), although it has yet to be tested in Hawai'i. Furthermore, starting distance (the distance at which the observer begins the trial approach) has not been incorporated in studies of flight distance of targeted fishes, despite having been shown to have a strong relationship with FID in terrestrial species (Samia et al. 2013). In order to validate the relationship of fishing pressure and fish wariness in Hawai'i and enable application for SDMs, I use a diver operated stereo-video system (stereo-DOV) to conduct direct measurements of FID, starting distance, and a novel measure of direct minimum approach distance (dMAD) in a marine reserve and heavily fished area. I investigate the role of starting distance and a number of other co-variables in measuring targeted fish wariness, compare FID and dMAD, and incorporate escape response data to explore how flight behavior changes under different levels of fishing pressure.

#### Species distribution models which incorporate fish behavior (Chapter 5)

Chapter five addresses the primary question of the thesis: Does incorporating fish behavior improve accuracy of species distribution models? To answer this question, I use a stereo-DOV to conduct belt transects and record minimum approach distance (MAD) of targeted fishes inside and outside of two marine reserves. Two previous studies have shown MAD to be related to fishing pressure/marine protection (Lindfield et al. 2014a, Goetze et al. 2017). I compare MAD inside the reserves to MAD in the fished areas to test the assumption that it provides a proxy for fishing pressure, then compare the accuracy of SDMs with include MAD as a predictor to SDMs that do not. The specific aims of this final data chapter are to evaluate the MAD of targeted reef fishes as a proxy for fishing pressure and determine if including MAD as a predictor in SDMs of targeted reef fish biomass improves model accuracy.

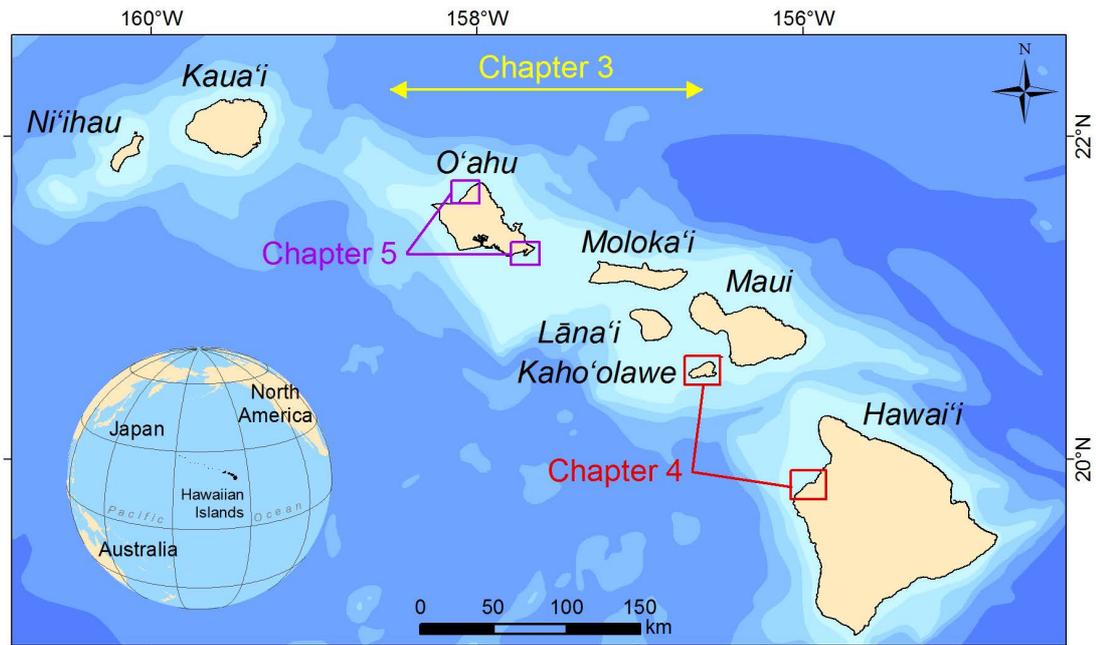
#### General discussion (Chapter 6)

In this chapter I summarize the main outcomes of each of the data chapters. I also critique my research and highlight its limitations as well as discuss the implications

for conservation and fisheries management. Finally, I present future research avenues arising from my work.

## **Study area**

All research presented in this thesis took place in the main Hawaiian Islands (MHI). The Hawaiian Islands comprise the most isolated island archipelago in the world and span a total distance of over 2,400 kilometers. The Hawaiian Archipelago is by convention split into two separate sub-regions, the MHI and the northwest Hawaiian Islands (NWHI). The NWHI are geologically older than the MHI and consist of a series of low-lying atolls and smaller islands or islets which are remote, unpopulated, and protected from fishing since 2005. In contrast, the MHI consist of eight large, geologically young, high volcanic islands. With exception of Kaho‘olawe and Ni‘ihau, they have relatively high human populations, with over 70% of the state inhabitants residing on O‘ahu and over seven million tourists visiting the islands each year (Friedlander et al. 2008). The coral reefs of the MHI, particularly those in shallow water, have been impacted by multiple stressors as a result of human influences which include habitat destruction, nutrient runoff, overfishing, and invasive species (Grigg 1994, Smith et al. 2002, Dollar and Grigg 2004, Friedlander et al. 2008). Chapter three encompasses the entire MHI, chapter four compares two sites on the islands of Hawai‘i and Kaho‘olawe, and chapter five focuses on two locations on the island of O‘ahu (Figure 1.2).



**Figure 1.2** Site map showing the spatial extents for each chapter.

# **CHAPTER 2 - Data requirements and tools to operationalize marine spatial planning in the United States**

## **Abstract**

The U.S. is adopting a Marine Spatial Planning (MSP) approach to address conflicting objectives of conservation and resource development and usage in marine spaces. At this time MSP remains primarily as a concept rather than a well-defined framework, however expanding anthropogenic impacts on coastal and marine areas reinforce the need to adopt an MSP approach to manage societal demands while preserving the marine environment. The development of theory and methods to implement MSP are on the rise across the nation to address coastal and marine environmental challenges. Critical components of marine spatial planning are (1) spatial data collection, (2) data management, (3) data analysis, and (4) decision support systems. Advances in geotechnology have increased access to spatial data enabling the development of decision support tools to organize, analyze, and inform the MSP process by projecting future scenarios. A review of the current literature reveals the available technological and methodological tools that are best suited for marine spatial planning, as well as suggests areas for further research in order to better inform this process in the U.S.

## **Introduction**

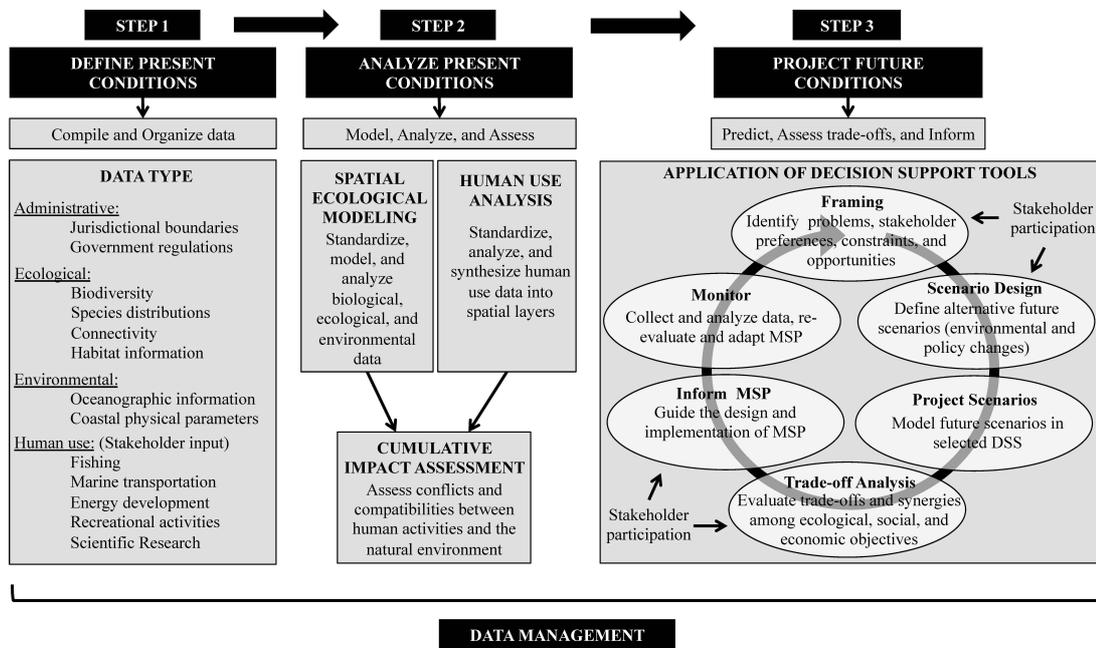
Marine spatial planning is a concept that has rapidly gained momentum. Regional MSP projects are currently underway in the United States and abroad (Allnutt et al. 2012, Collie et al. 2013). According to the United Nations Educational, Scientific, and Cultural Organization, “marine spatial planning is a public process of analyzing and allocating the spatial and temporal distribution of human activities in marine areas to achieve ecological, economic, and social objectives that are usually specified through a political process”. In June of 2009 the Obama administration created a Task Force to develop a framework for coastal and marine spatial planning. In December of that year, the U.S. Interagency Ocean Policy Task Force released an Interim Framework for Effective Coastal and Marine Spatial Planning. They

summarize Coastal and Marine Spatial planning (CMSP) as “a public policy process for society to better determine how the oceans, coasts, and great lakes are sustainably used and protected now and for future generations.” CMSP encompasses nearly identical concepts as MSP and may be more accurate given that coastal and marine space and processes are inextricably linked and should not be considered as distinct in a planning process. For the purpose of simplicity however, the more widely used term of MSP will be used in this paper.

The practice of marine spatial planning is made possible by the increasing availability of high quality spatial data (Collie et al. 2013). Various software and other tools allow for the management and analysis of this data and give practitioners the ability to create alternate management scenarios upon which planning decisions are made (Melbourne-Thomas Jessica et al. 2011, Guerry et al. 2012, Weijerman et al. 2013). It is important to remember that MSP is not a simple linear progression but rather a dynamic process with many feedback loops. Analyses of existing and future conditions will evolve as new information is identified and incorporated into the planning process (Yee et al. 2014). Understanding and utilization of the proper tools is essential for successful MSP endeavors (Halpern et al. 2012). The purpose of this review is to present and describe the kinds of tools that are available for MSP and provide examples from the current literature. Much discussion has occurred regarding MSP policy, frameworks, and best practices. As existing federal and state agencies prepare to shift their practices towards an MSP approach, a comprehensive review of data requirements and available tools is timely.

A primary goal of MSP is to support current and future uses of ocean ecosystems and maintain the availability of valuable ecosystem services for future generations (Douvere 2008). An MSP process also addresses the legal, social, and economic aspects of governance, including the designation of authority, stakeholder participation, financial support, enforcement, monitoring, and adaptive management (UNEP 2011). Key steps include (Ehler and Douvere 2009) (Figure 2.1):

1. Defining existing conditions through data collection;
2. Analyzing existing conditions using spatial ecological modeling, human dimension research methods, and cumulative impact assessments; and
3. Projecting future conditions using decision support tools.



**Figure 2.1** Key steps within the MSP process related to data and information, adapted from Ehler and Douvere (2009).

Information generated throughout this process informs the preparation of a spatial management plan (Ehler and Douvere 2009). These critical steps are facilitated by the use of data, software tools, or other well-defined spatially explicit methodologies (Papathanasiou and Kenward 2014, Shucksmith and Kelly 2014), which we will collectively refer to as “tools”. They fall into four major categories as relevant to MSP and will be the basis upon which this review is organized. The categories are: 1) data collection; 2) data management; 3) data analysis; and 4) decision support systems.

### Data collection

The collection of pertinent spatial data is critical to the MSP process (Ehler and Douvere 2009). For the purpose of this review we will make a distinction between the tools and technologies used for collecting primary data and the tools utilized by

MSP practitioners to define, manage, and analyze this information. Ehler and Douvère (2009) identify five primary sources of data relevant to MSP, which include scientific literature; expert scientific opinion or advice; government sources; local knowledge; and direct field measurement. Most spatial planning efforts rely heavily on the first three sources (Ehler and Douvère 2009). However local knowledge is increasingly recognized as an important source of information (Thornton and Scheer 2012) and methods are in development to collect and incorporate this knowledge in the planning process (St. Martin and Hall-Arber 2008). Direct-field measurements are typically outside the scope of MSP practitioners, though are sometimes necessary if significant knowledge gaps are identified. However, given that many MSP projects have a large scope, it can be difficult to obtain datasets that are consistent across the area of interest. This issue is particularly pronounced for ecological and human use data.

Current technology and methods have made available a great deal of spatially explicit data for use in MSP, especially in terms of ecological and environmental information. Palumbi et al. (2003) describe the application of some of the tools currently used in oceanography and marine ecology to inform the design of ocean reserves, which have implications for all aspects of MSP. Remote sensing data is a major source of ecological and environmental information. Human dimensions, including (spatial) information about human activities, have been less studied and often represent a knowledge gap in MSP (St. Martin and Hall-Arber 2008). With the current proliferation of MSP initiatives this “missing layer” is increasingly becoming addressed through various techniques (Collie et al. 2013).

A critical consideration for the collection of data for MSP is the issue of scale (Hughes et al. 2005, Kendall and Miller 2010, Kendall et al. 2011), similarly to natural ecosystems and social processes; MSP should address multiple scales (Hughes et al. 2005, Cumming et al. 2006). According to sustainability theory and recent experiences, MSP should adopt a hierarchical approach to define its planning units (Kay et al. 1999, Spalding et al. 2007, McCay and Jones 2011) so issues and information are considered at multiple levels and each level provides context to the lower one. This enables more coordinated management (Gilliland and Laffoley 2008) and a more effective institutional arrangement (Ostrom 1990).

In the U.S., these planning levels have been defined as: Federal, Regional (nine Regional Planning Bodies have been tasked with implementing MSP), and State (Halpern et al. 2012). In addition to the challenges of defining the scale of planning units, how to define coastal and offshore boundaries is also subject to discussion (Gilliland and Laffoley 2008). According to an ecosystem-based approach and for planning purposes, those boundaries should be established based on natural ecosystem borders and their delineation should incorporate biogeography, oceanography, connectivity, and habitat (Spalding et al. 2007, Crowder and Norse 2008, Foley et al. 2010, Toonen et al. 2011); while also reflecting socio-cultural (Olson 2010), socio-political, and administrative conditions (Crowder and Norse 2008, Gilliland and Laffoley 2008). Identifying areas where ecosystem and governance boundaries converge and diverge is also necessary to identify measures to maintain planning coherence (Gilliland and Laffoley 2008).

This transition to a more holistic and coordinated management of ocean spaces and marine resources generates two key planning challenges: (1) Maintaining coherence across the nested hierarchy in terms of linking policy goals, objectives, management tools, and actions without gaps; and (2) ensuring coordination across planning unit boundaries (Halpern et al. 2012). Identifying and agreeing on the scales of the hierarchical nested planning units and the allocation of those boundaries will be necessary to inform the scale of the data collection process (Gilliland and Laffoley 2008, Halpern et al. 2012). It is often unproductive to collect fine-scale data sets for small parts of the planning unit area, because when put together they are frequently not compatible (Ehler and Douvère 2009). Types of spatial data that are necessary for marine spatial planning include administrative, ecological, environmental, and human use (Shucksmith and Kelly 2014). Each of these main data types will be discussed in turn along with key sources and tools utilized for their collection.

### Administrative

Administrative data includes jurisdictional boundaries and government regulations. Maritime boundaries and limits delineate the extent of a nation's exclusive rights and control over the maritime areas off its coast. In the U.S., these boundaries include a 12-nautical mile territorial sea, a 24-nautical mile contiguous zone, a 200-mile

exclusive economic zone, and the continental shelf. Government regulations regarding coastal and marine areas apply to specific legislative and jurisdictional zones and can be represented as spatial footprints. The combination of jurisdictional boundaries and the regulations that apply to the areas they delineate are essential to understanding existing legislative frameworks and place the MSP process in the current management context (Sanchez et al. 2010, UNEP 2011).

The Marine Cadastre is an online spatial database provided by the NOAA Coastal Services Center (CSC) and the US Department of the Interior's Bureau of Ocean Energy Management (BOEM) (NOAA CSC a 2014). It is a useful tool for the retrieval of administrative layers needed for MSP efforts including jurisdictional boundaries, restricted areas, laws, and marine infrastructure. This tool is accessible via the internet and features an online GIS, in which a user zooms into and selects their area of interest to identify available data resources, which they then have the option to download. A GIS application is necessary to view and analyze the downloaded spatial data.

### Ecological

Ecological data necessary for MSP include biodiversity, species distributions, connectivity, and habitat information (Crowder and Norse 2008, Foley et al. 2010). In most cases, these types of data are collected by scientific and/or government organizations. Various field methods are used to generate ecological distribution and biodiversity data as part of inventory and monitoring projects (Murphy and Jenkins 2010). The scale and extent of these datasets however, are often small and patchy (Hughes et al. 2005, Knudby et al. 2013), making them unsuitable for large scale MSP endeavors (Collie et al. 2013). Seascape properties, such as benthic cover and structural complexity can also be used as proxies or surrogates of important ecosystem properties, including biodiversity, species distributions, ecological processes, and ecosystem goods and services (Mumby et al. 2008, Pittman et al. 2010, Mellin et al. 2011). This information is increasingly obtained through remote sensing methods, allowing data collection on large scales (see [Diaz et al. \(2004\)](#) for a review of methods). This has important implications for MSP as it represents large scale, low cost means of collecting information useful for spatial ecological modeling (Knudby et al. 2010a) (further discussed in section 4.1) and essential for

identifying sensitive or ecologically important areas (Boström et al. 2011, Schmiing et al. 2013).

### Environmental

The marine environment is dynamic and complex (Hughes et al. 2005), and patterns and trends exist on different time and spatial scales (Boström et al. 2011). An understanding of ocean and near shore physical parameters is important for MSP (Ehler and Douvère 2009). Oceanographic information can include mean sea level change, temperature, ocean winds, circulation, currents, and water chemistry (Mellin et al. 2010). While historically much of this data was collected directly by ships, today remote sensing from satellites records the same data on the scale of whole ocean basins. On a much smaller scale, land-based remote sensing techniques, such as Coastal Ocean Dynamics Application Radar, allow precise measurements of surface currents within a few kilometers of shore (Palumbi et al. 2003). Marine environmental and circulation patterns are important for determining different uses for marine spaces (Ban 2009). In addition, knowledge of ocean currents can allow us to infer dispersal patterns for marine larvae (Hogan et al. 2012, Anadón et al. 2013), which is particularly important for the design of marine reserves (McLeod et al. 2009). Oceanographic maps for different parameters at appropriate scales are useful for spatial ecological modeling and informing MSP (McArthur et al. 2010). These are obtainable through U.S. government agencies such as the NOAA National Ocean Service (NOS) and the NASA Physical Oceanography Distributed Data Archive Center (PO.DAAC).

### Human use

Data regarding human activities in marine spaces is instrumental for marine spatial planning (Dalton et al. 2010, Ban et al. 2013). The social seascape however, is largely undocumented and often represents a "missing layer" in decision making (St. Martin and Hall-Arber 2008). Human uses of ocean and coastal areas encompass a broad range of activities which can include: fishing (commercial and recreational), aquaculture, marine transportation and shipping, oil and gas development and exploration, sand and gravel mining, offshore renewable energy, military operations, scientific research, as well as a range of recreational activities (Katsanevakis et al.

2011). At this stage, no convenient proxy exists for the delineation of human activities in marine spaces. Some of these activities are site specific and can be mapped fairly easily, others such as fishing and recreational uses, can be variable in time and space (Cummins et al. 2008, Tallis et al. 2012). Due to the proliferation of ecosystem-based management and marine spatial planning, researchers have begun to focus on quantifying and mapping these activities (Selkoe et al. 2009, White et al. 2012), and various initiatives are underway at the federal level to collect this information through stakeholder analysis and participatory mapping.

Data collection on human uses of the marine environment occurs by identifying the relevant stakeholders in all sectors and providing them with opportunities to contribute (Gilliland and Laffoley 2008), using a ‘stakeholder analysis approach’ (refer to Pomeroy and Douvère (2008) for a more comprehensive discussion and methodology for the identification of stakeholders). Participatory mapping draws on stakeholder and local knowledge to locate fishing communities at sea (St. Martin and Hall-Arber 2008) as well as collect other MSP relevant information (Scholz et al. 2004). Questionnaire surveys and/or interviews (Cummins et al. 2008) and shipboard surveys (Dalton et al. 2010) have been used to collect information about marine recreational activities. Vessel Monitoring Systems (VMS) are used to define principle areas for fisheries (Mills et al. 2007, Fock 2008, Lee et al. 2010). Similar to natural seascapes, social and cultural seascapes are often equally complex, heterogeneous, and dynamic (St. Martin and Hall-Arber 2008, Pungetti 2012). Currently available data collection techniques often fail to adequately represent them over space and time, in spite of the recognition that marine ecosystems-based approach should include human impacts, knowledge, and needs, which are dynamic and multi-scale (St. Martin and Hall-Arber 2008).

## **Data management**

Data management is nearly as important to successful marine spatial planning as are the data themselves (Ehler and Douvère 2009). Information and data collected and created in the MSP process may be underutilized without careful management and documentation. Organizing and managing spatially explicit databases is typically the most time-consuming aspect of planning activities. Data models and other resources

exist to assist practitioners during this phase. A well-organized inventory of available data facilitates analysis and subsequent planning steps. It should be refined during the planning process to reflect modified objectives and new sources of information.

A geodatabase or spatial database is designed to store, query, and manipulate geographic information and spatial data. This is the preferred method for managing MSP data specific to a particular area or project. Guidance on the theory and practice of designing geodatabases is provided by [Arctur and Zeller \(2004\)](#). A data model such as ArcMarine provides a basic template to implement a MSP geodatabase, and facilitates the process of extracting, transforming, and loading data. Users can build upon the common marine data types provided by the model to suit the needs of their project (Wright et al. 2007).

Regional and national initiatives to manage and make accessible coastal and MSP relevant data, utilize Spatial Data Infrastructures (SDI) (Rajabifard et al. 2005, Strain et al. 2006). An SDI is a system or framework that facilitates the exchange of spatial data. Benefits of developing SDIs include improved access to data, reduced duplication of effort in collecting and maintaining data, better availability of data, and interoperability between datasets (Strain et al. 2006). Examples of SDI's for the United States include the NOAA Coastal Services Center - Digital Coast ([NOAA CSC b](#)) and Multipurpose Marine Cadastre ([NOAA CSC a](#)). These are valuable resources for obtaining MSP relevant data, which are updated on a continual basis.

## **Data analysis**

Analyzing existing and future conditions represents another critical part of the MSP process (Ehler and Douvere 2009). Various tools have been developed for this purpose, all of which fall under the realm of Geographic Information Science (GISc), which is the foundation of Geographic Information Systems (GIS). Of the four primary data types discussed previously, ecological and human use data require additional analysis to maximize their usefulness in a MSP framework. These analyses include mapping important biological and ecological areas and human uses. Second order analysis draws on ecological, human use and environmental data to

assess possible conflicts and compatibilities among human activities and the natural environment.

### Spatial ecological modeling

Spatial ecological modeling is a type of analysis that compiles and summarizes all available biological, ecological and environmental information for a study area. It involves the characterization of seascapes and biological communities to identify ecologically important areas based on species–habitat associations (Kendall et al. 2004, Pittman et al. 2007b, Mellin et al. 2009). Recent research focusing on the relationship between benthic habitat and marine life assemblages utilized benthic habitat and seascape variables as predictors for diversity and abundance of fish and corals (García-Charton and Pérez-Ruzafa 2001, Gratwicke and Speight 2005, Pittman et al. 2007b, 2009, Wedding and Friedlander 2008, Walker et al. 2009, Knudby et al. 2010a, Mellin et al. 2011).

Spatial ecologists develop methods, ranging from linear to non-linear modelling and machine learning techniques, coupled with a Geographical Information System (GIS), to geographically extrapolate in-situ data on the distribution, diversity, and abundance of species based on seascape properties (Pittman et al. 2007b, Franklin 2010, Boström et al. 2011). Modelling techniques can be rule-based or quantitative, and can include multivariate ordination, generalized linear models, generalized additive models (Guisan et al. 2002, Knudby et al. 2010a), classification and tree ensemble techniques (Pittman et al. 2009, Knudby et al. 2010b), and artificial neural networks (Guisan and Zimmermann 2000, Pittman et al. 2007b). Therefore, developing spatial ecological models begins with observations of species distributions (often summarized in terms of biodiversity, biomass, or other ecological metrics), and the identification of environmental variables thought to influence habitat suitability, and therefore the distributions of the species in question (Mellin et al. 2006, Franklin 2010, Schmiing et al. 2013).

Predictive mapping, or geographical extrapolation provides cost-effective, quantitative, and spatially explicit information at multiple scales, on patterns of species distribution and abundance (Pittman and Brown 2011). Hence, this work and its resulting map products expand upon field-based measurements that are expensive

and spatially limited and produce spatial information of the scope and scale which are necessary for MSP. Spatial ecological modeling can allow managers and ecologists to undertake large-scale ecological assessments, gain better understanding of species-habitat associations, and inform management strategies, with a focus on areas of high ecological significance (Mellin et al. 2010, Shucksmith and Kelly 2014).

### Human dimensions

Human use data that is obtained as part of a MSP process needs to be standardized into spatial layers that can then be overlaid in a GIS to identify existing or potential conflicts between human activities. These are complex processes occurring across a variety of scales and to be accurately represented should integrate a temporal as well as a spatial component. Ongoing advances in geographic information systems (GIS), geographic positioning systems (GPS), and other technologies create new alternative methods to collect data on the human ocean uses (Dalton et al. 2010). Ehler and Douvère (2009) suggest a matrix method for identifying conflicts and compatibilities among existing human activities. The Atlas Project utilized a mixed methods approach to generate GIS data layers depicting fisher behaviors, which combined spatial analytical techniques with participatory research in the form of community-based workshops and interviews (St. Martin and Hall-Arber 2008). This method leveraged GIS advances while overcoming certain GIS limitations in terms of representing social processes and values. However, barriers remain in utilizing spatial data to represent the human dimensions of the marine environment.

Incorporating social seascapes into MSP requires new methodologies and data collection efforts capable of identifying and representing places of interests and/or cultural importance, stakeholders' level of dependencies on those places and resources, and temporal and spatial use patterns at multiple scales (St. Martin and Hall-Arber 2008, Dalton et al. 2010, Scholz et al. 2011). Until these are developed, it may well be necessary for MSP practitioners to utilize the techniques presented earlier to generate appropriate data. Spatial analysis of human activities is a critical part of MSP and a proportional amount of effort should be spent on this phase.

### Cumulative impact assessments

The next step consists in integrating this information into maps of human-uses to locate conflict areas and for comparison with other spatial attributes (Selkoe et al. 2008, 2009, Halpern et al. 2012). Assessing conflicts and compatibilities between human activities and the natural environment follows, informed by previous analyses of ecological and human use data (Maxwell et al. 2013). Analysis of cumulative human impacts in the marine environment is still in early stages but developing rapidly. A framework for evaluating the interactive and cumulative impacts of human activities is provided by (Halpern et al. 2008a). In a related study, (Halpern et al. 2008b) generated a global map of human impacts on marine ecosystems. The maps produced by this research can help to inform MSP efforts, though the scale is likely too broad for most marine planning efforts. The analytical process however, could be adapted to delineate human impacts at a finer scale by improving data and methods used to quantify, combine, and evaluate impacts from multiple stressors operating at multiple scales (Halpern and Fujita 2013).

### **Decision support systems**

Another key step in the MSP process is identification and evaluation of alternative management measures (Ehler and Douvère 2009). It is in this capacity that interactive decision support systems (DSS) have played an increasingly important role (Collie et al. 2013, Papathanasiou and Kenward 2014). Decision support systems constitute a class of interactive computer-based information systems that support decision-making activities. Interactive DSS can integrate, share, and contrast many people's ideas about planning options and help managers and stakeholders to visualize tradeoffs between different management strategies (TNC Global Marine Team 2009). They can also be made available online to further facilitate user collaboration (Villa et al. 2009, Guerry et al. 2012). The primary benefits of using DSS in the MSP decision process are their ability to centralize, integrate, and manage a wide range of spatial data (Fulton et al. 2011), the speed of processing those data, simplicity, and outputs easily understood by the users. Governing bodies must still make decisions among alternative solutions, but these alternatives can be defined and understood more quickly and easily, while evaluated in terms of trade-offs and synergies (Yee et al. 2014).

There are a myriad of complex trade-offs that exist between the various ecological, economic, and social objectives within MSP (Fulton et al. 2011). DSS tools can be used to compare alternative scenarios to identify potential ‘cost-effective’ solutions (Collie et al. 2013), assess tradeoffs, and identify areas of synergy (White et al. 2012). Trade-offs are analyzed with qualitative or quantitative methods coupled with expert judgment (Collie et al. 2013). Market and non-market economic components of trade-off analysis can also be useful to inform MSP (Sanchirico and Mumby 2009, Waite et al. 2014). DSS can make explicit tradeoffs, by assessing multiple ecosystem goods and services, their benefits, and values provided to different sectors (Hicks et al. 2009, White et al. 2012). Hence, the need for DSS increases with the number of planning objectives and potential tradeoffs.

Initial development of DSS was primarily for the purpose of conservation and more specifically, for the siting of marine reserves. Since that time, examples from the literature that describe the use of DSS to produce and evaluate future conditions are on the rise. DSS can model exploited marine ecosystems to foster understanding of system dynamics; identify major processes, drivers, and responses; highlight major gaps in knowledge; and provide a mechanism to evaluate management strategies before implementing them (Fulton et al. 2011, Stelzenmüller et al. 2013). Most commonly used tools predict the impacts of alternative stressors (climate change) and management interventions (marine reserve placement) scenarios on future ecosystem states (Francis et al. 2011). Existing tools range from relatively simple mapping tools (Guerry et al. 2012) to more sophisticated modeling approaches capable of also characterizing uncertainty (Villa et al. 2009, Melbourne-Thomas et al. 2011a, Francis et al. 2011, Stelzenmüller et al. 2013) (refer to Table 2.1 for summary on pros and cons of key existing DSS). Certain tools adopt an ecosystem services approach that explore cumulative impacts and benefits and are explicit about trade-offs and win-win scenarios to inform MSP (Guerry et al. 2012). U.S. agencies at multiple levels have expressed that DSS are more useful and more likely to be adopted in a structured decision-making context when they are GIS-based, MPA related, publicly available, and participatory (Pattison et al. 2004, Bremer et al. 2015).

**Table 2.1** Summary information of described DSS software (● – Yes; ◐ – Intermediate, ○ – No).

Model	Marxan <sup>1</sup>	Ecopath (Ecosim, Ecospace) <sup>2</sup>	Marine InVEST <sup>3</sup>	CORSET <sup>4</sup>	Atlantis <sup>5</sup>
Management purpose	Protected area design and monitoring	Fisheries effects & protected area design and monitoring	Ecosystem services trade-offs & policy design	Cumulative impact assessment & protected area design	Cumulative impact assessment & policy design
Ecosystems	All	All	All	Coral reefs only	All
Users expertise	Intermediate	Advanced	Minimal	Advanced	Advanced
Spatial	●	●	●	●	● (3D)
Temporal	○	●	○	●	●
Trophic interactions	○	●	○	●	●
Larval connectivity	○	●	○	●	●
Transferable & Flexible	●	●	●	●	●
Data intensive	◐	●	○	◐	●
Computational intensive	○	●	○	◐	●
Simple outputs	●	●	●	●	●
Documentation	●	●	●	●	◐
Ease of implementation and use	●	○	●	◐	○

1 (Ball and Possingham 2000), The University of Queensland (Australia),

<http://www.uq.edu.au/marxan/>

2 (Polovina 1984), National Oceanographic and Atmospheric Administration (NOAA),

<http://www.ecopath.org>

3 (Guerry et al. 2012), The Natural Capital Project, Stanford University, World Wildlife Fund, The Nature Conservancy, and the University of Minnesota,

<http://www.naturalcapitalproject.org/InVEST.html>

4 (Melbourne-Thomas 2010), Institute for Marine and Antarctic Studies (IMAS), The University of Tasmania, <https://ebmtoolsdatabase.org/tool/corset-coral-reef-scenario-evaluation-tool>

5 (Fulton et al. 2011), Commonwealth Scientific and Industrial Research Organisation (CSIRO) Marine and Atmospheric Research, <http://atlantis.cmar.csiro.au/>

### Marxan and Ecospace

Marxan is the most widely used conservation planning software in the world (Watts et al. 2009). It uses the simulated annealing algorithm (Kirkpatrick 1984) to minimize the total cost of a reserve system, while achieving a set of conservation goals. Similar to other reserve siting tools it provides two zoning options for each

planning unit: reserve and non-reserve. An extension called Marxan with Zones generalizes this approach by providing multiple zoning options for each planning unit. Each zone then has the option of its own actions, objectives and constraints. The purpose is to minimize total cost while ensuring a variety of (user-defined) conservation and multi-use objectives (Watts et al. 2009). Marxan provides a flexible approach capable of incorporating large amounts of data and use categories. It is computationally efficient, and lends itself well to enabling stakeholder involvement in the site selection process (Ball and Possingham 2000). This tool has been used for the design of multiple-use marine parks in Europe (Smith et al. 2009), North America (Klein et al. 2009, Ban et al. 2013) Western Australia (Watts et al. 2009), Africa (Allnutt et al. 2012), and Indonesia (TNC Global Marine Team 2009). One shortcoming of the Marxan approach is its inability to deal with issues of demographic connectivity. Marxan considers that including into a reserve system a site that contains a particular feature will ensure the persistence of that feature, even though surrounding sites may not have the same protection, and may therefore be ecologically compromised (Leslie et al. 2003).

Given Marxan shortcomings, the evaluation of the ecological components and tradeoffs of alternate planning scenarios may be better provided by another freely available DSS, Ecopath (Polovina 1984, Christensen and Pauly 1992). Ecopath was designed to investigate the impacts of fisheries on ecosystems' dynamics by translating changes in biomasses and trophic interactions in time (Ecosim) (Walters et al. 1997) and space (Ecospace) (Walters et al. 1999, Pauly et al. 2000). Ecospace is an ecosystem modeling approach that has been under constant development over the last quarter of a century (Polovina 1984, Christensen and Pauly 1992, Walters et al. 1997). During this time the approach has grown to become the most widely applied ecosystem modeling technique (Christensen and Walters 2004). The most recent version of Ecospace (EwE6) incorporates a new optimization module based on a seed cell selection approach, where the spatial cell selection process is influenced by geospatial information (Christensen et al. 2009). The new sampling procedure may be complementary to the Marxan approach in that Ecospace provides a robust evaluation of ecological processes, including spatial connectivity, due to its trophic modeling foundation. These topics are not fully developed in the Marxan analysis. Christensen et al. (2009) advocate that the two approaches, with their

unique advantages and limitations, be applied in conjunction. Further research should reveal the efficacy of the updated Ecospace approach and how it compares with the already well-established Marxan with Zones.

### Marine InVEST

Marine Integrated Valuation of Ecosystem Services and Tradeoffs (InVEST) tool was developed to map, quantify, and value changes in the delivery of multiple ecosystem goods and services generated by seascapes, including renewable energy, seafood supply, aesthetic, recreation, carbon sequestration, water quality, and habitat risk (Tallis et al. 2008, Guerry et al. 2012, Arkema et al. 2013). It estimates changes across a suite of services under different management and climate change scenarios and investigates trade-offs, in both biophysical and monetary and/or non-monetary value terms (Guerry et al. 2012). The tool is a flexible and scientifically grounded set of computer-based models with a modular, tiered approach to accommodate a range of data availability and the state of system knowledge (Tallis 2011), however the platform is static. Hence, InVEST is best used in an iterative and interactive fashion with stakeholders, and was applied to the west coast of Vancouver Island, British Columbia (McKenzie et al. 2014) and Belize to inform the design of their Coastal Zone Management Plans (Ruckelshaus et al. 2015). Efforts are on the way to expand and improve marine InVEST on three primary fronts (Ruckelshaus et al. 2015): (1) Further model testing and improved communication of uncertainty; (2) develop new models and improve the functionality of existing models; and (3) expand existing options for model outputs (i.e., connecting biophysical metrics to more valuation metrics) and synthesize outputs to better examine trade-offs and win-win opportunities.

### CORSET

CORSET (Coral Reef Scenario Evaluation Tool) is a biophysical model suited to inform coral reef management decisions. It was specifically developed with 3 primary goals: (1) Build a generic modeling structure, transferable across biogeographic regions supporting coral reefs, while still capturing coral reef ecological dynamics of interest to management; (2) model reef dynamics at a range of spatial (sub-regional to regional) and temporal (years to decades) scales; and (3) generate outputs understandable to non-experts (Melbourne-Thomas et al. 2011a,

2011b). CORSET couples larval connectivity to coral reef ecological dynamic processes (functional and trophic group interactions) and links observed conditions to terrestrial or marine-based drivers, such as sedimentation and fishing activities at the regional scale (~1000 km) in a spatially explicit manner and over simulated future projections (Melbourne-Thomas et al. 2011a, 2011b). Although only applied in the Quintana Roo region (Mexico), CORSET can be coupled with a spatially explicit socioeconomic agent-based model (SimReef) (Perez et al. 2009) structured around fisheries, urbanization, and tourism drivers (Melbourne-Thomas et al. 2011c). Stochastic simulation models are of particular value in decision support, because they facilitate the projection of potential future outcomes under alternative resource management scenarios (Melbourne-Thomas et al. 2011c, 2011a). However, CORSET is best applied at a regional scale due to the spatial and ecological resolution of the processes being modeled.

#### Atlantis

Atlantis is a dynamic modelling framework that links a biophysical system to the users of the system (industry), and socioeconomic drivers of human use and behavior (Fulton et al. 2011). It is a full ecosystem simulation model that incorporates climate, oceanography, nutrient availability, food web interactions, and other ecological factors in a spatially explicit way. Atlantis is best used as a strategic tool (long-term decision-making) to explore ecosystem dynamics (including marine habitat, nutrients, and biodiversity) and test different fisheries management approaches in terms of tradeoffs between and among species, fishing gear types, management goals, and the direct and indirect effects of different management policies (Fulton et al. 2011, Kaplan et al. 2012). The Atlantis DSS has been used in these roles for a decade, primarily in Australia and North America (Link et al. 2010, Kaplan et al. 2012), and is regularly being modified and applied to new questions (e.g. it is being coupled to climate, biophysical and economic models to help consider climate change impacts, monitoring schemes and multiple use management) (Fulton et al. 2011). Like many tools, Atlantis has weaknesses, including poor ease of use, patchy documentation, large data demands, difficult implementation, and long run and calibration times (Fulton et al. 2011).

#### Other software

Some marine spatial plans are using GIS-based mapping tools (e.g. SITES, Marine Atlas, Habitat Suitability Modeling) (Airamé et al. 2003, Pattison et al. 2004, Collie et al. 2013). For instance, (Airamé et al. 2003) used a computer-based siting tool (DSS) called SITES to generate potential options for the no-take reserve network in the California Channel Islands. The computer used previously compiled geographic information to create a network of randomly placed reserves and then improved it slightly, searching progressively for layouts that were closer to the specified criteria. The outputs were used as a starting point for discussions about where to implement individual reserves, and what trade-offs would be necessary in different potential network configurations (Pattison et al. 2004).

Other plans are using some form of quantitative index and/or decision tool, such as MarZone, MarineMap, or OceanMap (Pattison et al. 2004). For instance, OceanMap was specifically designed to allow for a participatory approach that incorporate local knowledge, collect spatially explicit-socioeconomic data, and integrate ecological, economic, and sociocultural data in the context of marine conservation planning (Pattison et al. 2004, Scholz et al. 2004). This tool was applied to inform the MSP planning process along the west coast of the U.S. (Scholz et al. 2011).

Other examples demonstrate the effectiveness of combining siting tools and GIS data in designing marine reserves in the Gulf of Mexico (Beck and Odaya 2001) and the Florida Keys (Leslie et al. 2003). These studies make it clear that there are multiple approaches to implementing marine reserves in a particular area. [Sarkar et al. \(2006\)](#) provide a review of conservation planning tools that can help inform potential users about their theory and utility. Initially, almost all of the theory for spatial conservation planning was focused on identifying no-take reserves. This trend translated into tool development such that most available DSS were designed to identify one type of zone (ie. marine reserves). Marine spatial planning seeks to develop multi-use zoning schemes for which a broad range of objectives is represented. Therefore, optimization tools or frameworks that allow for multiple zones have become increasingly available in recent years.

### Limitations of decision support systems

MSP needs to recognize and account for uncertainty and risk, arising from data gaps, scale mismatches, or lack of knowledge, given that DSS do not systematically include them (Fulton 2010). Conversely, the amount of data, technical challenges, and cost of tool implementation also increase (TNC Global Marine Team 2009). Most tools do not handle a wide array of sectors or ecosystem goods and services, lack mechanisms for modeling changes in the ecosystems and services delivery with changes in management or environmental stressors, and/or are not practical for MSP given the tendency to solely focus on fisheries management (Guerry et al. 2012). Tools should be instantiated to resolve real-life spatiotemporal dynamics (Melbourne-Thomas et al. 2011a). Remaining key challenges for implementing effective environmental DSS are now more socio-economic (data collection and data analyses) than technical, requiring also a more local- and place based-orientated attitude of researchers and government (Papathanasiou and Kenward 2014).

### **Conclusions**

Technological advances have enabled us to gather and share information about our environment and how it behaves. We use geographic information science to manage and explore this wealth of spatial data. MSP is a marriage of geographic information science, environmental management, and land use planning. It is a complex, data intensive process. Spatial analysis lies at the heart of MSP and is surpassed in importance only by stakeholder participation. To a large extent, the success of a MSP effort depends on the abundance and quality of its data, and the capacity for its analysis. Various tools can enable and facilitate different aspects of MSP. It is in the interest of all involved to make the best use of the technology available.

It is important to consider the scope and scale of the data collected for MSP which should, to the extent possible, have a consistent source, match the scope of the planning area and the scale of the planning units, and align with planning boundaries. Geographic information science has provided the tools needed to manage and analyze data for MSP. Practitioners should make full use of this capability and utilize geodatabases to maintain integrity of their spatial data in a consistent and accurate manner. Analytical methods such as spatial ecological modeling and cumulative

impact assessments allow for summarization and integration of a wide range of datasets for major planning components, enabling more efficient comparisons between them and providing a holistic view of the current state of ocean spaces. Interactive decision support systems can create alternate spatial management scenarios, along with a clear evaluation of the tradeoffs associated with each, making them available for the consideration of stakeholders. Proper use of these tools can greatly streamline the MSP process and support its iterative nature.

MSP represents a new global paradigm in spatial management. Though its roots lie in the familiar realm of land use planning, it presents many unique challenges and opportunities. As the practice of MSP continues, there will be continual insight into its organization, tools, and best practices. Even if MSP is a collaborative process and the organization and cooperation of stakeholders is paramount, the analytical component of the process is nearly as critical for its success. The stakes are high as we increasingly look to the development of ocean and coastal resources to support global consumption. Successful management of our marine spaces is less of a choice than a necessity.

## **CHAPTER 3 – Seascape models reveal places to focus coastal fisheries management**

### **Abstract**

To design effective marine reserves and support fisheries, more information on fishing patterns and impacts for targeted species is needed, as well as better understanding of their key habitats. However, fishing impacts vary geographically and are difficult to disentangle from other factors that influence targeted fish distributions. We developed a set of fishing effort and habitat layers at high resolution and employed machine learning techniques to create regional-scale SDMs (seascape models) and predictive maps of biomass and body length of targeted reef fishes for the main Hawaiian Islands. Spatial patterns of fishing effort were shown to be highly variable and seascape models indicated a low threshold beyond which targeted fish assemblages were severely impacted. Topographic complexity, exposure, depth, and wave power were identified as key habitat variables which influenced targeted fish distributions and defined productive habitats for reef fisheries. High targeted reef fish biomass and body length were found in areas not easily accessed by humans, while model predictions when fishing effort was set to zero showed these high values to be more widely dispersed among suitable habitats. By comparing current targeted fish distributions with those predicted when fishing effort was removed, areas with high recovery potential on each island were revealed, with average biomass recovery of 517% and mean body length increases of 59% on Oahu, the most heavily fished island. Spatial protection of these areas would aid recovery of nearshore coral reef fisheries.

### **Introduction**

Coastal marine ecosystems are in decline worldwide due to multiple interacting stressors operating from global to local scales (Lotze et al. 2006, Norström et al. 2016). Fishing is one of the most direct of these stressors and removes fish biomass, distorts trophic and size structure, and alters community composition resulting in the loss of ecological functions and ecosystem services (Jackson et al. 2001). These demonstrated impacts point to a need for better management of fisheries worldwide, including the implementation of additional marine reserves to recover fish biomass

and restore key ecosystem functions (Edgar et al. 2014). Numerous studies have documented the benefits of spatial protection on exploited fish assemblages, such as increased biodiversity and resilience (Mellin et al. 2016), resistance to invasive species (Giakoumi and Pey 2017), and fisheries enhancement (Weigel et al. 2014). Increases in biomass and size of targeted fish species in marine reserves have been particularly well documented (Lester et al. 2009). Current research includes a focus on maximizing reserve benefits by incorporating connectivity, the demographic linking of local populations through dispersal of individuals as eggs, larvae, juveniles or adults, and habitat quality as explicit considerations in marine reserve design (Almany et al. 2009, Green et al. 2015). As larval export from marine reserves has been shown to replenish stocks in fished areas (Harrison et al. 2012), reserves that support healthy spawning populations which act as larval sources may be key for fisheries recovery. Thus, identifying areas with habitats that have the potential to support reproductive populations of targeted fishes is critical to the design of effective place-based fisheries restoration strategies.

Rarely, however, do studies of coastal marine ecosystems integrate local context and stressors in estimates of recovery potential. Specifically, fishing patterns must be considered to inform effective placement of marine reserves intended to enhance fisheries. Fishing effects vary geographically and are difficult to disentangle from other factors that influence targeted fish distributions, creating a spatially complex challenge for understanding patterns of fishing impacts on these assemblages (Taylor et al. 2015, Nash and Graham 2016). Spatial ecological modeling techniques, where predicted variable distributions are mapped across geographical space, have proven useful to examine spatial trends and fill gaps in coverage of empirical datasets (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009). Models can be calibrated using ecological field survey data to establish relationships between fish species and/or assemblage characteristics and remotely sensed habitat and environmental variables. These calibrated models, referred to here as seascape models, can then be used to make spatial predictions of fish, or fishery indicators, across the area of interest (Pittman and Knudby 2014). However, these approaches have yet to incorporate spatially explicit estimates of fishing pressure and are rarely applied to prioritize areas to inform fisheries replenishment strategies in coastal marine ecosystems.

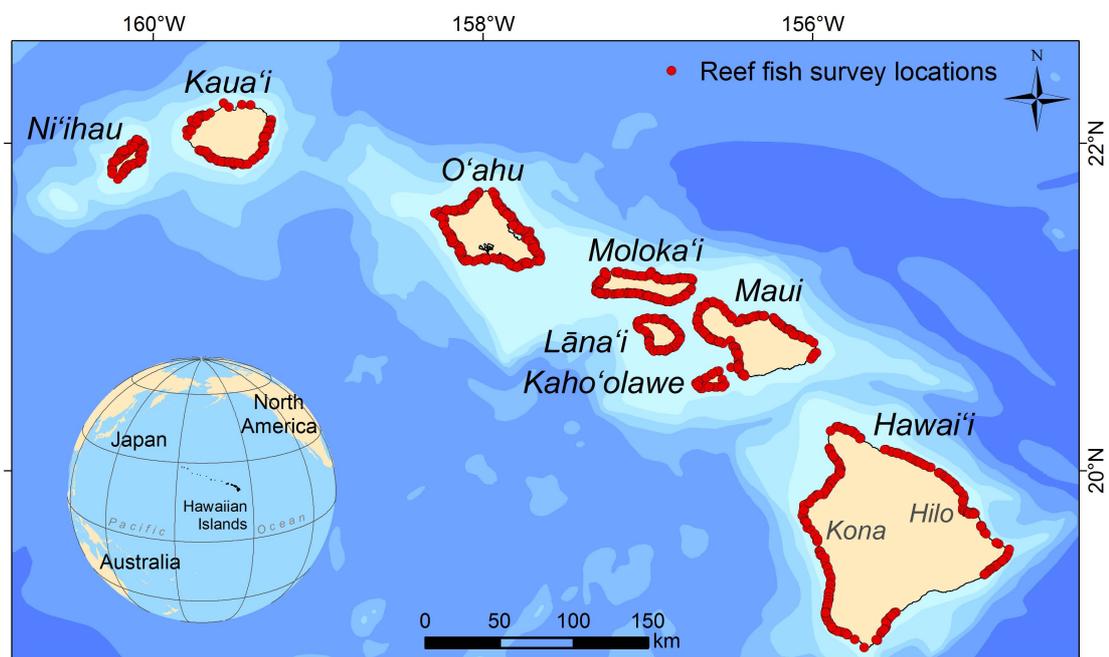
Seascape variables such as seafloor topography, benthic cover, and wave exposure, at varying spatial scales, have been shown to be important predictors of fish assemblages (Friedlander et al. 2003, Bouchet et al. 2015, Galaiduk et al. 2017). Impacts from fishing have been inferred by comparing fish populations in populated versus remote areas (Friedlander et al. 2018) and by using proxies such as local human population density and distance to markets (Williams et al. 2008, Cinner et al. 2013). Fishing effects have also been investigated through studies of fish populations along gradients of protection ranging from gear restrictions (Campbell et al. 2018), to rotational closures (Cohen and Foale 2013), to marine protected areas (MPAs) including full no-take marine reserves (Sciberras et al. 2015). Due to increased availability and coverage of empirical and remotely sensed datasets, there is opportunity to build on these studies by using seascape models to better understand fish habitat relationships in the context of fishing impacts and make realistic and spatially explicit estimates of recovery potential.

We address these knowledge and capacity gaps by developing a set of fishing effort map layers at high resolution and employing machine-learning techniques to create regional-scale seascape models and predictive maps of targeted reef fish biomass and body length for the Main Hawaiian Islands (MHI). We use a large and geographically comprehensive database of reef fish surveys and of predictor variables that includes measures of two-dimensional and three-dimensional spatial patterning of the seafloor and the distribution of wave energy. Study objectives were to 1) quantify and map fishing effort and habitat patterns around the MHI, 2) identify and characterize key habitat variables which promote high targeted fish biomass and body length, 3) model and quantify the recovery potential of targeted fish assemblages in the absence of fishing pressure (in terms of mean biomass and body length), and 4) identify areas with the highest recovery potential to prioritize for management actions.

## Methods

### Study area

The Hawaiian Islands are located near the center of the Pacific Ocean and are the most isolated archipelago in the world. The MHI consist of high volcanic mountain peaks, with steep topographic relief to the coastline and fringing reefs accreting on the submerged slopes. There are eight islands that comprise the MHI, six of which were evaluated in this study (from north to south): Kaua'i, Ni'ihau, O'ahu, Moloka'i, Maui, and Hawai'i islands (Figure 3.1). The islands of Lāna'i and Kaho'olawe were not included due to the lack of high-resolution bathymetry data.



**Figure 3.1** Main Hawaiian Islands study domain with reef fish survey locations used for modeling.

### Reef fish survey data

A spatially comprehensive dataset of reef fish surveys of the MHI conducted between 2010 and 2016 was contributed by the Pacific Islands Fisheries Science Center's Coral Reef Ecosystem Program (Coral Reef Ecosystem Program; Pacific Islands Fisheries Science Center 2016). Fish surveys utilized a paired stationary point count (SPC) protocol and were conducted on hard bottom habitat, stratified by reef zone and depth (McCoy et al. 2017). A total of 1,184 independent survey locations across the MHI were used for modeling (Figure 3.1). Spatial predictions were generated on a 60x60 m resolution grid to account for the dimensions of the

survey method and the positional uncertainty of the global positioning systems used to navigate to survey locations.

Targeted species of the MHI nearshore fishery were defined as coral reef fishes having  $\geq 450$  kg of annual recreational or commercial harvest for the past 10 years (2000-2010), or otherwise recognized as important for recreational, subsistence, or cultural fishing (<http://dlnr.hawaii.gov/dar/fishing/hmrfs/>). Biomass was estimated using the allometric length-weight conversion:  $W = aTL^b$ , where parameters  $a$  and  $b$  are species-specific fitting parameters, TL is total length (cm), and W is weight (g). Parameters were obtained from a comprehensive assessment of Hawai'i length-weight fitting parameters (M. Donovan, unpublished data) and FishBase (Froese and Pauly 2017). Cryptic and soft-bottom species were excluded due to low sampling effectiveness. Planktivores were excluded due to patchy distributions and weak benthic-habitat relationships, as were pelagic species (Supplement 3.1). Targeted species biomass was calculated as the sum biomass of modeled species at each survey location. Targeted species body length was calculated as the average recorded body length of modeled species at each survey location.

#### Predictor data

##### *Fishing effort*

We modeled and mapped spatial patterns of fishing effort based on non-commercial island-scale effort estimates (McCoy 2015), following the methods of Lecky (2016). This previous work mapped spatial patterns of catch, though did not incorporate measures of human population in the distribution of shore-based fishing estimates. We did not consider nearshore commercial fishing because it only represents a small fraction of total estimated effort and data quality is questionable (McCoy 2015). Furthermore, commercial fishing data are recorded for large reporting blocks that would obscure fine-scale spatial patterns of fishing effort. Shore and boat fishing were modeled separately by major gear type (line, net, and spear), which were assumed to have different spatial footprints. Despite different magnitudes, patterns of total shore effort hours between gear types were very similar among islands (Supplement 3.3) and both shore and boat fishing effort layers were highly correlated among gear types ( $> 0.8$  Pearson  $r$ ). Because spear fishing had the largest spatial footprint, highest catch per unit effort, and targets the greatest variety of

species, it was used as a proxy of total effort for both shore and boat fishing, respectively.

We used average annual fishing effort (hrs/yr) for reef fish by island from ten years of recreational fishery data (2004-2013) compiled by McCoy (2015) and distributed these values into the nearshore marine area based on weighting factors related to accessibility to fishers. Fishing effort showed a declining trend over time for all islands with the exception of Lānaʻi (McCoy 2015), so values may be overestimates of current fishing effort levels based on available data. Marine managed areas where fishing is prohibited were set to zero. For shore fishing, proximity and type of roads along with shoreline steepness were used as proxies for accessibility, and values were weighted by human population within 30 km. To model spear fishing, a logistic decay function was used so effort decreased with depth to a maximum distance of 2 km from shore. The parameters of the function were set based on discussions with fishing experts in Hawaiʻi and assume the vast majority of spearfishing effort is shallower than 20 m and there is no effort beyond 40 m (Lecky 2016). For boat fishing, accessibility measures were based on distance to boat launch/harbor weighted by human population within 30 km. There was no recreational fishery data available for Niʻihau (pop. 170) and while subsistence fishing does occur, shore fishing effort was assumed to be zero. To ground-truth the fishing effort maps, estimated shore-based spear fishing effort values were compared to total shore fishing effort values from 12 independent fishing (creel) survey locations across the MHI. Total shore fishing effort values were obtained from Delaney et al. (2007) and compared to derived spear fishing effort maps based on the sum of pixel values within polygons matching the description of each survey area. Empirical boat-based fishing effort estimates were not available for comparison.

#### *Habitat variables*

A set of 62 gridded environmental datasets at 60x60 m resolution was generated for each island as potential predictor variables used to model reef fish assemblage metrics (Stamoulis et al. 2016). Selection of predictors was based on an extensive literature review and input from experts in Hawaiian reef ecology (Delevaux 2017). There were four types of predictor variables: seafloor topography, benthic habitat composition, geographic, and wave energy. Oceanographic variables including sea

surface temperature, chlorophyll a, and irradiance were included in preliminary models and had low explanatory power. These variables were excluded from further analysis.

Seafloor topography variables were included to account for variation in reef fish distributions due to direct and indirect effects of depth and seafloor structure. A gridded synthesis of multibeam sonar and Light Detection and Ranging (LiDAR) bathymetry at 5 m resolution was used as the depth variable and to derive the suite of seafloor topography metrics. For example, the morphometric, slope-of-the-slope (a second derivative of bathymetry), measures the maximum rate of change in slope between cells within the specified analytical neighborhood. Slope-of-the-slope is a measure of surface topographic complexity, sometimes called terrain roughness, and has been shown to be positively correlated with finer scale *in situ* measures of rugosity such as chain-tape measurements (Pittman et al. 2009, Pittman and Brown 2011). The modeled area was limited by gaps in the LiDAR bathymetry data. For this reason, the islands of Lānaʻi and Kahoʻolawe were not modeled, as well as much of the nearshore area around Niʻihau, and large portions of the north-east and south-east coasts of Hawaiʻi island.

Benthic habitat composition variables from existing habitat maps (Battista et al. 2007) were included to account for variation in reef fish assemblages arising from the direct and indirect effects of the spatial configuration of benthic habitats. Geographic variables were used to account for variation in reef fish assemblages arising from spatial location. Wave energy variables were included to account for variation in reef fish assemblages arising from the direct and indirect effects of ocean wave dynamics.

A pairwise correlation analysis was performed on the full set of predictors for the whole study area (MHI). Highly correlated predictors (Spearman  $|\rho| > 0.7$ ) were identified, and those highly correlated with two or more other predictors were removed. In cases where only two predictors were highly correlated, those with greater ecological importance (based on expert opinion and scientific literature) were retained. After the correlation analysis, 25 out of 62 seascape predictors were retained for model development (Table 3.1, Supplement 3.2).

**Table 3.1** Final predictor datasets used in model development. Number of individual datasets of each type indicated in parenthesis. A pairwise correlation analysis was performed on the full set of predictors for the whole study area (MHI). Highly correlated predictors (Spearman  $|\rho| > 0.7$ ) were identified, and those highly correlated with two or more other predictors were removed. See Supplement 3.2 for more details.

Predictor dataset types	Datasets	Description
Fishing (2)	Boat fishing spear, Shore fishing spear	Boat and shore based fishing effort represented by spearing effort.
Seafloor topography (12)	Depth, Slope, Slope of slope, Aspect, Planar and profile curvature, BPI	Seafloor topography metrics derived from bathymetry including depth, slope, structural complexity, exposure, curvature and bathymetric position index (BPI). Slope, slope of slope, and BPI were calculated at two scales.
Benthic habitat composition (7)	Percent cover of CCA, Macroalgae, Turf, and Soft bottom, Proximity index, Shannon's diversity index	Percent benthic cover of major cover types. Seascape fragmentation/patch isolation. Habitat diversity.
Geographic (3)	Latitude, Longitude, Distance to shore	Geographic location and distance from shore.
Wave energy (1)	Wave Power	Wave height * wave period.

### Seascape models

Boosted regression trees (BRT) were used to estimate relationships between targeted fish assemblage metrics (biomass and length) and the predictor datasets (De'ath 2007, Elith et al. 2008). These modeled relationships were then used to create spatial predictions of targeted fish biomass and body length. Each metric was modeled independently at the archipelago scale. To make predictions with fishing pressure removed, fishing predictors were set to zero. Statistical models and spatial predictions were generated in R (R Core Team 2014) using the *dismo* (Hijmans et al. 2014) and *raster* (Hijmans 2014) packages. BRT is effective at modeling nonlinearities, discontinuities (threshold effects), and interactions between variables (Breiman 1996, 2001, De'ath and Fabricius 2000).

BRT can accommodate many types of response variables. Since the targeted fish assemblage metrics were continuous variables, they were modeled using a Gaussian (normal) distribution, and appropriate data transformations were applied to improve normality. Targeted fish biomass was fourth root transformed and targeted fish body

length was square root transformed. Prior to model fitting, reef fish survey data were randomly divided into model training (70%) and test (30%) subsets. The test data set was withheld from model fitting and used only to evaluate predictive performance (map accuracy). Although boosting makes BRT models less prone to overfitting (Friedman 2002, Elith et al. 2008), predictive performance was evaluated using the test data to measure how well the model generalized to new data.

Model fitting and selection was accomplished following the procedures detailed in Elith et al. (2008). To increase parsimony, selected models were then simplified to remove less informative predictor variables. This was accomplished by dropping the least contributing predictor, re-fitting the model, and computing the change in predictive deviance relative to the initial model (Elith et al. 2008). The predictive deviance indicates the amount of variation in the response variable not explained by the model. This process was repeated, and the predictive deviance was plotted over the full range of predictors. The final number of predictors was selected at the inflection point in the predictive deviance curve, where change in predictive deviance increased relative to previous values. In general, this resulted in removal of predictors which explained  $< 5\%$  of the variation in the response variable.

Bootstrapping was used to create spatially explicit predictions and calculate prediction precision. The model training dataset was repeatedly sampled with replacement to create 20 bootstrap samples. Using the optimal parameter value combination and simplified set of predictor variables, a BRT model was fit to each bootstrap sample and used to make predictions to a spatially explicit gridded map using the values of the predictor variables at each grid cell. This resulted in a total of 20 spatial prediction grids that were used to calculate the mean and coefficient of variation (CV) in each grid cell (Leathwick et al. 2006), where low CV values indicate high precision. Prediction means and CVs were plotted against each other to visualize the relationship between the magnitude and precision of predictions. The mean of the bootstrapped predictions was used for interpretation and further analysis.

Model performance was evaluated using the cross-validation percent deviance explained (PDE) and test PDE. The cross-validation PDE is the 10-fold cross-validation estimate of the percent deviance explained for the best model (as

described above). Similarly, the test PDE was determined by calculating the percent deviance explained by the model when evaluated using the model test dataset. Both metrics indicate overall model fit, but the test PDE also provides a measure of model performance when predicting data that were independent of model fitting. To better understand the relationship between measured and predicted values, average measured values by island were compared with predicted values under current fishing levels and with fishing pressure removed. Finally, the relative importance of predictor variables for each model was evaluated and partial dependence plots were generated for each predictor variable to interpret their individual effects on the response variables (De'ath 2007, Elith et al. 2008).

#### Recovery potential in the absence of fishing

Final BRT models were used to generate gridded predictions of targeted fish biomass and body length across the MHI study area (60x60 m resolution) under current fishing levels and with fishing pressure removed. Values from these layers were used to create distribution curves of predicted biomass and body length under each fishing scenario for each island. Differences were assessed visually and tested using a two-sample Kolmogorov-Smirnov test. Overall change in spatial patterns of high predicted targeted fish biomass and body length were assessed using maps of predicted values. Finally, means and percent change between predicted values across all modeled habitats for present conditions and with fishing effort set to zero were calculated by island to estimate recovery potential at the island scale.

#### Spatial prioritization for management

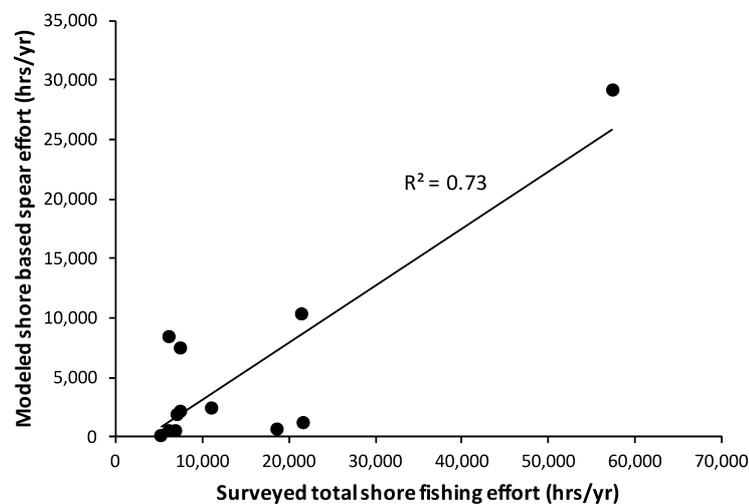
To identify places that could be prioritized for management actions which would support fisheries restoration, we evaluated spatial differences between predictions of targeted fish biomass and body length under current fishing levels and predictions with fishing effort set to zero. We assumed that areas with the greatest differences have the highest potential for fisheries replenishment if fishing pressure were limited or removed through management actions. To identify areas where predictions differed significantly between models, we applied the methodology of Januchowski et al. (2010) using the SigDiff function in the R package SDMTools (VanDerWal et al. 2014). We computed the significance of the pairwise differences (for each grid cell) for the response variables (biomass and length) relative to the mean and

variance of all differences for each island. The resulting probability values represent the area under the curve of a Gaussian distribution defined by the mean and variance across all cells for that island. The spatial grids representing the individual significance values were reclassified to indicate cells where predictions with fishing pressure removed were significantly higher than present predictions ( $p < 0.10$ ). Mean absolute difference and mean percent change relative to modeled values under current fishing pressure were calculated for cells showing significant increase by island. Finally, the spatial grids representing regions of significant increase for biomass and body length were combined into a single map for interpretation.

## Results

### Fishing and habitat patterns

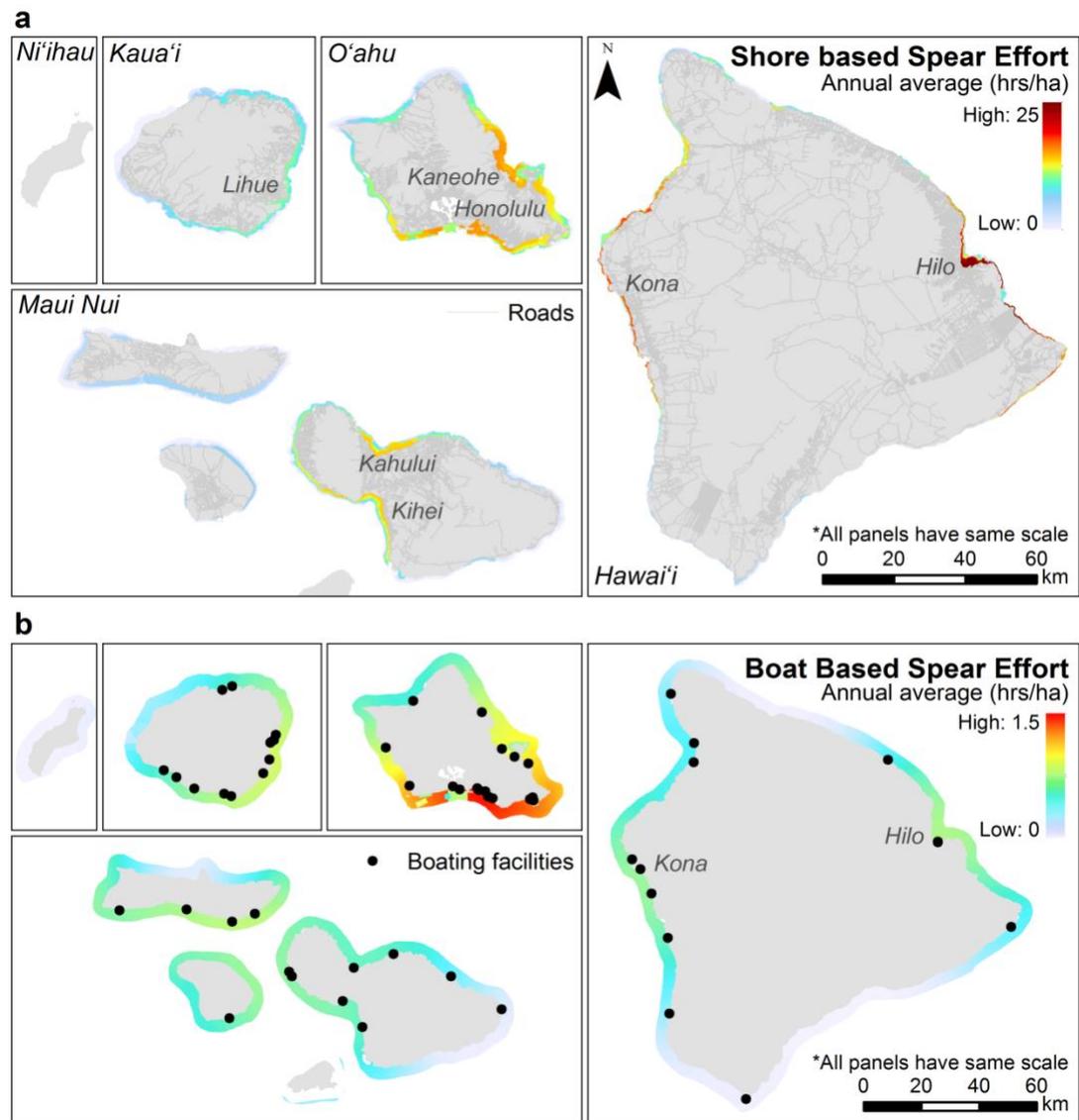
Modeled shore spearing effort values under-estimated total shore effort from creel surveys by a factor of two. However, there was a strong positive relationship ( $r^2=0.7$ ) across all sites indicating that this measure of shore spearing effort provides a reliable proxy for overall shore fishing effort (Figure 3.2).



**Figure 3.2** Comparison of modeled shore fishing effort with empirical fishing survey values from 12 sites across the MHI (Hawai‘i - 4, Maui - 2, O‘ahu - 5, Kaua‘i - 1). Total fishing effort values were obtained from Delaney et al. (2017) and compared to derived spear fishing effort maps based on the sum of pixel values within polygons matching the description of the survey area in each report. The equation of the fitted line is  $y = 0.48x - 1660$ .

The highest intensity of shore fishing effort was estimated to be near the highly populated areas of Hawai‘i Island near Hilo and Kona, followed by the south and

southeast shores of O‘ahu and near the populated areas around Kahalui and Kihei on Maui (Figure 3.3a). Boat fishing effort for reef fish was generally much lower than shore fishing effort (Figure 3.3b). The highest values for boat fishing effort were found offshore of south O‘ahu. Moderate boat fishing effort was found along the southwest shore of Kaua‘i, south Moloka‘i, northwest Maui, and near Kona and Hilo on Hawai‘i Island (Figure 3.3b).



**Figure 3.3** Shore fishing effort around the MHI as represented by a) shore based spear effort (hrs/ha). Boat fishing effort around the MHI as represented by b) boat based spear effort (hrs/ha). Maui Nui encompasses the islands of Maui, Moloka‘i, and Lāna‘i.

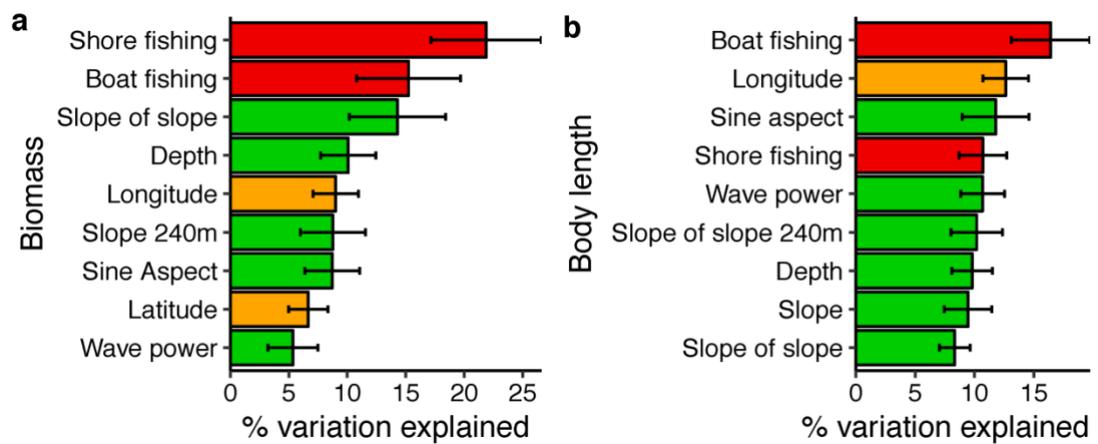
While a more complete description of marine habitat patterns in the MHI is outside the scope of this study, here we focus on several key variables shown to be important determinants of targeted fish biomass and body length. Seafloor topographic

complexity (slope of slope) was highly variable within islands. Generally, areas with low values (indicating flat bottom) encompassed the greatest area, while high values (indicating complex structure) were few and widely dispersed. Islands with more shallow water habitat such as O‘ahu tended to have more flat bottom. Sine aspect (sine circular mean aspect, Supplement 3.2) represents the E/W exposure of benthic habitats. The highest values were located on east-facing shores and the lowest values on west-facing shores. Eastern exposures are most exposed to the predominate trade winds and associated short-period swells. Wave power was highest on the north shores of all islands, with the exception of Hawai‘i Island, and generally decreased among islands from north to south. Depth increased with distance from shore on all islands, and the largest shallow water areas were found on O‘ahu and the south shore of Moloka‘i.

#### Seascape models

The final BRT model for targeted fish biomass had nine predictors. Cross-validation PDE was 37.5%, and test PDE was 35.3%. The final BRT model for targeted fish body length had nine predictors, a cross-validation PDE of 21.2%, and a test PDE of 21.4%. Based on these metrics, the biomass model fit better than the length model, and had higher predictive accuracy. Plots of prediction means vs CVs showed that higher predicted values generally had higher precision ( $CV < 0.5$  – Supplement 3.4). When predictions for biomass and length under present fishing levels were compared to fish survey data at the island level, BRT predictions tended to underestimate means of field measured values within one standard deviation (Supplement 3.5). This effect increased with the magnitude of the measured values. However, the BRT predicted values well represented the relative differences between islands (Supplement 3.5).

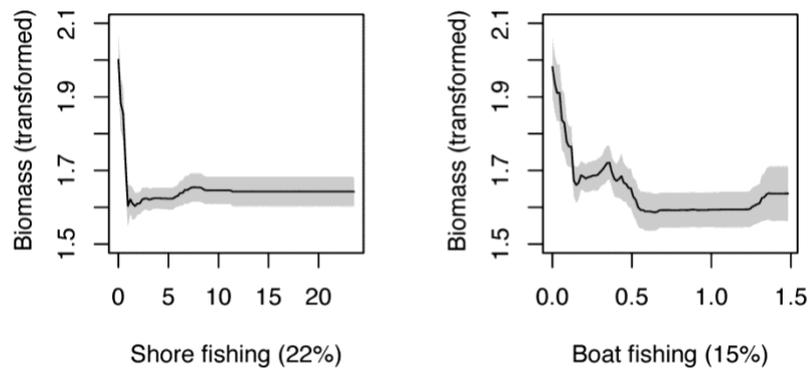
Modeled biomass was largely driven by shore fishing, while length responded primarily to boat fishing (Figure 3.4). In terms of habitat, biomass was primarily driven by topographic complexity (slope of slope) and length was most associated with exposure (sine aspect). Depth and wave power were other key habitat variables that influenced both targeted fish biomass and body length (Figure 3.4). These habitat variables all had positive relationships with the assemblage indicators, whereas the fishing variables had negative relationships (Figure 3.4).



**Figure 3.4** Final predictors for MHI models based on BRT model results for a) biomass and b) body length. Relative percent variation explained is shown on the x-axis and the color represents the directionality of the relationship (red: negative, green: positive, orange: non-directional).

#### Effects of fishing and habitat on fish biomass and body length

Targeted fish biomass and body length had similar negative relationships with fishing predictors. Both declined rapidly from 0-2 hrs/ha/yr of shore (spear) fishing effort and 0-0.2 hrs/ha/yr of boat (spear) fishing effort, then were relatively flat across a wide range of increasing effort values (Figure 3.5, Supplement 3.7). Areas of shore fishing effort < 2 hrs/ha/yr include the less populated islands, Ni‘ihau, Moloka‘i, and Lāna‘i, as well as remote and difficult to access areas of the more populated islands such as west Kaua‘i, east Maui, and south Hawai‘i Island (Figure 3.3a). Areas of low boat fishing effort (< 0.2 hrs/ha/yr) included Ni‘ihau, northwest Kaua‘i, north O‘ahu, north Moloka‘i, west Lāna‘i, and north and south Hawai‘i (Figure 3.3b).



**Figure 3.5** Partial dependence plots of fishing predictors for the targeted reef fish biomass model. Y-axis is transformed biomass (4<sup>th</sup> root) and x-axis is boat and shore fishing effort (hrs/ha/yr). Plots represent the relationship of biomass with each predictor individually when all other predictors are held at their mean. Lines are the mean of bootstrapped models plus and minus the standard deviation.

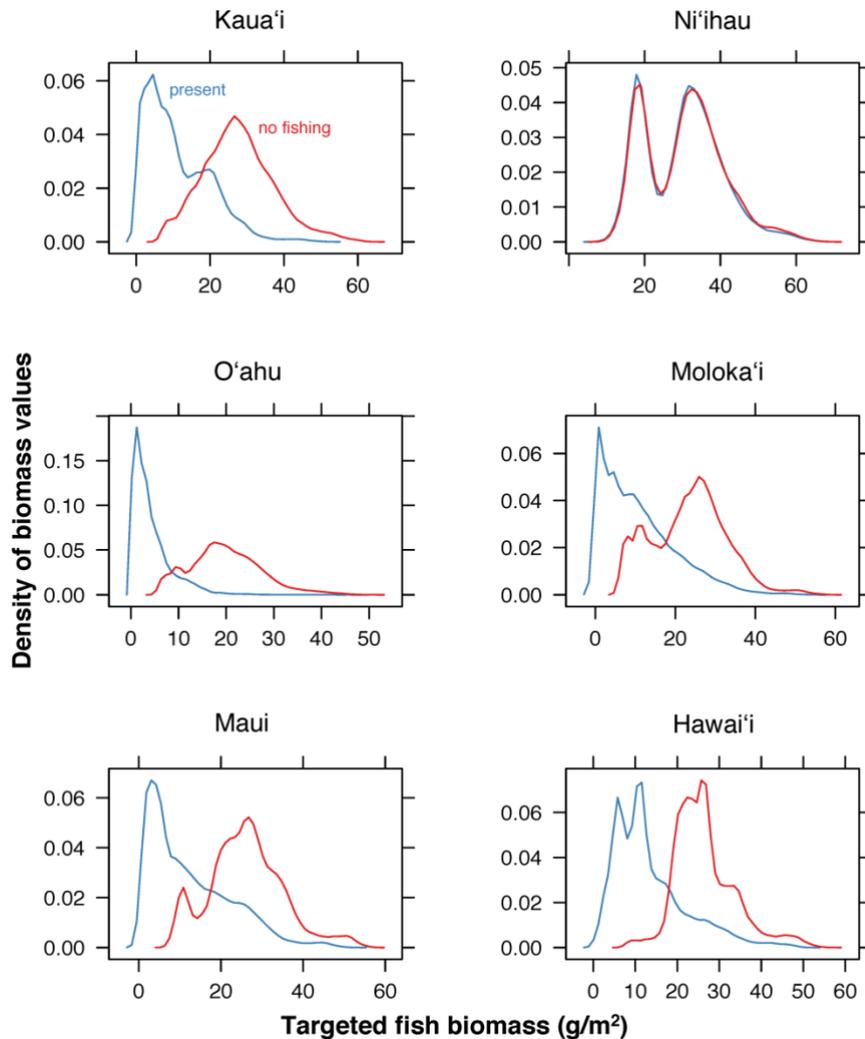
Slope of slope, a measure of topographic complexity, was the most important habitat predictor for targeted reef fish biomass, which increased rapidly at the low end of the scale (0-8°) (Supplement 3.6). Seafloor depth had a strong positive relationship with targeted fish biomass, which increased with depth before leveling off at around 17 m. Maximum slope in a 240 m radius was also positively related to biomass with a steep increase from 0-10°. Sine aspect (exposure) was positively related to biomass, which increased linearly from -1 (west facing) to 1 (east facing), and wave power, responding more at higher levels (> 10,000 kW/hr, Supplement 3.6). Predictor relationships for fish body length were similar to those for biomass (Supplement 3.7). However, there was a stronger relationship with wave power and a weaker relationship with slope of slope. In addition, the relationship of average body length and sine aspect was not linear and length increased with depth up to 25 m before leveling off. Targeted fish body length was also positively related to maximum slope of slope within a 240 m radius, peaking between 25-40°; and slope, increasing from 0-5° (Supplement 3.7). Thus, in the absence of fishing pressure, targeted fish biomass and body length were generally predicted to reach their highest values in habitats with slope of slope > 8°, eastern exposures (sine aspect > 0), wave power > 10,000 kW/hr, and at depths > 17 m.

### Recovery potential in the absence of fishing

All islands except for Ni‘ihau (which was assumed to have negligible fishing pressure) showed a significant increase in predicted biomass when the influence of fishing was removed (Table 3.2, Figure 3.6). Biomass predictions for these islands under present fishing levels had distributions that were right skewed, indicating primarily low biomass levels. When fishing effort was set to zero, these distributions flattened out, shifted right, and became more symmetrical, indicating overall increases in mean biomass (Figure 3.6). Targeted fish biomass was highest in areas less accessible to humans such as the north shores of most islands and the east shore of Maui. However, when fishing pressure was removed biomass increased across all suitable habitats with the highest increases in deeper areas with high topographic complexity (Supplement 3.8 & Supplement 3.9). O‘ahu (the most populated island, with highest overall fishing effort) showed the largest predicted increase in biomass, followed by Kaua‘i, Moloka‘i, Maui, Hawai‘i, and then Ni‘ihau (Table 3.2).

**Table 3.2** Predicted mean biomass and percent increase for targeted reef fishes under present conditions and with fishing pressure removed. N is the sample size representing total number of spatially predicted grid cells per island. SD is standard deviation. Islands are ordered from north to south.

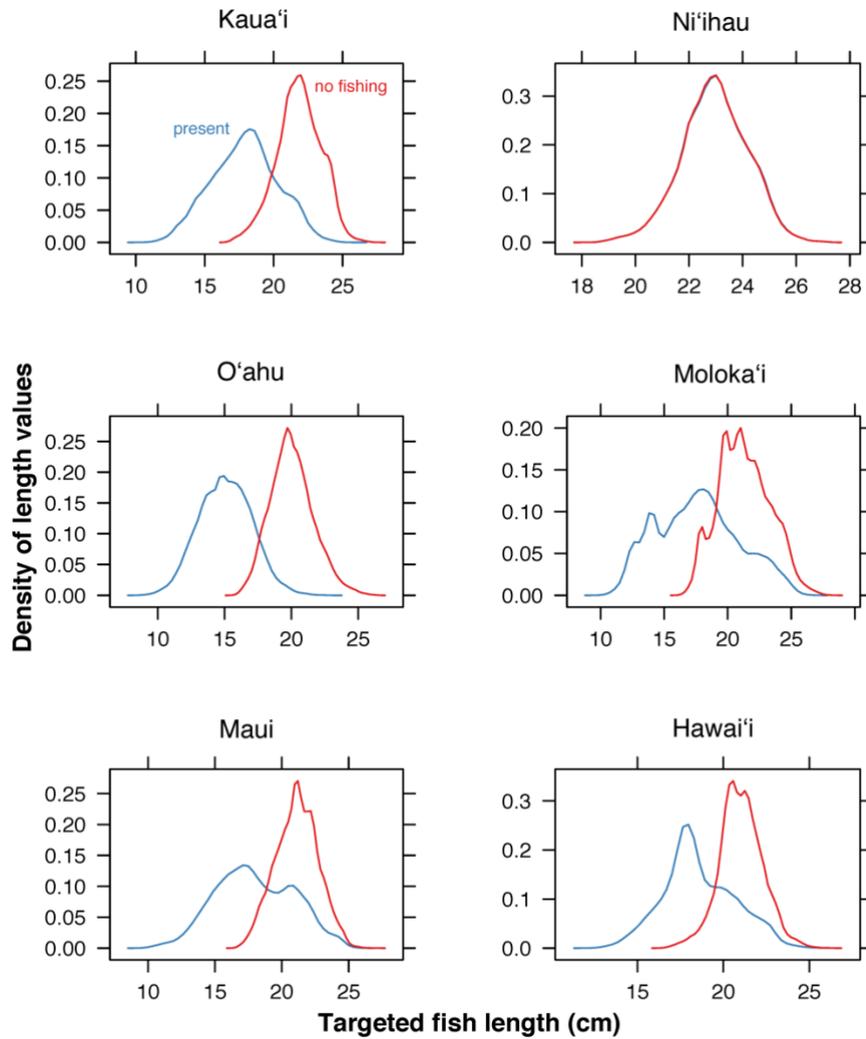
<b>Biomass (g m<sup>-2</sup>)</b>	N	Present		No fishing		% Increase
		mean	SD	mean	SD	
Kaua‘i	67,967	11.2	8.7	27.6	9.7	147%
Ni‘ihau	10,677	30.0	10.2	30.5	10.4	2%
O‘ahu	84,870	4.2	4.1	19.9	7.6	370%
Moloka‘i	38,220	10.9	9.2	23.5	9.4	116%
Maui	43,830	12.5	10.0	26.1	9.1	110%
Hawai‘i	30,702	13.4	8.7	26.6	7.3	98%



**Figure 3.6** Distributions of predicted biomass values under present fishing levels and with fishing removed for each island. X-axis is biomass values per 60x60 m grid cell and y-axis is frequency of biomass values as a proportion of the total number of grid cells per island (density).

All islands except for Ni'ihau showed a significant increase in predicted fish body length when the influence of fishing was removed (Table 3.3, Figure 3.7). Under current fishing levels, the shapes of predicted fish length distributions varied by island. When fishing effort was set to zero, predicted length distributions maintained their general shape and shifted to the right indicating an increase in average body length (Figure 3.7). Similar to biomass, larger fishes were located in areas that are less accessible to humans such as north shores of most islands and the east shore of Maui (Supplement 3.10 & Supplement 3.11). When fishing effort was set to zero, fish length increased in all areas with the highest increases along eastern exposures and areas with high wave power. As with biomass, O'ahu showed the largest relative

increase in fish body length when fishing pressure was removed; the other islands showed smaller increases (Table 3.3).



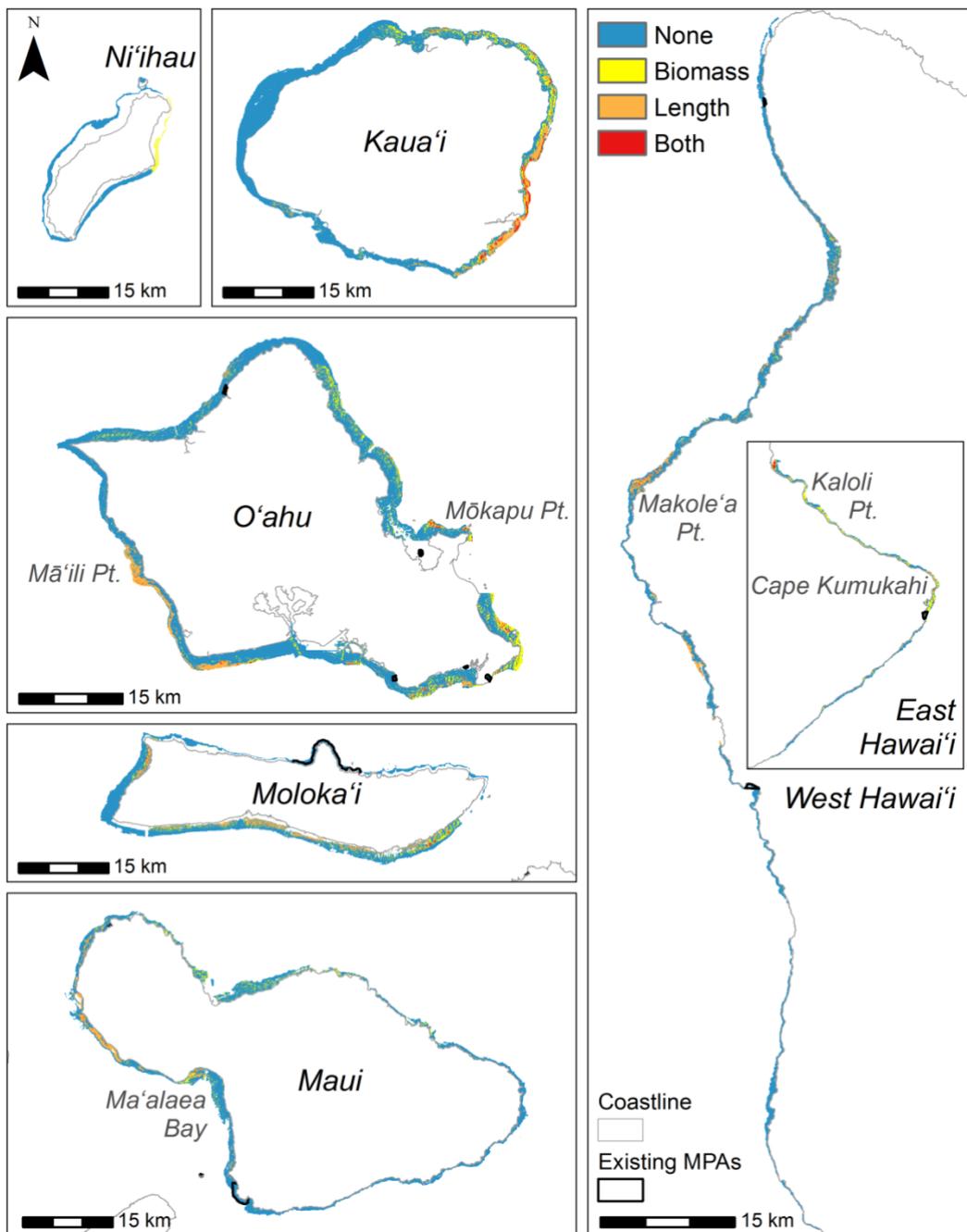
**Figure 3.7** Distributions of predicted length values under present fishing levels and with fishing removed for each island. X-axis is length values per 60x60 m grid cell and y-axis is frequency of length values as a proportion of the total number of grid cells per island (density).

**Table 3.3** Predicted mean body length and percent increase for targeted reef fishes under present conditions and with fishing pressure removed. N is the sample size representing total number of spatially predicted grid cells per island. SE is standard error of the mean.

<b>Length (cm)</b>	N	Present		No fishing		% Increase
		mean	SD	mean	SD	
Kaua‘i	67,967	17.9	2.4	21.8	1.6	22%
Ni‘ihau	10,677	23.0	1.2	23.0	1.2	0%
O‘ahu	84,870	15.1	2.0	20.0	1.6	33%
Moloka‘i	38,220	17.7	3.2	21.3	2.0	21%
Maui	43,830	18.0	2.9	21.1	1.6	17%
Hawai‘i	30,702	18.6	2.1	21.0	1.3	13%

#### Spatial prioritization for management

These analyses identified areas with the highest recovery potential (i.e., areas with high quality habitat and currently under high fishing pressure), which would be expected to respond positively to management of fishing effort. Because current fishing effort was assumed to be zero in existing marine reserves, these areas were not selected. Areas with highest recovery potential for targeted reef fish biomass tended to be patchy, while areas with highest projected recovery for body length were more continuous. Locations with high recovery potential for targeted fish biomass and body length were usually found in the same areas, though often with little direct spatial overlap (Figure 3.8). In general, these areas were located on the east-facing shores of Kaua‘i and O‘ahu, the southeast shore of Moloka‘i, and the west shore of west Maui (Figure 3.8). In addition, the prioritization analysis identified areas on the north shore of Kaua‘i, around Mōkapu point and the southeast shore of O‘ahu, Mā‘ili point on west O‘ahu, northwest Moloka‘i, Ma‘alaea bay on Maui, west Hawai‘i Island just north of Makole‘a point, and east Hawai‘i Island around Cape Kumukahi and north of Kaloli point (Figure 3.8). The largest relative change in biomass for regions of significant increase were on O‘ahu and Kaua‘i, while largest relative increases in body length for these areas were on O‘ahu, with smaller levels of increase on Kaua‘i, Moloka‘i, and Maui (Table 3.4). Ni‘ihau showed minimal change in biomass and body length.



**Figure 3.8** Regions of significant increase ( $\alpha = 0.1$ ) in MHI model predictions of biomass and length after removal of fishing. Existing no-take reserves and restricted access areas are outlined in black.

**Table 3.4** Biomass ( $\text{g m}^{-2}$ ) and fish length (cm) mean, standard deviation (SD), mean percent increase, and standard deviation of percent increase between MHI model predictions for regions of significant difference shown in Fig. 3.8.

	Biomass Increase				Length Increase			
	Mean	SD	Mean %	SD %	Mean	SD	Mean %	SD %
Kaua‘i	29.4	2.6	<b>383%</b>	184%	6.5	0.6	<b>45%</b>	7%
Ni‘ihau	3.6	0.9	<b>11%</b>	2%	0.0	0.0	<b>0%</b>	0%
O‘ahu	25.9	2.8	<b>517%</b>	268%	7.3	0.5	<b>59%</b>	10%
Moloka‘i	21.6	2.2	<b>349%</b>	200%	5.8	0.2	<b>43%</b>	4%
Maui	23.4	2.2	<b>256%</b>	125%	6.2	0.6	<b>46%</b>	9%
Hawai‘i	21.9	2.1	<b>203%</b>	114%	4.5	0.4	<b>29%</b>	4%

## Discussion

Inferred fishing effort patterns were highly variable around the MHI and seascape models indicated a low threshold beyond which targeted fish assemblages were severely impacted. Sparsely populated islands Ni‘ihau and Moloka‘i had fishing effort below this threshold, as did large, and often remote, areas on the other islands. Seascape models also identified seafloor topographic complexity, exposure, wave power, and depth as the key variables that influenced the distribution of high targeted fish biomass and body length and characterized productive habitats. Fish biomass was most sensitive to shore and boat-based fishing, as well as topographic complexity, whereas average body length responded primarily to boat fishing and was strongly influenced by exposure. While the highest targeted reef fish biomass and body lengths were mostly restricted to areas not easily accessed by humans; when fishing effort was set to zero, high values of biomass and body length were widely distributed among suitable habitats. By comparing modelled current targeted fish distributions with those predicted when fishing pressure was removed, areas with high recovery potential were revealed, with significant increases in average biomass and length across the MHI (Table 3.4).

### Fishing effort

An integral component of this research was the application of spatially continuous fishing effort layers developed for the MHI. We chose to use fishing effort rather than catch because derived catch estimates incorporate catch per unit effort (CPUE) which varies in relation to a number of factors including fish abundance (Maunder et al. 2006). Because fish biomass is also related to fish abundance, fish catch - unlike

fishing effort – would not be independent of our response variable. Our derived fishing effort layers represent the most spatially comprehensive, high resolution, and broad-scale products yet created to quantify spatial patterns of coral reef fishery effort. However, a number of simplifying assumptions were made in order to develop these layers, primarily that fishers are more likely to frequent accessible areas, more likely to fish close to home, and that numbers of fishers are proportional to total population (Stewart et al. 2010). For these reasons, our fishing effort maps may possibly capture additional impacts related to accessibility and proximity to humans, such as land-based source pollution. Though our fishing layers were strong predictors of fishery indicators and have been corroborated with fine scale effort data from creel surveys, there is considerable scope to improve them further. Future studies should focus on testing large-scale drivers of fishing effort based on local-scale empirical data.

Our results show the greatest impacts on targeted reef fishes within the first 10% of modeled ranges for shore and boat fishing effort. This is supported by previous research indicating that the greatest impacts from fishing occur at low fishing levels (Jennings and Polunin 1996, Jennings and Kaiser 1998). There are few examples in the literature showing this relationship for coral reef fisheries; it has important implications for management as it highlights the importance of no-take MPAs and suggests that fishing effort in rotational closures should be carefully managed.

#### Fish response variables

Biomass and size of targeted fish species have often been used to evaluate the effects of fishing pressure (Nicholson and Jennings 2004, Dulvy et al. 2004). The theoretical basis is that larger fishes are generally more targeted; the accumulated effects of fishing mortality reduce the number of older, and therefore larger, fishes in a population; and that large-bodied species are more vulnerable to fishing due to slow population turnover (Jennings et al. 1998, 1999). Both biomass and fish length are thought to represent the relative abundance of large and small individuals (Shin et al. 2005). However, our results suggest they are not interchangeable and instead capture different aspects of the fished assemblage. Biomass was more sensitive to fishing compared to mean length. While higher average length always reflects greater relative abundance of large individuals, high biomass can also result from high

abundance of small individuals. This was supported by the fact that slope of slope (60 m) was the top habitat predictor for biomass, while maximum slope of slope in a 240 m radius explained more variability in average length. Larger individuals and species generally have a broader geographical range of movements and thus respond to broader-scale measures of seascape structure (Pittman et al. 2007a, Wedding et al. 2008, Kendall et al. 2011). It is important to consider both fished assemblage biomass and size distribution because large individuals represent high-value species and high reproductive capacity (Birkeland and Dayton 2005).

Our response variables were derived from pooling all targeted coral reef fish species (49) for which we had adequate data. These species represent a range of trophic guilds, life history traits, and vulnerability to fishing (Supplement 3.1). The majority were herbivores (23), followed by mobile invertivores (15), piscivores (9), and detritivores (2). Maximum species sizes ranged from 19 cm to over two meters and known life-spans from 4 to 50 years. This level of variability is common in coral reef fisheries and managers are in need of simple, yet meaningful metrics to guide management actions (Nash and Graham 2016). While species differences in terms of life-span and age at maturity will influence timelines of recovery, habitats characteristics which support targeted fish assemblages can be identified and used to select priority areas for management (Pittman and Knudby 2014). In addition to their practicality, a significant advantage of using assemblage level metrics for spatial modeling is the low prevalence of null values which improves model performance (Wisiz et al. 2008). Furthermore, using a large number of species provides more stable spatial solutions when conducting multi-species prioritization (Kujala et al. 2017).

### Habitat and waves

Of the 27 seascape predictors selected for model development, slope of slope, sine aspect, wave power, and depth were selected as final predictors and showed positive relationships for both targeted fish biomass and body length. Topographically complex habitats offer more potential niches and provide refuges from predation (Hixon and Beets 1989, Almany 2004). Slope of slope is a measure of topographic complexity, which along with related LiDAR derived metrics, has been shown to be highly correlated with in-situ rugosity (Wedding et al. 2008, Stamoulis and

Friedlander 2013) and a strong positive spatial predictor for the distribution of fish biomass (Wedding and Friedlander 2008, Pittman et al. 2009). Depth has also been shown to be a key predictor of fish distributions with higher fish biomass generally associated with greater depths (Friedlander and Parrish 1998a, Pittman and Brown 2011), suggesting that deeper waters may represent a refuge from fishing (Lindfield et al. 2014b).

Both targeted fish biomass and body length showed strong positive relationships with sine aspect. Sine aspect measures east/west exposure with the highest values facing east towards the prevailing trade-winds. Windward reefs may be more productive due to nutrient inputs from increased terrestrial runoff (Ringuet and Mackenzie 2005, Giambelluca et al. 2012), and predominantly rough seas along eastern shores likely limit boat and shore fishing activity. In contrast, wave power is highest along north and northwest facing shores due to winter storms in the north Pacific (Fletcher et al. 2008). The positive relationships between wave energy and targeted fish biomass and body length have several possible explanations. High waves may provide a refuge from fishing pressure (Branch and Odendaal 2003, McLean et al. 2016) and flush reefs and mitigate land based source pollution, thus improving habitat quality (Fabricius 2005, 2011). Highly wave exposed areas also have less small-scale structure such as from branching corals and support fewer small species, while larger fishes are stronger swimmers and thus able to subsist in areas with high wave energy (Friedlander and Parrish 1998b, Friedlander et al. 2003). Further research is needed to confirm these patterns and identify causal mechanisms.

Productive habitats for targeted fishes were characterized by eastern exposures and a combination of high topographic complexity, wave power, and depth. Topographic complexity provides ecological benefits, though it may also provide some refuge from fishing. High wave power, wind exposure, and depth likely provide refuges from fishing pressure due to reduced accessibility, which may in part explain why targeted fish biomass and body length showed strong positive relationships with these factors.

### Recovery patterns in the absence of fishing

Our comparison of predicted targeted fish distributions under current fishing levels and with fishing pressure removed clearly shows the strong limiting influence of fishing. Because our fishing effort layers were partly based on accessibility to humans and human population, some of the variability they account for in models of targeted fish assemblage indicators may be due to human impacts other than fishing. While current productive and healthy targeted fish assemblages were largely restricted to areas less accessible to fishers, when fishing pressure was removed they expanded throughout all suitable habitats. This is supported by previous research which showed that structurally complex habitats harbored greater fish biomass (Graham and Nash 2013, Darling et al. 2017). When converted to percent depletion, our island-scale estimates of biomass recovery potential are generally lower than estimates of depletion reported by Williams et al. (2015), though relative differences among islands were fairly consistent. This is unsurprising given that models used in Williams et al. (2015) estimated total fish biomass and were calibrated on a suite of Pacific Islands ranging from pristine to highly degraded. Our models were calibrated only on the main Hawaiian Islands, which are far from pristine. Also Ni‘ihau was assumed to have negligible fishing impact, which is not strictly accurate as subsistence fishing occurs on the island (pop. 170), and there are reports of fishing from boats based on Kaua‘i. Furthermore, due to gaps in the bathymetry datasets the shallow nearshore areas around Ni‘ihau were not included in our analysis.

Areas with significant projected biomass and length recovery had little direct spatial overlap. This is because they represent different aspects of the fished assemblage and are primarily influenced by different seascape predictors, especially in terms of fishing effort. Shore fishing explained the most variability in targeted fish biomass, while boat fishing was most important for fish body length. As a result, when fishing pressure was removed, predicted biomass increase was highest in accessible, nearshore areas with currently high shore fishing effort, and body length showed greatest projected increases in well populated areas close to boating facilities with currently high boat fishing effort. After fishing effort, high biomass was primarily driven by high topographic complexity (slope of slope) which is patchily distributed. This resulted in fragmented patterns for areas of high biomass recovery potential. In contrast, top habitat predictors for body length were high exposure (sine aspect) and

wave power which have more continuous patterns, resulting in similarly unbroken spatial patterns for areas with high length recovery potential.

### Management applications

In September, 2016 the governor of Hawai‘i made a commitment at the International Union for Conservation of Nature (IUCN) World Conservation Conference to effectively manage 30% of Hawai‘i’s nearshore waters by 2030 (Ige 2016).

“Effective management” will be achieved through a broad suite of approaches including area closures for fisheries replenishment, as well as identifying areas that are already healthy (Hawaii Division of Aquatic Resources 2016). Therefore, identifying presently productive areas and those with high recovery potential is a priority, and an effective approach to accomplish this at the scale of the MHI is timely and could serve as a template for similar efforts elsewhere.

The prioritization approach presented in this study incorporates current fishing levels into estimates of recovery potential, thus identifying areas where management actions will be most effective in restoring coral reef fisheries. This was a result of comparing spatial predictions of fishery indicators under current fishing levels with predictions after fishing is removed. Each of these predicted maps also has utility for management. Spatial patterns of targeted fish biomass and body length under current fishing levels allows for identification of areas that presently harbor healthy fish assemblages. Effectively managing fishing in these areas would ensure that they continue to supplement adjacent fisheries, through larval export and spillover of adults and juveniles (Harrison et al. 2012, Stamoulis and Friedlander 2013). Because these areas generally have low fishing pressure, management actions would incur minimal cost in terms of fisher displacement. Predicted maps of targeted fish distributions with fishing removed identify habitats capable of supporting high biomass and larger fishes. This information can be used to characterize these essential habitats for coral reef fisheries. Comparing predictions with and without fishing pressure reveals areas to focus fisheries management and provides estimates of recovery potential. Targeted fish biomass recovery in these areas represented a 517% increase on average relative to current values for O‘ahu with smaller increases for the other islands where fishing pressure is not as high. These areas show potential mean targeted fish size increases of up 59% on O‘ahu with smaller increases for the

other islands. Long-term monitoring data shows over a ten-fold increase in total fish biomass during the first 16 years of protection at Hanauma Bay, the oldest no-take reserve on O‘ahu (Friedlander and Brown, 2004), suggesting that these estimates are likely conservative.

The intrinsic rate of population growth ( $r$ ) is the major driver of population recovery after fishing pressure is removed (Jennings 2000). However, the rate of population recovery also depends on the size of the remaining population and degree of compensation or depensation, as well as other factors (Jennings 2000). In the absence of this information, rough estimates of recovery rates inside no-take marine reserves can be inferred from life history traits such as trophic level, maximum body size and longevity (Abesamis et al. 2014). The targeted reef fish species included in this analysis exhibit a broad range of life history characteristics (Supplement 3.1) and thus timelines of recovery will vary. The first species likely to recover are the goatfish (Mullidae) and several of the parrotfish (Scaridae -  $A_{\max} < 7$  yrs) based on their short lifespans, and full recovery for these species may be possible within 10 years (Abesamis et al. 2014). In overfished regions such as the MHI, full recovery of moderate to highly vulnerable targeted reef fish such as jacks (Carangids), wrasses (Labrids), surgeonfish (Acanthurids), and large parrotfish is likely to take 20-40 years (Abesamis et al. 2014).

Areas with significant ( $\alpha=0.1$ ) projected biomass and length recovery were selected for prioritization, though the threshold could be adjusted based on management needs. Spatial predictions of high biomass and fish body length generally had high precision ( $CV < 0.5$ ), providing confidence in the results. This prioritization approach identified areas where management actions will have the most scope to restore fisheries and could be used as a starting point for marine reserve selection. These areas are capable of supporting high numbers of large fishes which constitute high reproductive capacity (Berkeley et al. 2004, Birkeland and Dayton 2005). The next most important criteria to consider is larval connectivity to ensure that adequate portions of larvae are exported into fished areas (Green et al. 2015). While larval transport modeling is still in its infancy, recent work has modeled potential connectivity based on oceanographic circulation in the Hawaiian islands and identified potential larval sources and sinks at 4 km<sup>2</sup> resolution (Wren et al. 2016).

Places that are capable of supporting high spawner biomass, which are also important larval source areas for connected reefs, would be good candidates for enhanced fishery management or protection. Such areas, identified by these ecological criteria, should be additionally evaluated based on social, economic, and other considerations important for management (Smith and Wilen 2003, Charles and Wilson 2009, Jones et al. 2013).

## **Conclusions**

The development of spatially continuous and comprehensive fishing effort layers, combined with seascape models of targeted fish assemblage indicators for the entire MHI, allowed us to make spatially explicit estimates of recovery potential and thus identify areas that would benefit most from focused coral reef fisheries management. These areas are generally located on the east-facing shores of Kaua‘i and O‘ahu, the southeast shore of Moloka‘i, the west shore of west Maui, and isolated locations in west and east Hawai‘i Island. However, the high-resolution maps show considerable spatial heterogeneity in the geographical distribution of recovery potential as defined by habitat and fishing patterns. While targeted fish biomass and body length were chosen here to characterize key attributes of reef fisheries, this approach could also be applied using other fish response variables that are important to managers. The information provided is well suited for both local scale management and regional marine spatial planning efforts that aim to sustain and enhance coastal fisheries.

This study is the first of its kind to develop regional-scale seascape models that integrate spatially explicit estimates of fishing pressure. The high resolution of our model inputs and predictions (60x60 m) is consistent with movement patterns of most targeted fish species and fishers (Weeks et al. 2017). Tree-based modeling approaches are well suited to handling non-linear relationships and high-order interactions of complex ecological data (De’ath and Fabricius 2000). The ability to make spatial predictions, or predictive mapping, expands upon field-based measurements that are expensive and spatially limited, and produces spatial information at the scope and scale necessary for large-scale assessments and marine spatial planning (Chapter 2). Spatially comprehensive, continuous input and output datasets eliminate the need for the simplifying assumptions common in traditional

approaches that can increase uncertainty when results are extrapolated across the area of interest. Predictive mapping fills gaps in survey coverage, allows for testing of management scenarios, and provides spatially comprehensive information for managers including estimates of prediction precision (Pittman and Knudby 2014). Finally, the approach is flexible so that it can be applied anywhere where demersal fish populations are targeted, and any response variable derived from fish survey data can be modeled depending on the research or management question.

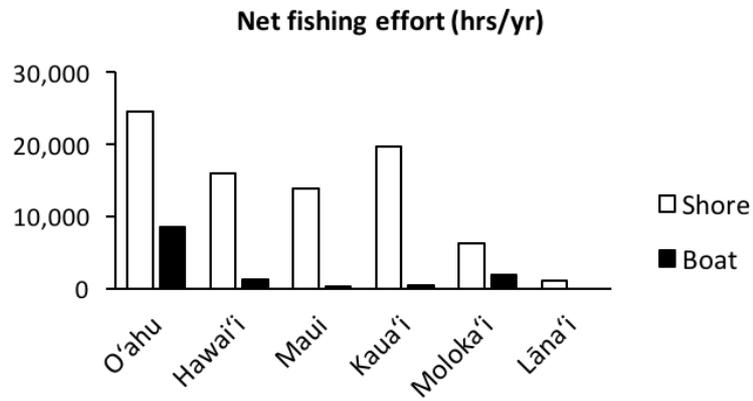
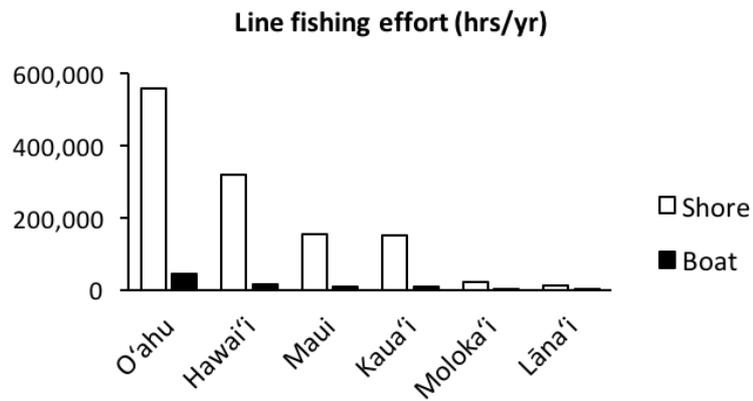
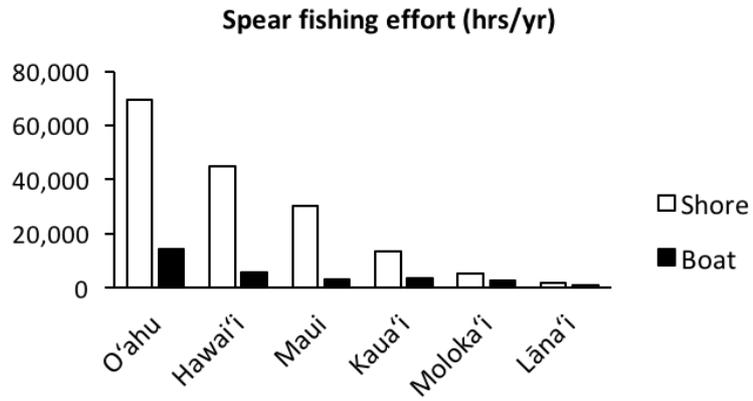
## Supplementary Material

**Supplement 3.1** List of targeted fish species included in modeling. Trophic level (T): H-herbivore, D-detritivore, M-mobile invertivore, P-piscivore. Maximum observed length (L) in cm. Maximum age (A) in years if available. \*Endemic, +Introduced

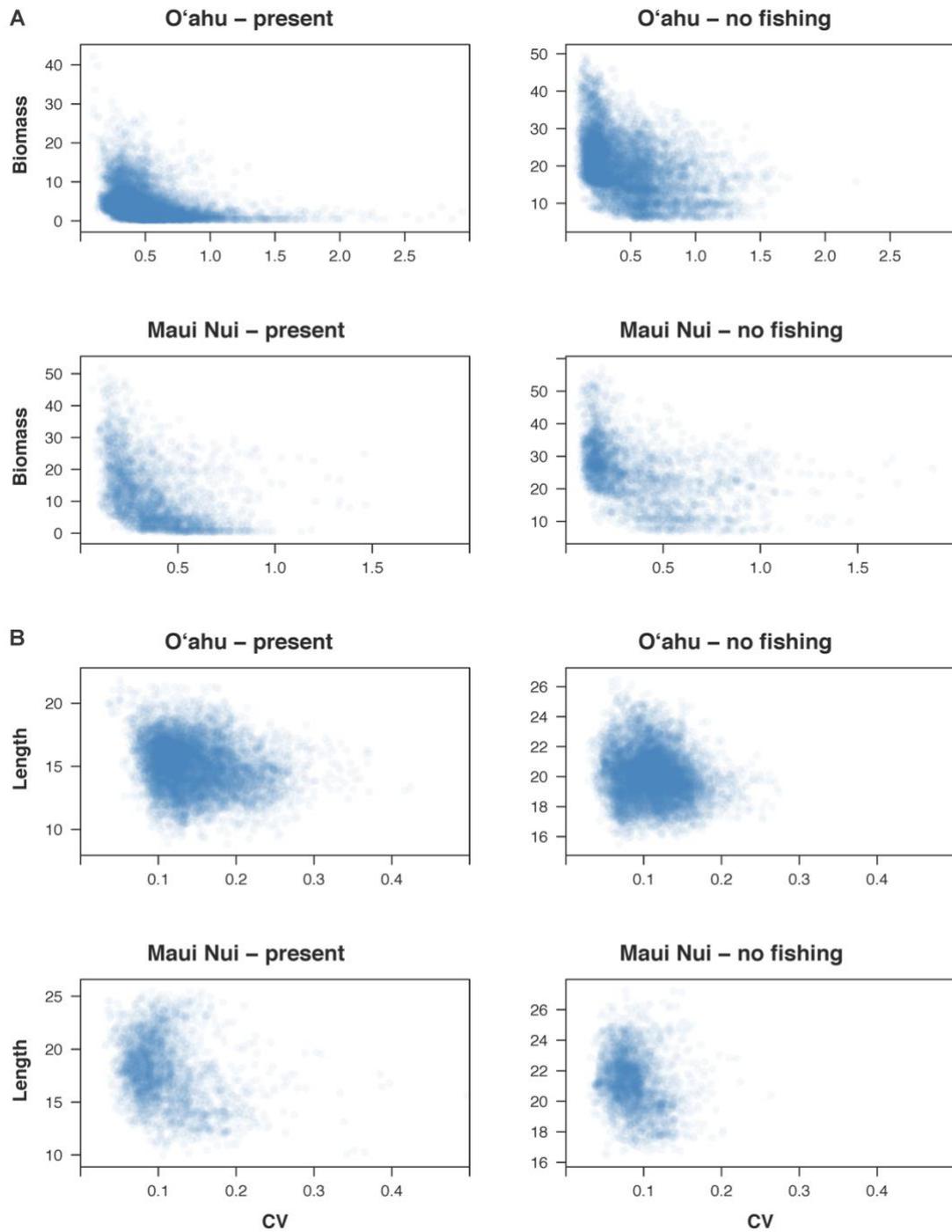
<u>Family/Taxon</u>	<u>T</u>	<u>L</u>	<u>A</u>	<u>Family/Taxon</u>	<u>T</u>	<u>L</u>	<u>A</u>
<u>Acanthuridae</u>				<u>Lethrinidae</u>			
<i>Acanthurus achilles</i>	H	25		<i>Monotaxis grandoculis</i>	M	63	21
<i>Acanthurus blochii</i>	H	43	35	<u>Lutjanidae</u>			
<i>Acanthurus dussumieri</i>	H	46	28	<i>Aphareus furca</i>	P	70	
<i>Acanthurus guttatus</i>	H	26		<i>Aprion virescens</i>	P	110	31
<i>Acanthurus leucopareius</i>	H	25		<i>Lutjanus fulvus</i> +	M	43	19
<i>Acanthurus nigroris</i>	H	25		<i>Lutjanus kasmira</i> +	M	40	8
<i>Acanthurus olivaceus</i>	H	30	33	<u>Mullidae</u>			
<i>Acanthurus triostegus</i>	H	26		<i>Mulloidichthys flavolineatus</i>	M	40	6
<i>Acanthurus xanthopterus</i>	H	65		<i>Mulloidichthys vanicolensis</i>	M	38	5
<i>Ctenochaetus hawaiiensis</i>	D	25		<i>Parupeneus cyclostomus</i>	P	50	5.4
<i>Ctenochaetus strigosus</i>	D	19		<i>Parupeneus insularis</i>	M	33	6.4
<i>Naso lituratus</i>	H	46	25	<i>Parupeneus multifasciatus</i>	M	29	
<i>Naso unicornis</i>	H	70	50	<i>Parupeneus pleurostigma</i>	M	33	
<i>Zebrasoma veliferum</i>	H	40	27	<i>Parupeneus porphyreus</i> *	M	50	6
<u>Carangidae</u>				<u>Scaridae</u>			
<i>Carangoides ferdau</i>	M	53		<i>Calotomus carolinus</i>	H	50	4
<i>Carangoides orthogrammus</i>	P	70	11	<i>Calotomus zonarchus</i> *	H	30	
<i>Caranx ignobilis</i>	P	217	11	<i>Chlorurus perspicillatus</i> *	H	61	19
<i>Caranx melampygus</i>	P	100	7	<i>Chlorurus spilurus</i>	H	40	11
<u>Fistulariidae</u>				<i>Scarus dubius</i> *	H	36	13
<i>Fistularia commersonii</i>	P	160		<i>Scarus psittacus</i>	H	30	6
<u>Kyphosidae</u>				<i>Scarus rubroviolaceus</i>	H	70	22
<i>Kyphosus cinerascens</i>	H	51		<u>Serranidae</u>			
<i>Kyphosus hawaiiensis</i>		41		<i>Cephalopholis argus</i> +	P	60	25
<i>Kyphosus sandwicensis</i>	H	60					
<i>Kyphosus vaigiensis</i>	H	60					
<u>Labridae</u>							
<i>Anampses cuvier</i> *	M	36					
<i>Bodianus albotraeniatus</i> *	M	51					
<i>Coris flavovittata</i> *	M	38					
<i>Oxycheilinus unifasciatus</i>	P	46					
<i>Thalassoma ballieui</i> *	M	40					
<i>Thalassoma purpureum</i>	M	43					

**Supplement 3.2** Final predictor datasets used in model development. A pairwise correlation analysis was performed on the full set of predictors for the whole study area (MHI). Highly correlated predictors (Spearman  $|\rho| > 0.7$ ) were identified, and those highly correlated with two or more other predictors were removed. See Stamoulis et al. (2016) for further details.

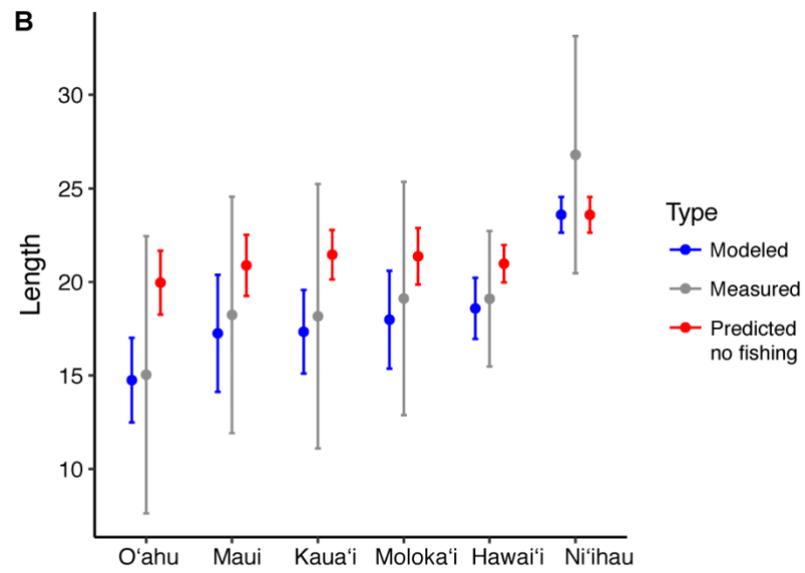
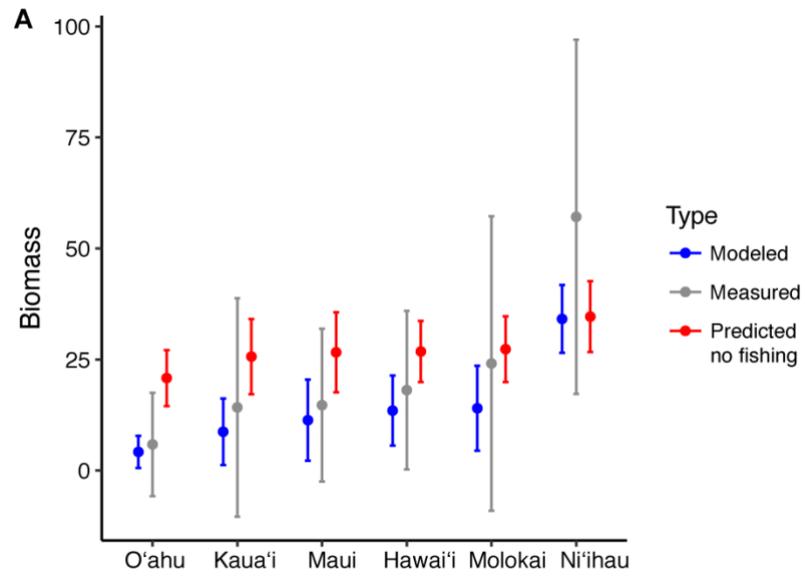
Type	Dataset	Description	Units
<b>Fishing</b>	Boat fishing	Vessel based spearfishing effort	hrs/ha/yr
	Shore fishing	Shore based spearfishing effort	hrs/ha/yr
<b>Seafloor Topography</b>	Depth 60m	Mean seafloor depth	m
	Slope 60m, 240m	Mean maximum rate of change in seafloor depth between each grid cell and its neighbors, maximum slope in 240m radius	Degree
	Slope of Slope 60m, 240m	Mean maximum rate of change in seafloor slope between each grid cell and its neighbors, maximum slope of slope in 240m radius	Degree
	Aspect 60m	Downslope direction of maximum rate of change in seafloor depth between each grid cell and its neighbors: Sine circular mean (E/W), cosine circular mean (N/S), circular SD	Unitless
	Planar curvature 60m	Mean seafloor curvature perpendicular to the line of maximum slope; value indicates whether flow will converge or diverge over a point; values can be - (concave), + (convex), or 0 (flat)	Radians/m
	Profile curvature 60m	Mean seafloor curvature along the line of maximum slope; value indicates whether flow will accelerate or decelerate over the curve; values can be + (concave), - (convex), or 0 (flat)	Radians/m
	Bathymetric position index (BPI) 60m, 240m	Mean difference in seafloor depth and the mean seafloor depth in an annular neighborhood of specified inner and outer radii; values indicate a location's position relative to the surrounding area; values can be + (ridges), - (valleys), or 0 (flat areas or areas of constant slope)	m
<b>Benthic Habitat composition</b>	Percentage of landscape 60m	Percent of grid cell (60m) composed of each cover type: Coral, CCA, Macroalgae, Turf, Soft bottom	Percent
	Proximity index 60m	Values indicate the spatial context of both the degree of patch isolation and degree of seascape fragmentation; a value of 0 indicates no neighbors of the same cover class within the search radius, and values increase as patches of the same class become more numerous, closer, and more contiguous	Unitless
	Shannon's diversity index 60m	Values indicate habitat diversity in terms of the number of different cover classes present (richness) and the proportional distribution of area among the different cover classes (evenness); a value of 0 indicates only 1 patch (no diversity) and values increase as either the number of different cover classes increases or area becomes more evenly distributed among classes	Unitless
<b>Geographic</b>	Latitude	Latitude at each model grid cell centroid	Meters
	Longitude	Longitude at each model grid cell centroid	Meters
	Distance to shore	Straight line (Euclidean) distance to the shoreline	Meters
<b>Wave energy</b>	Wave power 60m	Mean wave power (wave height x wave period) derived from a 1 year (2000-2009) hind-cast wave model	Kilowatts per meter



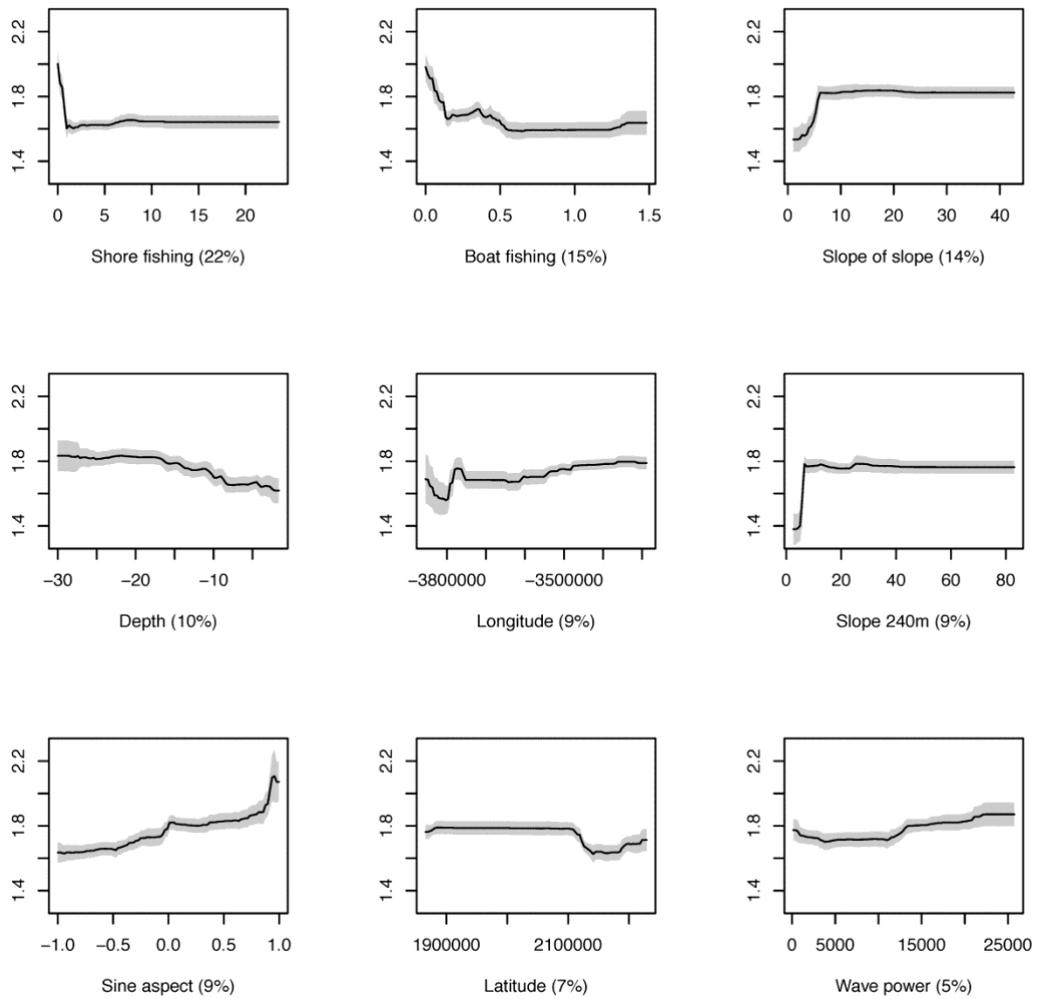
**Supplement 3.3** Total expanded shore effort by gear type by island from McCoy (2015).



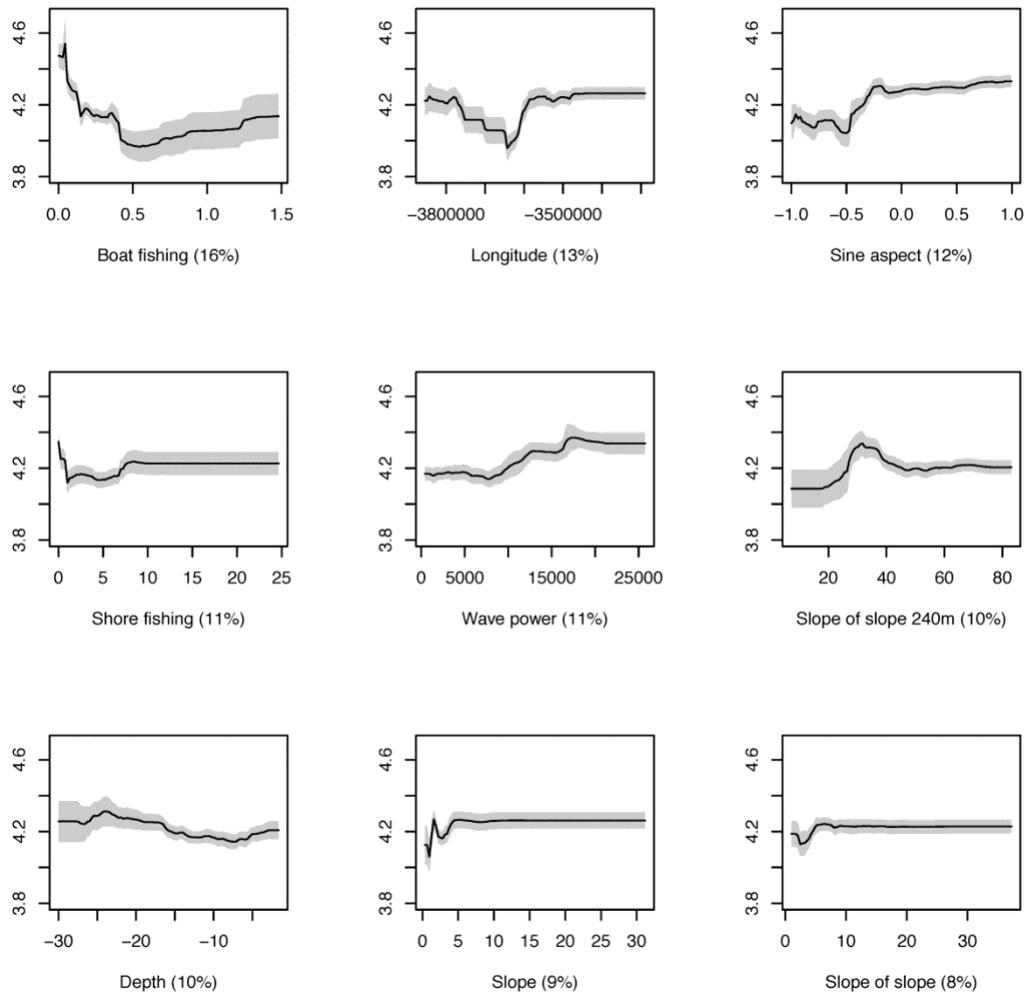
**Supplement 3.4** Coefficient of variation (CV) of predictions vs mean of predictions for A) biomass and B) length for O'ahu and Maui Nui. Maui Nui encompasses the islands of Maui and Moloka'i.



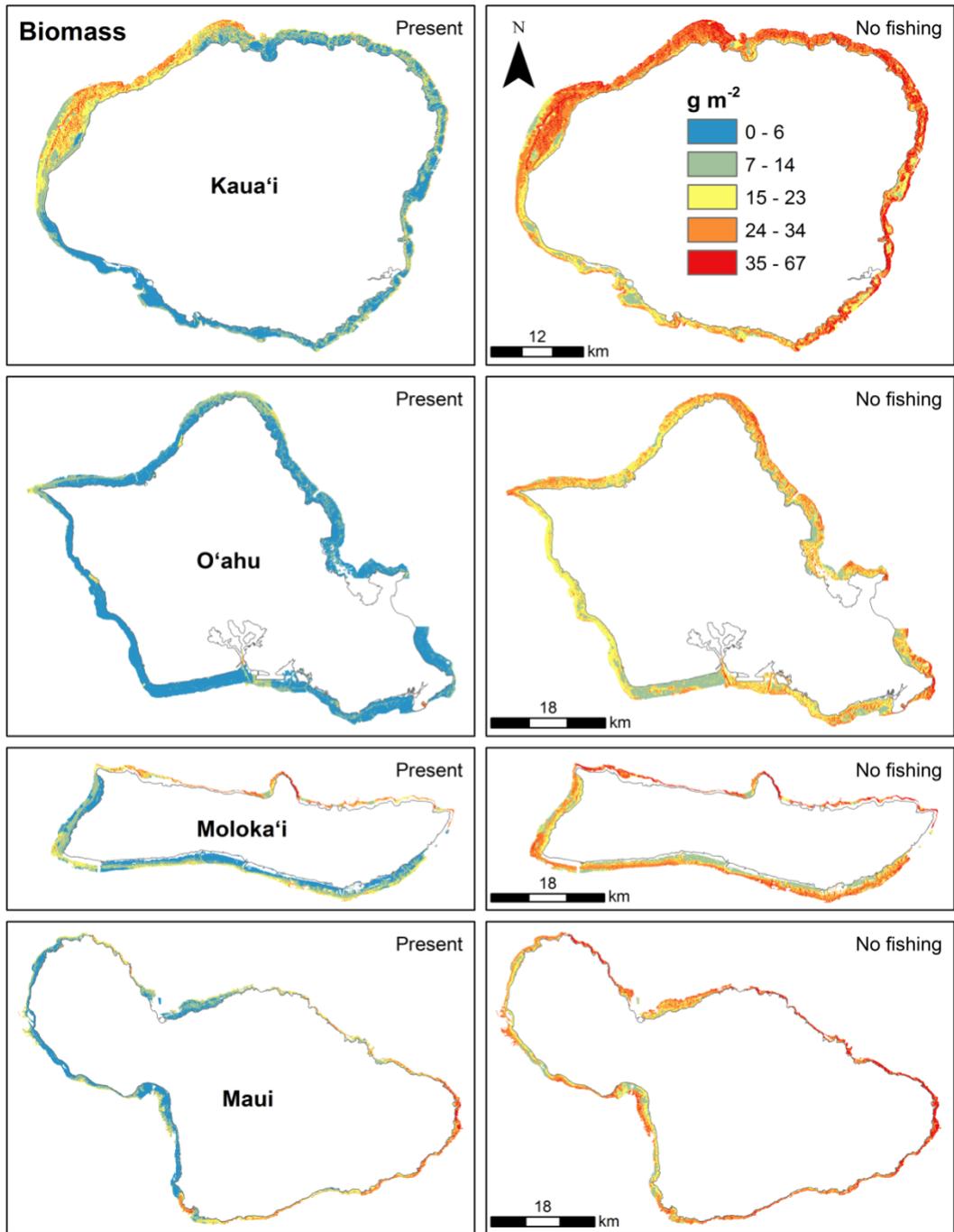
**Supplement 3.5** Comparison of modeled, measured, and predicted values with fishing pressure removed for (A) biomass and (B) length, averaged by island. Error bars represent standard deviation of the mean.



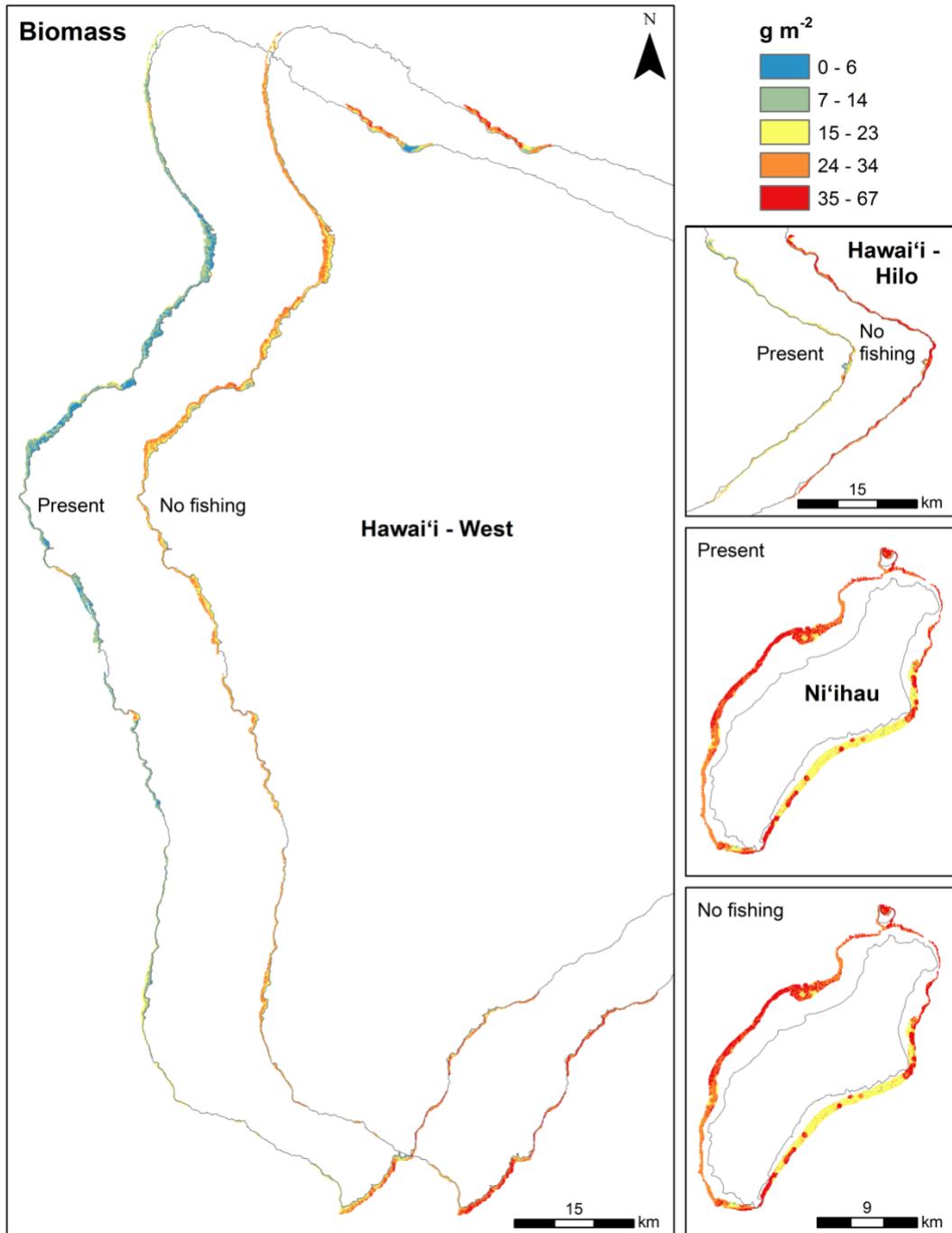
**Supplement 3.6** Partial dependence plots for biomass. Y-axis is transformed biomass (4<sup>th</sup> root) and x-axis is the predictor variable (units in **Supplement 3.2**). Plots represent the relationship of biomass with each predictor individually when all other predictors are held at their mean. Lines are the mean of bootstrapped models plus and minus the standard deviation.



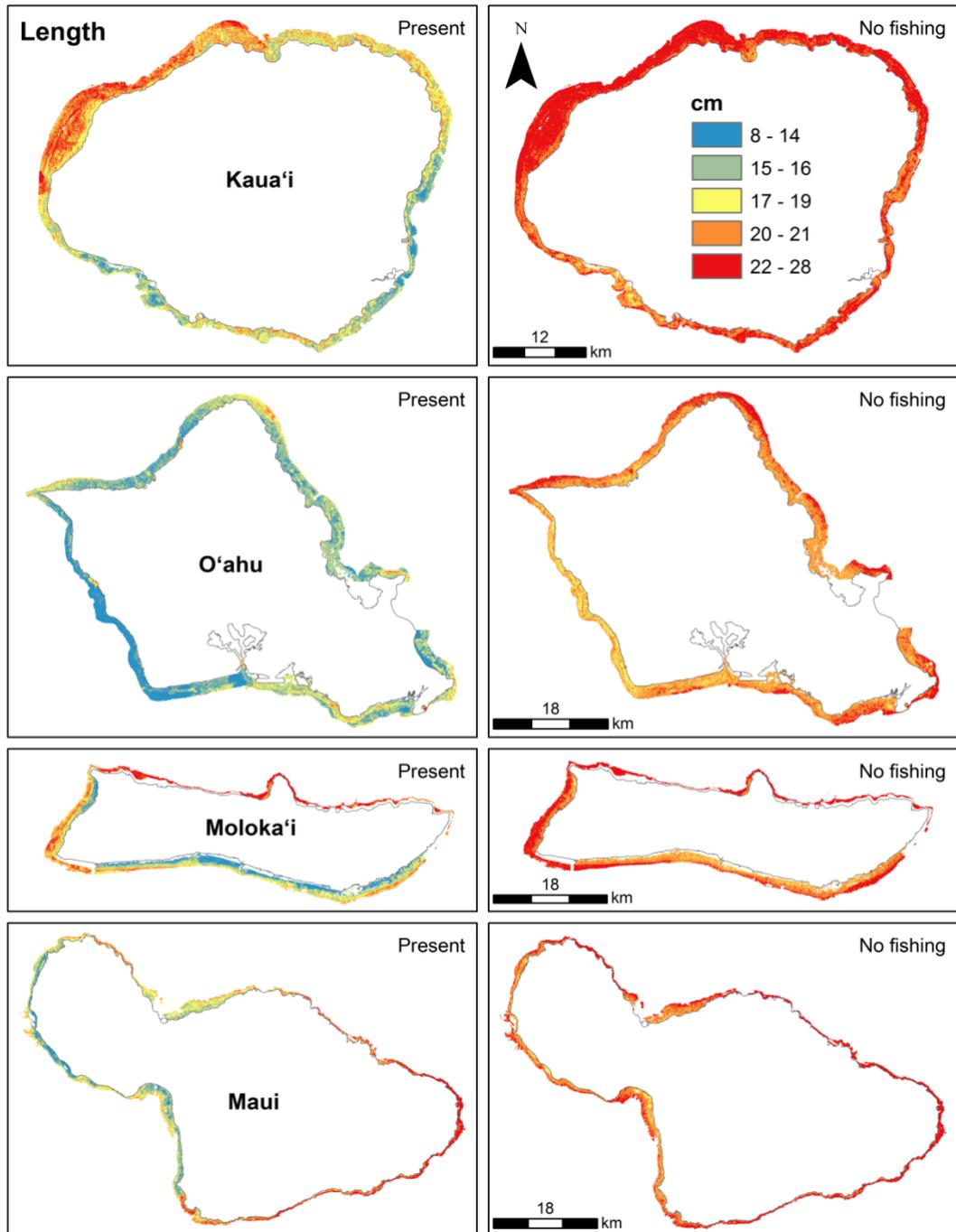
**Supplement 3.7** Partial dependence plots for body length. Y-axis is transformed length (square root) and x-axis is predictor variable (units in Supplement 3.2). Plots represent the relationship of length with each predictor individually when all other predictors are held at their mean. Lines are the mean of bootstrapped models plus and minus the standard deviation.



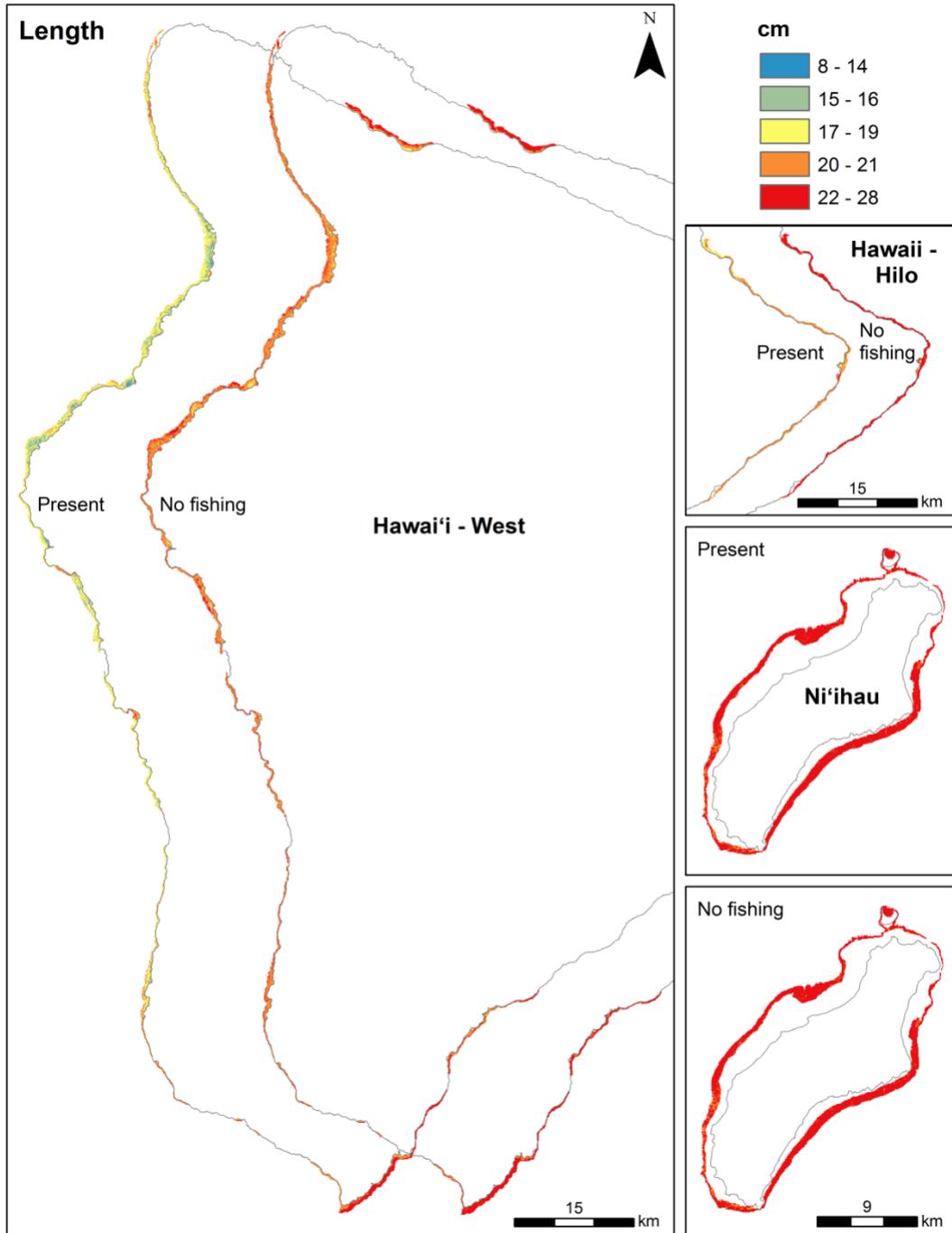
**Supplement 3.8** MHI predicted biomass for present conditions (left) and with fishing pressure set to zero (right) for Kaua'i, O'ahu, Moloka'i, and Maui. Classification (symbology) is consistent across all islands.



**Supplement 3.9** MHI predicted biomass for present conditions (left) and with fishing pressure set to zero (right) for Hawai'i and Ni'ihau. Classification (symbology) is consistent across all islands.



**Supplement 3.10** MHI predicted length for present conditions (left) and with fishing pressure set to zero (right). Classification (symbology) is consistent across all islands.



**Supplement 3.11** MHI predicted length for present conditions (left) and with fishing pressure set to zero (right) for Hawai'i and Ni'ihau. Classification (symbology) is consistent across all islands.

## **CHAPTER 4 - Flight behavior of targeted fishes depends on fishing and other key variables**

### **Abstract**

Behavioral changes due to human predation can affect the functional role of targeted fishes and has implications for ecosystem and fisheries management. Wariness of targeted fishes towards divers, often measured as flight initiation distance (FID), has been shown to increase in areas where spear fishing pressure is higher. Additional research is required to understand how these patterns vary among different species and places. To support such studies, there is a need to explore the relationship of approach starting distance (SD) and other variables that influence measures of fish wariness. We used diver-operated stereo video (stereo-DOV) to record FID, a new direct measure of minimum approach distance (dMAD), and escape responses of targeted reef fishes in a marine reserve and heavily fished area in Hawai'i. We investigated the role of SD and 15 other variables in influencing FID and dMAD and tested differences between the reserve and fished area. SD explained a large portion of the variability in FID and somewhat less variability in dMAD. FID and dMAD were higher when fishes were travelling (vs feeding), increased with fish body length, and decreased with depth. When including these co-variates in models of FID and dMAD of targeted reef fishes, we found significant differences between study sites for dMAD, though not for FID. We also found differences in escape responses between sites. Based on these results, we recommend using stereo-DOV to conduct measures of dMAD as a complement or alternative to FID, while simultaneously collecting additional data such as escape response. Relative effect sizes of SD and, to a lesser extent, other co-variates were large in comparison to site. Studies that use similar methods and do not control for or incorporate SD may produce biased results with regard to the effects of fishing pressure on flight behavior of targeted fishes.

### **Introduction**

Fishing alters the structure and function of fish communities, influencing trophic composition (Robinson et al. 2016), biomass (Friedlander et al. 2018), abundance (Kelaher et al. 2014) and diversity (Mora et al. 2011), with consequences for food security and ecosystem function (Bridge et al. 2013, Brown and Mumby 2014).

However, there has been comparatively little research on the effects of fishing on fish behavior and the resulting implications for fisheries and ecosystem management. Behavioral changes can influence the functional role that fishes play in the ecosystem (Madin et al. 2010, 2011), and may affect sexual selection (Biro and Post 2008) and habitat usage (Lindfield et al. 2014b). For example, Rizzari et al. (2014) showed that the presence of a predator led to the localized cessation of macroalgae removal by herbivorous fishes, due to the perceived risk of predation. Fish behavior can also influence estimates of fish assemblage metrics as measured by underwater visual census (UVC) (Kulbicki 1998, Pais and Cabral 2017), especially across gradients of fishing pressure and when evaluating MPA effectiveness (Lindfield et al. 2014a, Gray et al. 2016). This potential source of bias could also influence other applications of UVC data such as studies of fish/habitat relationships and species distribution modelling (Monk et al. 2012).

Reef fish wariness towards divers has been estimated by measuring flight initiation distance (FID) in a limited number of studies (eg. Gotanda et al. 2009) using methods adapted from terrestrial experiments where the subject is approached directly until it flees (Frid and Dill 2002, Cooper 2005). Lindfield et al. (2014a) used a passive measure; minimum approach distance (MAD) to estimate reef fish wariness, where minimum distance was recorded for every fish encountered on a transect. These studies have documented differences in fish wariness between marine reserves and fished areas and along gradients of fishing pressure (Januchowski-Hartley et al. 2015). Fish wariness has also been shown, in some circumstances, to be more sensitive to changes in management than measures of abundance, length, or biomass (Goetze et al. 2017). Measures of fish wariness have the potential to be used as proxies for fishing pressure and indicators of marine reserve compliance (Bergseth et al. 2015). However, there is a need for additional research to see if findings are consistent across geographies and species and to establish regional baselines.

Starting distance (SD) - the distance at which the observer begins the trial approach - has been shown to have a strong and consistent relationship with FID in terrestrial species (Samia et al. 2013). Nevertheless, SD has not been incorporated in studies of flight distance of harvested fishes (but see Tran et al. 2016). Previous studies of FID for coral reef fishes have standardized SD by setting a minimum range, however, it is

necessary to understand the influence of SD on flight distance of fishes to support continuing research and aid interpretation. In addition, factors such as fish body size have been recognized to be important determinants of flight behavior and there is a need to explore additional variables that may explain variation in flight distance besides fishing pressure.

In order to fill these knowledge gaps and support future flight behavior research on marine fishes, we used stereo-video to conduct measurements of SD, FID, and dMAD, and investigated the role of SD and other co-variables on targeted reef fish wariness in a marine reserve and heavily fished area in Hawai'i. In addition, we recorded escape (post flight) responses of targeted reef fishes. Our objectives were to: 1) investigate the role of SD and other variables in measuring flight distance in coral reef fishes, and 2) compare measures of FID and dMAD and incorporate escape response data to explore how flight behavior changes under different levels of fishing pressure.

## **Methods**

### Site descriptions

Measurements of fish behavior were conducted at two locations in the main Hawaiian Islands: Ka'ūpūlehu-Kīholo on Hawai'i Island and around the island of Kaho'olawe. Ka'ūpūlehu-Kīholo, hereafter referred to as Ka'ūpūlehu, lies on the west coast of Hawai'i Island, approximately 20 km north of a main population center, Kailua-Kona. Surveys of fish behavior were carried out in September, 2013 shortly before a regional ban on SCUBA spearfishing was implemented (DLNR 2013) and well before the more recent enactment of a 10-year fishing moratorium that went into effect July 29, 2016. Based on previous UVC surveys, average biomass of targeted reef fishes in the area was low ( $27.1 \pm 1.6$  (SE)  $\text{g}/\text{m}^2$ , Minton et al. 2015) compared with statewide estimates among fished areas ( $50.0 \text{ g m}^{-2}$ , Friedlander et al. 2018). Combined estimates of spearfishing effort for this area prior to the ban equaled more than  $5,000 \text{ hrs yr}^{-1}$ , making it among the highest of the 18 locations in the state with fisheries creel survey data (Delaney et al. 2017). Kaho'olawe is the smallest of the eight main islands of Hawai'i, it is located southwest of Maui and southeast of Lāna'i. Surveys of targeted fish behavior were

conducted there in June, 2015. The island was a *de facto* marine reserve during World War II, and since 1990, it has been under the administration of the state Kaho‘olawe Island Reserve Commission (KIRC), with only limited take of marine life permitted for cultural and subsistence purposes (Friedlander et al. 2014). Average biomass of targeted reef fishes on Kaho‘olawe ( $92.0 \pm 13.7$  SE g/m<sup>2</sup>, Minton et al. 2016) is over three times higher than at Ka‘ūpūlehu, and it has been used as a near-unfished baseline for the main Hawaiian Islands (Friedlander et al. 2018). Targeted species of the MHI nearshore fishery were defined as coral reef fishes having  $\geq 450$  kg of annual recreational or commercial harvest for the past 10 years (2000-2010), or otherwise recognized as important for recreational, subsistence, or cultural fishing (<http://dlnr.hawaii.gov/dar/fishing/hmrfs/>).

#### Sample design and methodology

Surveys of fish behavior were conducted using SCUBA at pre-selected, random locations on hard-bottom habitat at each site. Survey locations were accessed by small boat and spaced a minimum of 60 m apart, though adjacent locations were rarely surveyed on the same day. Behavior surveys were carried out in parallel with underwater visual census (UVC), thus three divers were present at each survey location. Two divers worked together to conduct belt-transects of fishes and benthos, while the third diver carried out surveys of fish behavior. The fish behavior diver maintained visual contact with the UVC divers but maintained a distance of at least 10 m. Diver operated stereo-video (stereo-DOV) was used to conduct surveys of fish behavior that were later analyzed in the lab. Fish behavior surveys were based on those of Gotanda et al. (2009). The fish behavior diver (hereafter 'observer') swam slowly about the site holding the stereo-DOV unit in front of them and searching for any targeted reef-fish species that was foraging or moving slowly and in a position where it could be approached directly. When a suitable individual was located, the observer approached horizontally at the same depth as the fish and at a steady swimming speed. The approach was continued until the fish started to flee, as indicated by an increase in speed and often a change in direction, or until the observer could not get any closer to the fish. About 20 minutes was spent at each survey location, thus the number of behavior trials varied based on the density of targeted species present, resulting in differing sample sizes by species/family and site.

### Video analysis

EventMeasure software (SeaGIS) was used to analyze stereo-video data and enabled precise measurements of distance and fish length. Fish species, conspecific group size, and activity (feeding or travelling), was recorded at the beginning of each trial approach. Fish length was measured at the closest point where the fish was orientated perpendicular to the observer. SD was measured at the beginning of each trial approach. This was determined as the farthest point of the approach where the line of site between observer and fish (and vice-versa) was unobstructed. Flight response was identified as a change in speed and often direction. FID was measured as distance from observer (stereo-DOV) to the nearest part of the fish, usually the tail, immediately before the observed flight response. If there was no observable flight response, FID was recorded as the minimum distance between the observer and fish. dMAD was measured separately as the minimum distance from the observer to the fish at any time during the approach. Thus, dMAD was always less than or equal to FID. Often dMAD coincided with FID, however sometimes it occurred before, or after, an observed flight response.

Escape response was classified into five categories, based on video observations. These can be roughly organized from most-wary to least-wary behaviors listed as follows: “spook” – large burst of speed, “shelter” – take shelter in the substrate, “evade” – evasive maneuvers side to side and/or in and out of structure, “flee” – increase speed and swim away in a single direction, usually toward deep water, and “none” – no visible escape response.

### Data analysis

#### *Data cleaning*

The full suite of variables influencing flight behavior were investigated using the dataset from the fished area (Ka‘ūpūlehu). Observations of the generally smaller-bodied, non-targeted surgeonfishes (Acanthuridae) and wrasses (Labridae) were removed so we could treat those families as being ‘targeted’ by spearfishers. Families with very small sample sizes ( $N < 5$ ) were also removed, as were all soldierfishes (Holocentridae) due to their close affinity to shelter. To investigate the effect of SD on FID and dMAD and examine differences in targeted reef fish flight

behavior related to fishing pressure, data from the reserve and fished area were combined. To ensure a robust comparison, data for families with  $N < 10$  for either site were removed. Species that were not sampled at both sites were also removed.

#### *Variables influencing flight behavior*

Previously tested and novel variables that potentially influence flight behavior were identified based on a review of the literature and grouped into three main categories: aspects of observer/observation trial, aspects/attributes of fish under observation, and environmental factors (Table 4.1).

**Table 4.1** Variables tested with potential influence on flight behavior.

<b>Variable</b>	<b>Type</b>	<b>Units</b>	<b>Description/ justification</b>
<i>Observer</i>			
Bubble	True/False	-	If flight response coincided with SCUBA exhale. A potential confounding variable.
Observer	Categorical	-	Most observations were conducted by a single observer, though a small number were conducted by a different observer. A potential confounding variable.
Starting distance	Continuous	m	The distance between the fish and the observer at the beginning of the trial approach.
<i>Fish</i>			
Activity	Categorical	-	Fish activity during trial approach, either travelling or feeding.
Family	Categorical	-	Previous research has shown differences in flight response by fish family.
Group size	Continuous	fishes	Predator theory predicts differences in flight response based on group size.
Length	Continuous	cm	Shown by previous research to influence flight response. Larger individuals have higher reproductive value, and thus are warier of predation.
Maximum size	Continuous	cm	Maximum recorded size of species. Larger bodied species tend to be more targeted by fishers.
Mobility	Categorical	-	Range of daily movements of fish species (Friedlander and Parrish 1998a). Transient: move rapidly over relatively large distances, semi-vagile type I: tens of meters - butterflyfishes and small wrasses, semi-vagile type II: potentially hundreds of meters – large surgeonfish and parrotfish.
Targeted	True/False	-	If species is targeted by spear fishing (Koike et al. 2015).
Trophic level	Categorical	-	Primary, secondary, top predator (Froese and Pauly 2017).
<i>Environment</i>			

Depth	Continuous	m	Deeper areas are less accessible to spear fishers.
Distance to shore	Continuous	m	Areas far from shore are less accessible to spear fishers.
Rugosity	Continuous	m	A measure of seafloor complexity. The length of chain lain along the seafloor surface profile corresponding to a 10 m transect. Fish wariness is thought to increase in areas with less shelter available.
Visibility	Continuous	m	Estimated from video. Furthest distance where objects/fishes can be distinguished from background.
Wave power	Continuous	kW/m	Areas with high waves have been shown to harbor targeted fish populations and are thought to provide a refuge from fishing pressure.

Influence of these variables on measures of FID and dMAD in the fished area were investigated using distance-based linear models (DistLM) (Anderson et al. 2008). DistLM is based on a resemblance matrix and we used Euclidean distances so the resulting  $F$  ratio and  $R^2$  values are equivalent to those obtained from traditional multiple linear regression. However, an important distinction of the DistLM routine is that the  $P$ -values are obtained by permutation, thus avoiding the traditional assumption that errors be normally distributed (Anderson et al. 2008). Distributions of continuous variables were examined to ensure they were not heavily skewed or contained extreme outliers and collinearity between variables was evaluated. Group size was 4<sup>th</sup> root transformed. Marginal tests were performed to evaluate the independent influence of each predictor on FID and dMAD. Final combined models were identified using a step-wise selection procedure with AIC model selection criteria and models were run with 9,999 permutations.

The relationship of SD with FID and dMAD was analyzed using quantile regression on the combined dataset. Due to the constraint that  $FID/dMAD \leq SD$  (escape cannot occur before the experiment starts), the relationship could not be modeled using ordinary least squares (OLS) linear regression as it violates the assumption of homoscedasticity and a spurious positive relationship is likely to be produced (Chamaillé-Jammes and Blumstein 2012). Quantile regression overcomes problems with the estimation of regression models that exhibit heteroscedasticity (non-constant variance) and is robust to outliers. The natural rate of leaving ( $\lambda$ ) is a critical determinant of the slope of the FID/dMAD-SD relationship. As animals become more likely to leave when approached, FID/dMAD become closer to SD and the

slope increases towards 1. Thus, conducting flight distance experiments is difficult on mobile species because false escapes will be recorded (Chamaillé-Jammes and Blumstein 2012). When the value of  $\lambda$  is unknown one must assume that the likelihood of the animal leaving before the observer reaches FID/dMAD is negligible. Under this assumption, the most robust approach is to test whether the slope of the lowest quantiles differs significantly from zero (Chamaillé-Jammes and Blumstein 2012). In addition, the use of quantile regression on upper quantiles can provide information as to the relative value of  $\lambda$  (Chamaillé-Jammes and Blumstein 2012). The relationship of water visibility and SD was visualized using OLS linear regression. Distributions of SD and water visibility for each site were compared using one-way Analysis of Variance (ANOVA) tests. SD was  $\ln(x)$  transformed to meet assumptions of normality, while water visibility did not require transformation.

#### *Fishing effects on flight behavior*

In order to incorporate the variation among survey locations and fish species, the effect of fishing on flight behavior was determined using linear mixed models where survey location and species were included as random factors. Key variables identified using the DistLM analysis were included as fixed factors. These were SD, length, depth, group size, family, activity and site (fishing level). Visibility was also included as a fixed factor. While shown to be significant variables in the DistLM models, maximum species size and mobility guild were not included in the linear mixed models because they were not measured in the field and the variability associated with these variables relates directly to species level differences.

Preliminary models indicated that observer was a significant factor, so observations by the secondary observer (n=43) were removed. FID and dMAD were  $\ln(x)$  transformed prior to modeling to meet assumptions of normality. Continuous variables were centered and scaled prior to modeling by subtracting the column means (omitting NAs) of x from their corresponding columns and dividing the (centered) columns of x by their standard deviations. A significance test of fixed factors was performed with a type III F-test, a marginal test that asks how much variation a predictor explains after the other predictors are accounted for. Degrees of freedom were estimated using the Kenward-Roger approximation.

### *Escape response*

Due to larger sample sizes, observations of three families: Acanthuridae, Mullidae, and Scaridae were selected for analysis of flight response. A Chi-squared test of independence of escape response by site and family was conducted and a mosaic plot was built based on these results. The plot shows relative occurrences of each escape response category by family and site and shows which combination of factors are significantly associated.

## **Results**

Measures of flight behavior were recorded for a total of 760 fishes comprising 58 species from 15 families at 40 independent locations in the fished area (Ka‘ūpūlehu) and 23 independent locations in the reserve (Kaho‘olawe). Variables influencing flight behavior were investigated for the fished area that, after cleaning, resulted in a total of 446 observations of 43 species from 9 families. The influence of fishing on flight behavior of targeted species was tested on a combined dataset from the reserve and fished area that, after cleaning, made up 489 observations of 14 species from five families (Supplement 4.1).

### Variables influencing flight behavior

DistLM marginal tests showed that all variables tested, with the exception of SCUBA bubbles, observer, and group size, were significant independent predictors of FID. Final combined DistLM results showed that SD had a disproportionately large effect on FID, accounting for 51% of total variation, followed by family (4.1%), fish length (3.4%), and activity etc. (Table 4.2).

**Table 4.2** DistLM results for FID, showing predictors identified as significant.

<b>Predictor</b>	<b>AIC</b>	<b>SS(trace)</b>	<b>Pseudo-F</b>	<b>P</b>	<b>Prop.</b>	<b>Cumul.</b>	<b>res.df</b>	<b>regr.df</b>
Start dist.	6322	6.61E+08	463.1	<0.001	0.511	0.511	444	2
Length	6292	4.37E+07	32.8	<0.001	0.034	0.544	443	3
Activity	6270	3.20E+07	25.3	<0.001	0.025	0.569	442	4
Family	6241	5.27E+07	5.7	<0.001	0.041	0.610	434	12
Targeted	6229	1.64E+07	14.6	<0.001	0.013	0.622	433	13
Depth	6217	1.49E+07	13.5	<0.001	0.011	0.634	432	14
Max size	6211	7.88E+06	7.3	0.006	0.006	0.640	431	15
Mobility	6206	9.90E+06	4.6	0.013	0.008	0.648	429	17

Whether a species was targeted by spear fishers was a significant predictor accounting for 1.3% of total variation. SCUBA bubbles, distance to shore, group size, observer, rugosity, trophic level, visibility, and waves were not significant predictors of reef fish FID. Marginal tests for MAD indicated that only SCUBA bubbles was not a significant independent predictor. Final combined DistLM results for dMAD also showed a large effect of SD, though it explained less variation (43%) compared to the FID model (Table 4.3). Length accounted for more variation in this model (5.5%), compared to the FID model and group size was a significant predictor, while other predictors showed similar results (Table 4.3). SCUBA bubbles, distance to shore, observer, rugosity, trophic level, visibility, and waves were not significant predictors of reef fish dMAD.

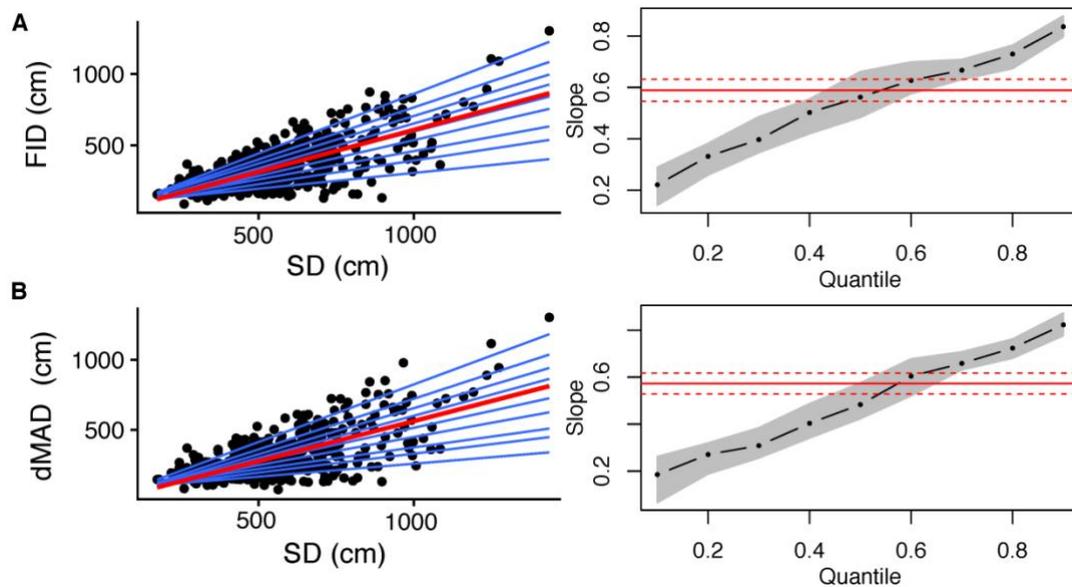
**Table 4.3** DistLM results for dMAD, showing predictors identified as significant.

<b>Predictor</b>	<b>AIC</b>	<b>SS(trace)</b>	<b>Pseudo-F</b>	<b>P</b>	<b>Prop.</b>	<b>Cumul.</b>	<b>res.df</b>	<b>regr.df</b>
Start dist.	6379	5.44E+08	335.0	<0.001	0.430	0.430	444	2
Length	6336	6.91E+07	47.0	<0.001	0.055	0.485	443	3
Family	6312	5.67E+07	5.2	<0.001	0.045	0.530	435	11
Activity	6290	3.03E+07	23.3	<0.001	0.024	0.554	434	12
Targeted	6277	1.85E+07	14.7	0.001	0.015	0.568	433	13
Depth	6268	1.36E+07	11.0	0.001	0.011	0.579	432	14
Max size	6259	1.32E+07	10.9	0.002	0.010	0.589	431	15
Mobility	6246	1.94E+07	8.3	0.002	0.015	0.605	429	17
Group size	6242	6.95E+06	6.0	0.015	0.006	0.610	428	18

#### *Starting distance*

Distributions of SD did not differ statistically between sites ( $F_{1,487}=0.74$ ,  $p=0.4$ ), though there were more high values in the fished area. Visibility had a significant positive relationship with SD (Supplement 4.2 A) and the fished area had significantly higher visibility ( $F_{1,487}=4.00$ ,  $p<0.05$ ), (Supplement 4.2 B). Quantile regressions revealed that the slope of fitted lines increased with higher SD (corresponding to higher FID and dMAD) (Figure 4.1). Slopes for dMAD were slightly lower for all quantiles compared to FID. The slope for the lowest (0.1) quantile was significantly different from zero (Figure 4.1). This result, however, was mainly driven by scarids which predominated in the dataset and did not hold for the other families measured (Supplement 4.3 ). The slope for the highest (0.9) quantile

was significantly  $< 1$  for scarids and mullids, though not for acanthurids, labrids, or lethinids (Supplement 4.3 ), though the small sample size for the latter two families urges caution in interpretation.



**Figure 4.1** Quantile regression of SD vs A) FID (cm) and B) dMAD. Left hand plots show regression lines fit to each of 9 quantiles of FID and dMAD (0.1 – 0.9) with the OLS fit in red included for reference. Right hand plots show slope of each fit with 95% confidence intervals. The slope of the ordinary least squares fitted line and confidence intervals are shown in red.

#### Fishing effects on flight behavior

In the linear mixed effects model of FID, SD, activity, length, and depth were significant. Group size, visibility, site, and family were not significant (Table 4.4).

**Table 4.4** Linear mixed effects model – FID, significant effects shown in bold.

	Sum Sq	Mean Sq	Num DF	Den DF	F	Pr(>F)
<b>Start dist.</b>	8.366	8.366	1	475.603	109.765	<b>&lt;0.001</b>
<b>Activity</b>	1.284	1.284	1	473.462	16.848	<b>&lt;0.001</b>
<b>Length</b>	1.020	1.020	1	472.903	13.388	<b>&lt;0.001</b>
<b>Depth</b>	0.598	0.598	1	59.939	7.843	<b>0.007</b>
Group size	0.133	0.133	1	453.373	1.746	0.187
Visibility	0.131	0.131	1	49.917	1.716	0.196
Site	0.098	0.098	1	72.959	1.281	0.261
Family	0.206	0.052	4	7.813	0.677	0.627

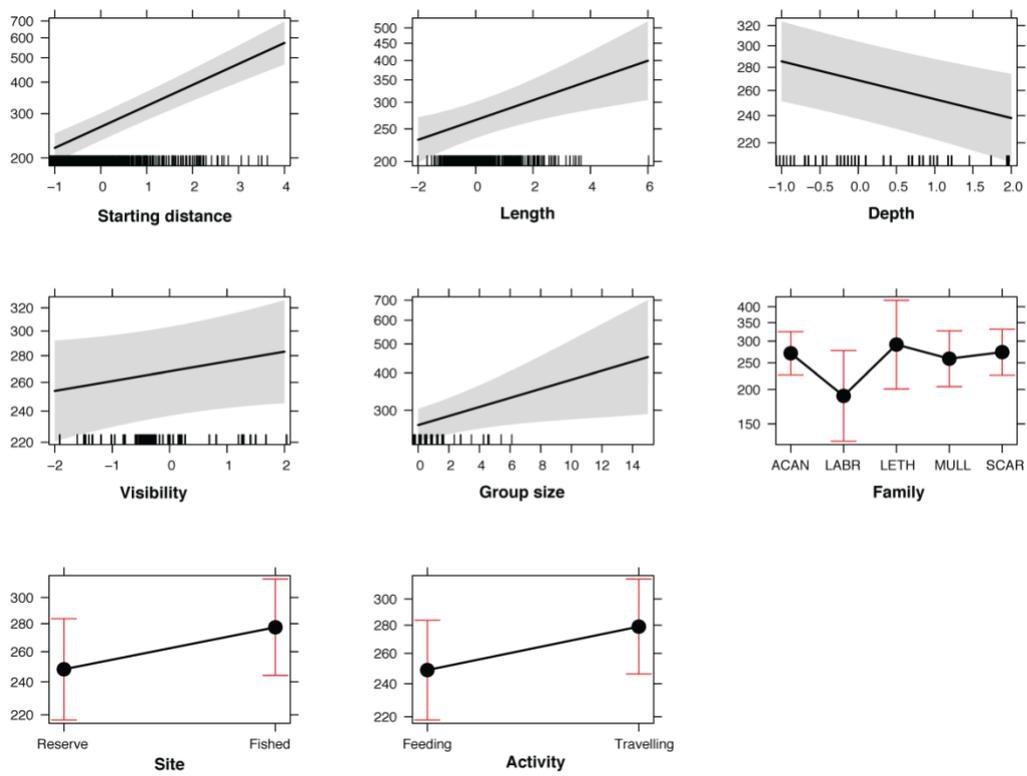
In the linear mixed effects model of dMAD, SD, activity, depth, length, site, and group size were all significant (Table 4.5). Effect of SD was smaller compared to

FID. More variability was attributed to site, and site was a significant factor in this model. Visibility and family were not significant (Table 4.5).

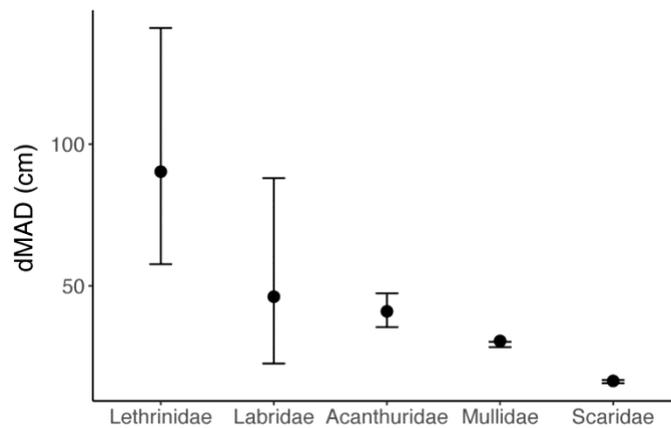
**Table 4.5** Linear mixed effects model – dMAD, significant effects shown in bold.

	<b>Sum Sq</b>	<b>Mean Sq</b>	<b>Num DF</b>	<b>Den DF</b>	<b>F</b>	<b>Pr(&gt;F)</b>
<b>Start dist.</b>	8.203	8.203	1	475.460	92.339	<b>&lt;0.001</b>
<b>Activity</b>	1.130	1.130	1	474.605	12.723	<b>&lt;0.001</b>
<b>Depth</b>	1.125	1.125	1	60.974	12.668	<b>0.001</b>
<b>Length</b>	0.909	0.909	1	469.711	10.227	<b>0.001</b>
<b>Site</b>	0.617	0.617	1	74.325	6.943	<b>0.010</b>
<b>Group size</b>	0.508	0.508	1	456.892	5.713	<b>0.017</b>
Visibility	0.212	0.212	1	48.833	2.384	0.129
Family	0.309	0.077	4	7.855	0.870	0.522

SD, length, visibility, and group size all had a positive relationship with dMAD while depth had a negative relationship (Figure 4.2). MAD was lower when fishes were feeding. While dMAD by family did not differ significantly, lethrinids had the largest average dMAD and labrids had the lowest (Figure 4.2). Average MAD for acanthurids, mullids, and scarids were very similar. Overall, targeted species in the fished area had significantly higher dMAD compared to in the marine reserve (Figure 4.2). Mean modeled family level differences in dMAD between sites ranged from 90.3 cm for lethrinids to 16.5 cm for scarids (Figure 4.3).



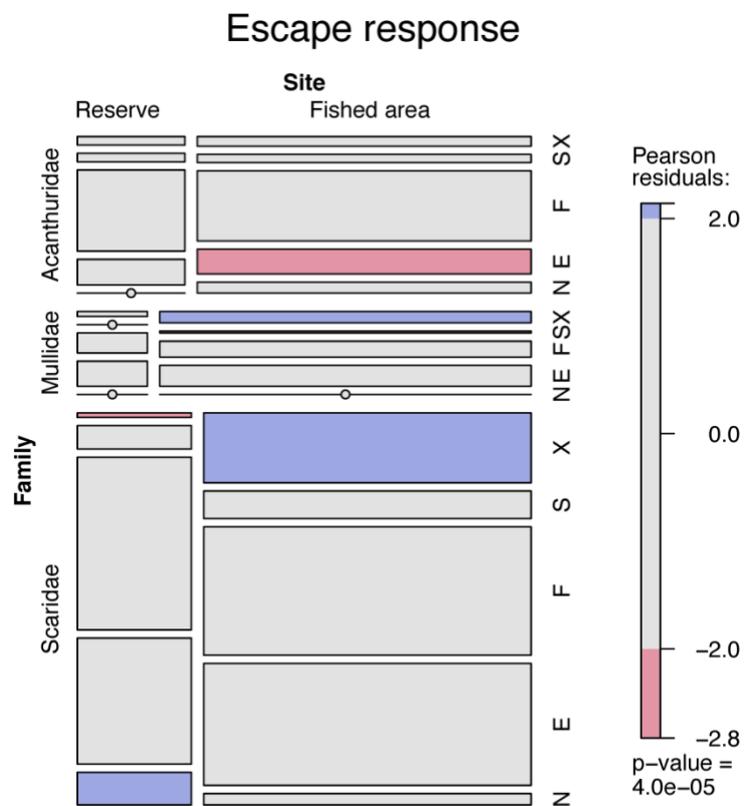
**Figure 4.2** Fixed effects for dMAD linear mixed effects model. Y-axis is  $\ln(\text{dMAD})$  in cm, x-axis represents scale of each fixed effect, units shown in Table 4.1. All continuous variables were centered and scaled prior to modeling. Family codes are as follows: ACAN – Acanthuridae, LABR – Labridae, LETH – Lethrinidae, SCAR – Scaridae.



**Figure 4.3** Family difference in effect size between sites: Fished area (Ka'ūpūlehu) – reserve (Kaho'olawe). Effect sizes are shown in centimeters, error bars represent 0.95 confidence intervals.

## Escape response

Analysis of escape response showed that surgeonfishes (Acanthuridae) had a significantly lower incidence of evasive flight in the fished area (Figure 4.4). Goatfish (Mullidae) and parrotfish (Scaridae) had a significantly higher incidence of “spook” in the fished area (Figure 4.4). Surgeonfishes predominately exhibited a ‘flee’ response. Overall, ‘evade’ and ‘flee’ were the most common escape responses across all three family groups. Taking shelter was relatively uncommon, but most common among parrotfish.



**Figure 4.4** Mosaic plot of fish escape response by site for families with the greatest number of observations. From least wary to most wary: N=none, E=evade, F=flee, S=shelter, and X=spook. The size of the cells represents the frequency of occurrences for that combination of levels. Cell colors represent the residual levels corresponding to the legend. Blue colors mean there are more observations than would be expected under the null model (independence), red colors mean there are fewer. Overall this plot shows which cells are contributing to the significance of the Chi-squared test result.

## Discussion

We found significant relationships between SD and both measures of flight behavior. SD explained a large portion of the variability in FID and somewhat less variability in dMAD. Other key variables were fish length, activity, and depth. When including these co-variables in models of FID and dMAD of targeted reef fishes, we found significant differences between a marine reserve and heavily fished area for dMAD though not for FID. Relative effect sizes of SD and, to a lesser extent, other co-variables were large in comparison to site. Consequently, studies that use similar methods and do not control for or incorporate SD may produce biased results with regard to the effects of fishing pressure on flight behavior of reef fishes.

### Starting distance

Behavior trials were conducted using a large range of SD, which enabled a robust evaluation of the relationship with measurements of flight behavior. By definition, an approached fish cannot initiate flight from a distance longer than SD. This constraint can potentially create an artefactual relationship between the variables if the variance increases with distance (Dumont et al. 2012). Nevertheless, there is support for a general rule of anti-predator behavior based on the relationship between SD and FID in other taxa, where animals should initiate flight soon after they detect a predator to minimize monitoring costs – the ‘flush early and avoid the rush’ hypothesis (Blumstein 2010, Samia et al. 2013). Recently, Tran et al. (2016) demonstrated a positive relationship between SD and FID in a non-targeted coral reef fish (*Ctenochaetus striatus*). We show this relationship holds across a number of targeted reef fish families. Furthermore, for scarids the slope for the lowest (0.1) quantiles was significantly different from zero, suggesting that SD does have a significant effect on FID and dMAD that is not artefactual (Chamaillé-Jammes and Blumstein 2012). The slope for the highest (0.9) quantiles was significantly  $< 1$ , suggesting a low natural rate of leaving (Chamaillé-Jammes and Blumstein 2012) for scarids and mullids, though not for acanthurids, labrids, or lethrinids. An important implication of these findings is that FID of fishes (as in other taxa) is dynamic and depends to a large degree on SD. Previous studies on flight behavior of coral reef fishes have controlled for SD by maintaining a narrow range of SD (eg. Bergseth et al., 2016; Feary et al., 2010; Januchowski-Hartley et al., 2011, 2015, 2013). Due in part to the

constraint on measures of FID from SD, our results show that measures of FID at higher SD are more variable. In addition, we show that SD is correlated with water visibility. Because it is difficult to standardize SD for behavior trials of fishes in the field, we recommend that future studies measure SD so that it may be accounted for in the analysis.

#### Other variables

In addition to SD, we found large and consistent effects on flight behavior from depth and activity, two variables that have not to our knowledge previously been tested for fishes. Depth had a negative relationship with flight distance. This could be because deeper areas are less intensively fished because they are harder for spear fishers to access, however, our models did not show a significant interaction between site and depth. Additionally, distance to shore also relates to accessibility to fishers and was not shown to be a significant predictor of flight behavior. Many fishes in our study fled towards deep water, thus perceived risk may increase in shallow water (where there is greater distance from potential refuge) leading to increased flight distances (Stankowich and Blumstein 2005). Fishes that were actively foraging prior to or during a trial approach had significantly lower flight distance, likely due to reduced ability to detect and react to the human predator while feeding (Krause and Godin 1996).

Fish length and group size were significant predictors of flight behavior. Fish length had strong positive relationships with both FID and dMAD. This is supported by optimal fitness theory (Cooper Jr. and Frederick 2007) and previous flight behavior research on coral reef fishes (Gotanda et al. 2009, Januchowski-Hartley et al. 2011, 2015, Miller et al. 2011, Bergseth et al. 2016). In our study, group size had a significant positive effect on dMAD but not FID. Previous studies have failed to find an effect of group size on FID (Gotanda et al. 2009, Benevides et al. 2016, Nunes et al. 2016) with the exception of Januchowski-Hartley et al. (Januchowski-Hartley et al. 2011) who found group size to be important for acanthurids, but not for other families. Our findings do not follow the theory that there is a dilution of risk with larger fish groups, leading to smaller flight distances (Godin 1986, Krause and Godin 1994). This may be because the coral reef fish species included in this study rarely

form large schools and may use conspecific behavior as cues of predation risk and thus flee at greater distances when in larger groups (Owens 1977).

Fish attributes of maximum size and mobility were shown to have positive relationships with flight distance, while trophic level was not a significant predictor. Larger-bodied species are generally more targeted by spear fishers (Pavlowich and Kapuscinski 2017), and thus more likely to have experience with human predation, leading to longer flight distances (Stankowich and Blumstein 2005). Fishes with higher mobility are more likely to be found farther from potential refuges, also leading to increased flight distances (Gotanda et al. 2009, Miller et al. 2011). Spearfishers caught the most diverse array of species across all trophic levels, compared to users of other fishing gear at Ka‘ūpūlehu (Koike et al. 2015). It is, therefore, not surprising that trophic level did not significantly influence flight behavior

Environmental variables of rugosity, visibility, and waves were not found to be significant predictors of flight behavior. Rugosity is an index of structural complexity that relates to refuge availability and thus might be expected to influence flight behavior. In contrast to our results, Januchowski-Hartley et al., (Januchowski-Hartley et al. 2015) and Nunes et al. (2015) showed a significant effect of structural complexity on parrotfishes and two labrid species, respectively. Likewise, visibility did not have a direct effect on flight behavior, though it did have indirect effects on flight behavior as we showed it to mediate SD. The limiting factor in terms of visibility in this study was the video resolution, which is less sensitive than both human and fish vision. Nevertheless, it is likely that visibility does have some effect on fish flight behavior, as fishes are less likely to detect predators under very low visibility. Waves have been shown to promote targeted fish biomass and abundance and are thought to provide a refuge from fishing pressure (Stamoulis et al. 2016). The lack of a significant effect of waves on flight behavior in this study could be due to the low range of wave power among Ka‘ūpūlehu sites, and future investigations would benefit from sampling across a larger gradient.

All behavior trials were conducted using SCUBA. Based on observations of fishes reacting to the diver exhalation/bubbles, we tested if FID and dMAD were

significantly influenced by the timing of diver exhalation (i.e., did FID/dMAD coincide with diver bubbles), and found no effects. Nevertheless, in order to avoid this potential factor, we recommend that observers on SCUBA measuring flight behavior take care to regulate their breathing. The majority of trial observations in our study were conducted by a single observer, however, a small subset (43) were conducted by an alternate observer. While observer was not a significant variable in DistLM models for the fished area dataset, when included in linear mixed models for the combined dataset it was a significant predictor of both FID and dMAD, and thus data from the second observer was excluded for the final models. Januchowski-Hartley et al. (2012) found small but significant differences in FID between observers using both SCUBA and free diving methods in a no-take marine reserve. Because the differences were not consistent in direction and did not occur between the same observers, they were considered a random source of error. Based on this previous work and our results, we recommend that observer effects be considered in future studies and care taken to standardize approach speed, diver behavior, and gear, to minimize these effects.

#### dMAD vs FID

We introduce dMAD as a compliment or alternative to FID. Video analysis procedures are very similar to MAD calculated from stereo-video transect surveys (Lindfield et al. 2014a, Goetze et al. 2017), though fishes were actively approached using the same methodology used to measure FID (Gotanda et al. 2009). Importantly, dMAD was significantly affected by differences in fishing pressure while accounting for other key variables, but FID was not. While patterns of dMAD were very similar to FID, we found dMAD to be less dependent on SD. One advantage of using dMAD as an alternative to FID is that flight responses in fishes are not always evident. For instance, a large proportion of parrotfishes showed no flight response within the reserve. In these cases, FID was assumed to be equal to dMAD. In addition, dMAD may solve some potential sources of error in FID. Spontaneous movement could produce an artefactual effect of SD on FID where probability of spontaneous movement increases with SD (Cooper 2005). In contrast to most other taxa for which FID has been studied, fishes rarely stop moving. Aggressive or evasive movements of fishes in response to other fishes may be

mistaken for a flight response. Because it ignores these nuances of fish behavior, dMAD may tend to minimize these potential sources of error.

#### Fishing effects on flight behavior

Studies of flight behavior of coral reef fishes have focused on the effects of (spear) fishing pressure as the primary variable of interest. Establishing a relationship between fishing pressure and flight behavior could provide useful applications for management of coral reef fisheries such as assessing compliance in no-take marine reserves (Bergseth et al. 2015). We show that four variables (SD, activity, depth, fish length) have larger effects on FID than fishing pressure, and only by considering an alternate measure of flight distance did we find a significant effect of fishing. Nevertheless, our results are consistent with previous studies showing higher flight distance of targeted species in fished areas compared to protected areas (Gotanda et al. 2009, Feary et al. 2010, Januchowski-Hartley et al. 2011, 2014, 2015, Bergseth et al. 2016). Species included in our analysis are known to be targeted in Hawai'i and have been shown to be components of spearfishing catch in the fished area (Koike et al. 2015).

We found no significant differences in FID or dMAD between reef fish families. Nevertheless, differences in mean effect size suggests that some families may be more sensitive to fishing pressure than others. Emperors (Lethrinids - represented by a single species in this study) had the largest mean effect size, suggesting that *Monotaxis grandoculis* could be a potential indicator species for spearfishing pressure in Hawai'i where this species is highly prized by spearfishers. In contrast, parrotfishes (Scaridae) had the lowest mean effect size and surgeonfishes (Acanthuridae) had intermediate effect sizes. This is supported by a previous study that showed surgeonfishes flight behavior to be more sensitive to differences in fishing pressure compared to parrotfishes (Januchowski-Hartley et al. 2014).

#### Escape response

Escape response behaviors of parrotfishes and goatfishes support the dMAD results. Parrotfishes and goatfishes had significantly higher proportion of 'spook' behavior at the fished area and parrotfishes had significantly higher proportion of 'no flight' behavior at the reserve. Spook behavior is an energetically costly flight response in

which the fish suddenly flees at high speed. For parrotfishes, this involves body and caudal fin swimming as opposed to using pectoral fins only (Miller et al. 2011). ‘No flight’ reflects a low level of perceived threat, where fishes are not seeking cover or increasing speed. Surgeonfishes showed a significantly lower proportion of ‘evade’ at the fished area and relatively higher proportion of ‘no flight’. This seems to contradict the dMAD results and suggests that escape response may not be a reliable indicator of perceived threat for acanthurids. Guidetti et al. (2008) showed that two species of sea breams more frequently sought shelter on protected reefs and more often escaped to open water on fished reefs in the Mediterranean. Our findings did not reflect this, as frequencies of shelter behavior were consistent between sites for each family. Nunes et al. (2015) reported that ‘run away’ behavior was the most common escape response in labrids. This is equivalent to ‘flee’ behavior in this study which was the most common escape behavior among acanthurids and scarids. Conversely, for labrids, ‘shelter’ was the most common escape response and ‘flee’ was among the least common. We suggest including escape response as a complement to flight distance in studies of flight behavior to help understand if the patterns described here are consistent across geographies and determine if escape response is a reliable indicator of fishing pressure for some fish families. The escape response categories developed for this study were refined over many repeated observations of the experimental trial video recordings. They represent consistent escape behaviors for coral reef fish and we recommend their use in future studies.

## **Conclusions**

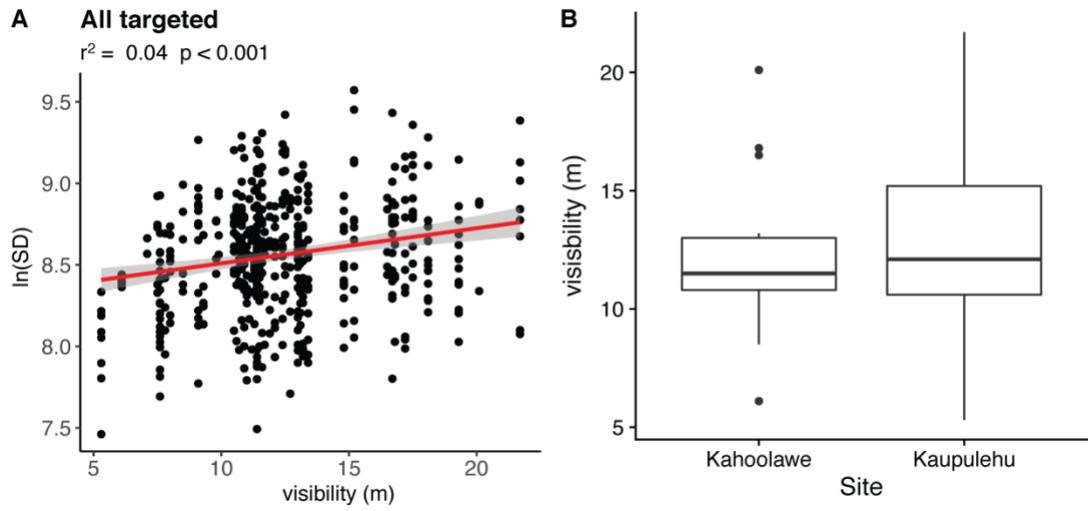
We show that SD, feeding activity, depth, and length have significant effects on flight distance which outweigh the effects of fishing pressure. Future studies investigating fishing effects on flight distance should include these variables in the analysis. SD in particular should be recorded to control for its impact on flight distance. Furthermore, we recommend using dMAD as a complement or alternative to FID. Stereo-video provides a means to accomplish these objectives with high precision and minimum effort in the field and can yield a variety of complementary data such as escape response. Research is needed to understand if incorporating fish behavior can improve measures of targeted fish assemblages such as abundance and biomass. This has implications for evaluating MPA effectiveness, studies of fish-

habitat relationships, species distribution modelling, as well as other applications. How flight behavior impacts ecosystem function of targeted fishes is another important area for study. In addition, flight distance is a potential indicator of spear fishing pressure that could be used as a tool to measure and monitor compliance in marine reserves. To address these topics, further research is needed to quantify flight distance of targeted species along gradients of fishing pressure, while controlling for key co-variables.

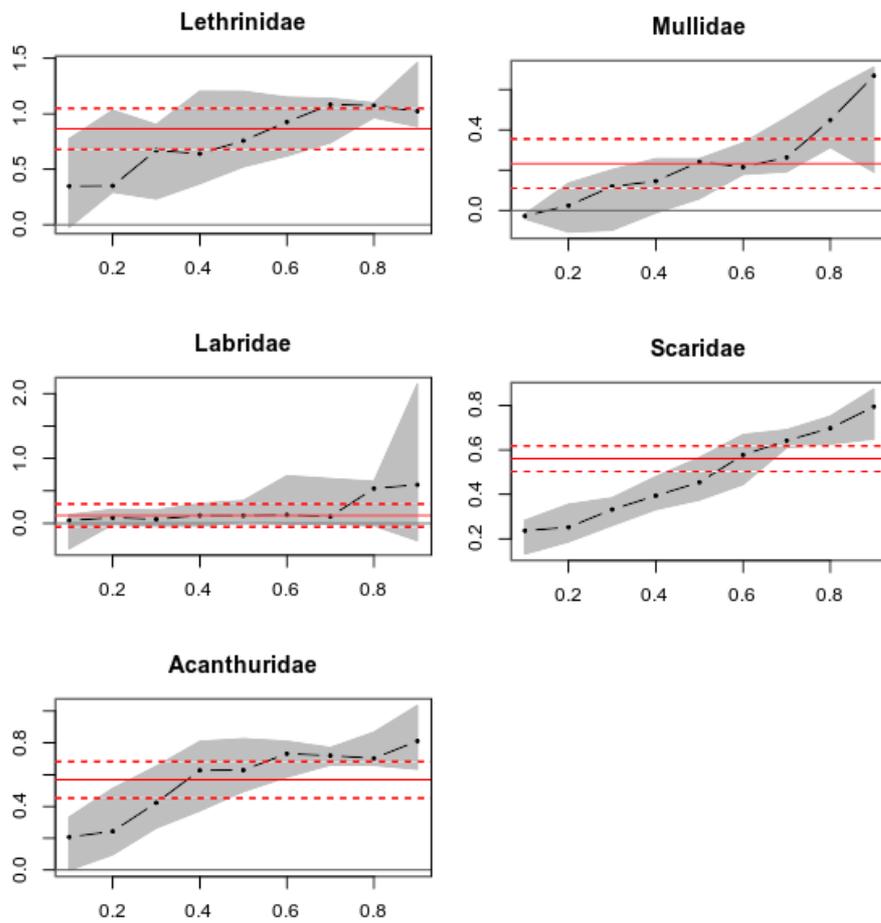
## Supplementary Material

**Supplement 4.1** Details of final combined dataset used for linear mixed effects models. Numbers refer to sample size by species/family. Endemic species are indicated with \*.

<b>Family/species</b>	<b>Kaho‘olawe</b>	<b>Ka‘ūpūlehu</b>
<b>Acanthuridae</b>	<b>29</b>	<b>75</b>
Acanthurus blochii	4	1
Acanthurus dussumieri	3	3
Acanthurus olivaceus	8	30
Naso lituratus	10	36
Naso unicornis	4	5
<b>Labridae</b>	<b>16</b>	<b>5</b>
Bodianus bilunulatus*	16	5
<b>Lethrinidae</b>	<b>18</b>	<b>11</b>
Monotaxis grandoculis	18	11
<b>Mullidae</b>	<b>10</b>	<b>46</b>
Mulloidichthys flavolineatus	2	4
Parupeneus insularis	4	2
Parupeneus multifasciatus	4	40
<b>Scaridae</b>	<b>77</b>	<b>202</b>
Chlorurus perspicillatus*	1	2
Chlorurus sordidus	33	143
Scarus psittacus	2	21
Scarus rubroviolaceus	41	36
<b>Grand Total</b>	<b>150</b>	<b>339</b>



**Supplement 4.2** Relationship between visibility (m) and  $\ln(x)$  transformed starting distance. B) Comparison of visibility (m) between sites.



**Supplement 4.3** Slopes of quantile regressions of SD vs MAD by family.

## **CHAPTER 5 - Incorporating fish behavior improves accuracy of species distribution models**

### **Abstract**

Species distribution models (SDMs) are used to interpret and map fish distributions based on habitat variables and other drivers. Fishing pressure is a major driver of fish behavior which has been shown to vary in the presence of divers. Diver avoidance behavior or fish wariness may spatially influence counts and other descriptive measures of fish assemblages. Because fish assemblage metrics are response variables for SDMs, measures of fish wariness may be useful as predictors in SDMs of targeted fishes. We used a diver operated stereo video system to conduct belt-transects and record minimum approach distance (MAD) of targeted reef fishes and inside and outside of two marine reserves on the island of O’ahu in the main Hawaiian Islands. We compared MAD in reserves to fished areas to test the assumption that it provides a proxy for fishing pressure. We then compare accuracy of SDMs including MAD as a predictor with SDMs that do not. MAD varied between sites and was lower inside reserves compared to fished areas, providing a proxy of fish wariness. When maximum values of MAD were used to represent sites with no targeted fishes present, MAD was correlated to estimated fishing pressure and greatly improved accuracy of SDMs.

### **Introduction**

A current focus in marine ecology has been to create species distribution models (SDMs) to explain and sometimes map fish distributions based on habitat drivers. This information can assist with marine protected area design and marine spatial planning (Shucksmith and Kelly 2014). Fish species respond to their habitat in different ways depending on their life-history strategies, predators, competitors, and food availability (Sale 1998, Boström et al. 2011). Fishing pressure is a primary driver, not only of fish distributions (Jennings and Polunin 1996, Friedlander and DeMartini 2002), but also fish behavior (Kulbicki 1998). Fish behavior has been shown to vary in the presence of SCUBA divers depending on prior experience of divers’ activities (ie. feeding vs spearing) (Cole 1994, Kulbicki 1998, Watson and Harvey 2007). Consequently, it is logical to expect that fish behavior may vary

spatially influencing counts and other descriptive measures of fish assemblages. Many shallow water surveys use underwater visual census (UVC) conducted by observers on SCUBA (Brock 1954). Despite earlier recognition of the potential behavioral biases associated with surveys of targeted fishes (Kulbicki 1998), only recently have there been attempts to quantify the impacts of diver avoidance behavior on measures of fish assemblages. Because fish assemblage metrics are response variables for SDMs, measures of fish behavioral responses to the presence of survey divers may be useful as predictors in SDMs of targeted fishes.

In locations with high fishing pressure, area-based fish survey methods may underestimate fish abundance of species targeted by spear fishers (Kulbicki 1998, Feary et al. 2010). Lindfield et al. (2014a) tested the magnitude of avoidance behavior by using a diver operated stereo video system (stereo-DOV) to survey fish populations inside and outside of two no-take reserves in Guam using standard open-circuit SCUBA and a closed-circuit rebreather (CCR) that produces no bubbles, and therefore, greatly reduces the disturbance caused by survey divers' presence. They recorded 'minimum approach distance' (MAD – the distance between the diver and the fish at its closest point) for each fish observed on belt transects, finding that fished sites sampled on SCUBA had the greatest average MAD for targeted fish groups. Overall, Lindfield et al. (2014a) found that abundance of targeted fishes was 2.6 times greater when surveyed on CCR compared to on SCUBA, demonstrating a dramatic impact of fish behavior on survey estimates. These effects were corroborated by Gray et al. (2016) who used a different UVC method and found that targeted reef fish estimates were significantly lower on SCUBA compared to CCR at high fishing pressure locations in the main Hawaiian Islands.

Fishing has obvious and direct effects on targeted fish populations (Jackson et al. 2001). Patterns of fishing pressure are difficult to measure and are rarely mapped (but see Chapter 3). Diver avoidance behavior of targeted fishes may provide a proxy for spear fishing pressure (Bergseth et al. 2015). Thus, inclusion of diver avoidance behavior in SDMs could have explanatory power beyond correcting underwater survey bias. Fishing pressure directly increases fish wariness and decreases true fish biomass, while increased fish wariness may decrease observed fish biomass, due to survey diver avoidance. In both cases, increased fish wariness results in decreased

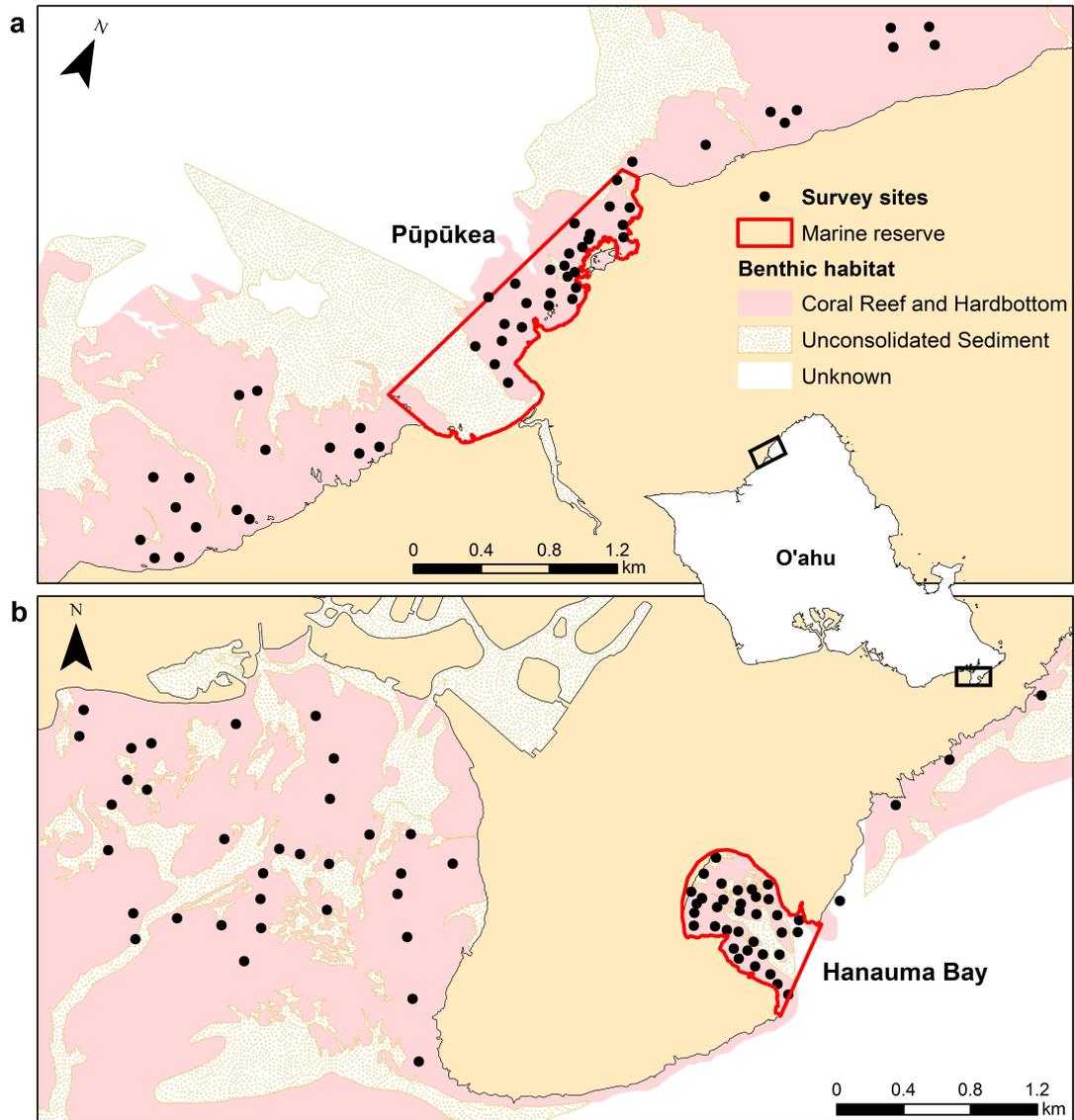
measures of fish biomass. Thus, including a measure of fish wariness should improve explanatory power and predictive accuracy of SDMs.

In order to test this hypothesis, we used a stereo-DOV to conduct belt-transects and record MAD of targeted reef fishes and inside and outside of two marine reserves on the island of O’ahu in the main Hawaiian Islands. We compare MAD in reserves to fished areas to test the assumption that it provides a proxy for fishing pressure, then compare the accuracy of SDMs including MAD as a predictor with SDMs that do not. The objectives of this study were to 1) evaluate MAD of targeted reef fishes as a proxy for fishing pressure, and 2) determine if including MAD as a predictor in SDMs of targeted reef fish biomass improves model accuracy.

## **Methods**

### Study sites

Samples were collected inside and outside of two no-take marine reserves on O’ahu in the Hawaiian Islands (Figure 5.1). Pūpūkea is located on the north shore of O’ahu and was originally established in 1983. It was only 10 ha when first established and allowed for a range of fishing activities. It was expanded in 2003 to encompass 71 ha and fishing activities were greatly restricted. Surveys of Pūpūkea were conducted during June-October 2016. Hanauma Bay is located on the south-east corner of the island and is the oldest MPA in the state, established in 1967. The entire bay is protected and encompasses 41 ha of marine habitats. Hanauma Bay was surveyed between February and May 2017.



**Figure 5.1** Survey locations at a) Pūpūkea and b) Hanauma Bay.

### Field surveys

Transect locations were randomly selected within management type (reserve and open) on hard-bottom habitats using ArcGIS (Figure 5.1). Pre-determined transect locations were uploaded to GPS units for use in the field. Two divers navigated to waypoints from shore or small boat and used a stereo-DOV to conduct a single 5 x 25 m belt transect on SCUBA. The transect began on the GPS point and followed the depth contour. Transect length was measured using a 25 m line reel which was secured to the substrate at the beginning of the transect and rolled out as progress was made. Survey time was standardized to 3 min per transect. The stereo-DOV system recorded imagery from which we calculated the abundance, length, and MAD

of all targeted reef fishes encountered within the transect. At each transect, one diver operated the stereo-DOV system while the second diver followed at least 10 m behind to avoid influencing the survey. The stereo-DOV surveys were conducted by the same researcher throughout. Targeted species of the MHI nearshore fishery were defined as coral reef fishes having  $\geq 450$  kg of annual recreational or commercial harvest for the past 10 years (2000-2010), or otherwise recognized as important for recreational, subsistence, or cultural fishing (Friedlander et al. 2018, Supplement 5.1).

Our stereo-DOV system used two Canon high-definition video cameras mounted 0.7 m apart on a base bar inwardly converged at  $7^\circ$  to provide a standardized field of view. The camera system was built by and purchased from <https://www.seagis.com.au/hardware.html>. Stereo video imagery was calibrated using the program CAL (SeaGIS), following the procedures outlined in Harvey and Shortis (Harvey and Shortis 1998). This allowed for measurements of fish length, distance (range) and angle of the fish from the center of the camera system, and standardization of the area surveyed. Fishes located further than 10 m in front or 2.5 m to the left or right of the stereo-DOV system were excluded based on minimum visibility encountered and transect dimensions.

### Video analysis

Pairs of videos from the stereo-DOV system were analyzed using the program EventMeasure (SeaGIS). The total length of each targeted reef fish encountered on the transect was measured at the closest point of the fish to the cameras and this distance was automatically computed by EventMeasure, thus obtaining an accurate measurement of MAD (Harvey et al. 2004). If this was not possible due to the angle of the fish or obstruction of the camera view, a '3D point' was recorded and used as the MAD for the measured fish (Lindfield et al. 2014a). In the case of large schools, a representative subset of 6-10 individuals was measured, and the remaining fishes in the school were allocated to those records based on size. Biomass was calculated from length estimates using the length-mass conversion:  $M = aTL^b$ , where parameters  $a$  and  $b$  are species-specific constants, TL is total length (cm), and M is mass (g). Length-mass fitting parameters were obtained from a comprehensive

assessment of length-weight fitting parameters for Hawaiian reef fish species (Froese and Pauly 2017).

#### Data analysis

To test effectiveness of the marine reserves included in this study, a two-way ANOVA was used to compare the effects of management and site on targeted fish biomass.

#### *Fish wariness (MAD)*

Linear mixed models were used to compare patterns of MAD of each fish between sites and management types and do not include transects where targeted fishes were not observed. Fish body length, angle of approach, and water depth were included as fixed factors in the models, while transect (location) and species were included as random factors. Linear mixed models were developed with the combined data from both sites and for each site separately. MAD values for each observation were  $\ln(x)$  transformed to meet assumptions of normality and continuous variables were centered and scaled prior to modeling. A significance test of fixed factors was performed with a type III F-test, a marginal test that asks how much variation a predictor explains after the other predictors are accounted for. Degrees of freedom were estimated using the Kenward-Roger approximation (Kenward and Roger 1997). A linear model was used to compare mean MAD of targeted species by transect among sites and management types with water depth included as a co-variable. Transects with no targeted fishes were excluded.

On transects where targeted species were not present, it was not possible to measure MAD. Because MAD represents the minimum distance to targeted fishes, when no targeted fishes are present within a transect, theoretically MAD is some value beyond the range of measurement. A number of transects in both study locations did not contain targeted fishes, resulting in biomass estimates of zero. In order to retain these data for model development and explore the implications of 1) missing MAD values and 2) substituting maximum MAD values, we separately developed SDMs with a predictor dataset retaining missing values for MAD and with a predictor dataset where MAD was set to the maximum value (10m) for those cases hereafter referred to as MAD<sub>10</sub>. Mean MAD by transect was compared to estimated fishing

pressure layers (Chapter 3) using Spearman rank correlation. The relationship of MAD and fishing pressure was evaluated for only transects where targeted fish were present and for all transects including those with no targeted fish where MAD was set to 10 m (MAD<sub>10</sub>).

#### *Species distribution models*

Boosted regression trees (BRT) were used to develop SDMs of the total biomass of targeted reef fish for each study area. BRT models and spatial predictions were generated in R (R Core Team 2014) using the *dismo* (Hijmans et al. 2014) and *raster* (Hijmans 2014) packages. BRT are effective at modeling nonlinearities, discontinuities (threshold effects) and interactions between variables (Breiman 1996, 2001, De'ath and Fabricius 2000). Targeted fish biomass was fourth root transformed prior to modeling. Model fitting and selection was accomplished following the procedures detailed in Elith et al. (2008). To increase parsimony, selected models were then simplified to remove less informative predictor variables (Elith et al. 2008). Simplified models generally had close to eight final predictors. Models with a large number of predictors generally have higher percent deviance explained, to simplify comparison the top eight predictors were retained for all models.

The model training dataset was repeatedly sampled with replacement to create 20 bootstrap samples. Using the optimal parameter value combination and simplified set of predictor variables, a BRT model was fitted to each bootstrap sample and used to make predictions based on the values of the predictor variables at each transect location. The mean of the bootstrapped predictions was used for interpretation and further analysis.

Habitat variables were those used in Chapter 3 following a pairwise correlation analysis (Spearman  $|\rho| > 0.7$ ) for the Main Hawaiian Islands. There were 23 total habitat variables of four broad categories: seafloor topography, benthic habitat composition, geographic (3), and wave energy (1) (Table 5.1, See Chapter 3 for further details and predictor generation methods). Four transects in the open area near Hanauma Bay did not have remotely sensed habitat data and were excluded from BRT models.

**Table 5.1** Habitat predictors used in SDMs. Number of individual datasets of each type indicated in parentheses.

<b>Predictor dataset types</b>	<b>Datasets</b>	<b>Description</b>
Seafloor topography (12)	Depth, Slope, Slope of slope, Aspect, Planar and profile curvature, BPI	Seafloor topography metrics derived from bathymetry including depth, slope, structural complexity, exposure, curvature and bathymetric position index (BPI). Slope, slope of slope, and BPI were calculated at two scales.
Benthic habitat composition (7)	Percent cover of CCA, Macroalgae, Turf, and Soft bottom, Proximity index, Shannons diversity index	Percent benthic cover of major cover types, seascape fragmentation/patch isolation, habitat diversity.
Geographic (3)	Latitude, Longitude, Distance to shore	Geographic location and distance from shore.
Oceanographic (1)	Wave Power	Wave height x wave period.

To determine whether including behavior as a predictor improved model fit and predictive performance, models were developed separately using predictor sets that included and excluded MAD. Models that included MAD were fit either with NAs for transects with no targeted species, or with MAD<sub>10</sub>. Furthermore, to determine if model performance increases due to MAD<sub>10</sub> were due only to accounting for zeros in the response variable, another set of models was developed with a binary variable representing presence of targeted fishes. In addition to the habitat variables described above, management type (reserve/open) was also included as a predictor. In summary, four BRT models were developed separately for each site to explain and predict targeted fish biomass; 1) habitat + management, 2) habitat + management + MAD, 3) habitat + management + MAD<sub>10</sub>, and 4) habitat + management + presence of targeted fishes. Model fit was evaluated using cross-validation percent deviance explained (CV PDE) and cross-validation standard error (CV SE). Predictive performance was assessed by comparing predicted values to observed values for each location. Accuracy of predictions was measured using R<sup>2</sup> and Gaussian rank correlation estimate (GRCE – (Boudt et al. 2012)), as well as root mean square error (RMSE) and symmetric mean absolute percent error (SMAPE), an alternate to mean absolute percent error that is robust to zero values.

## Results

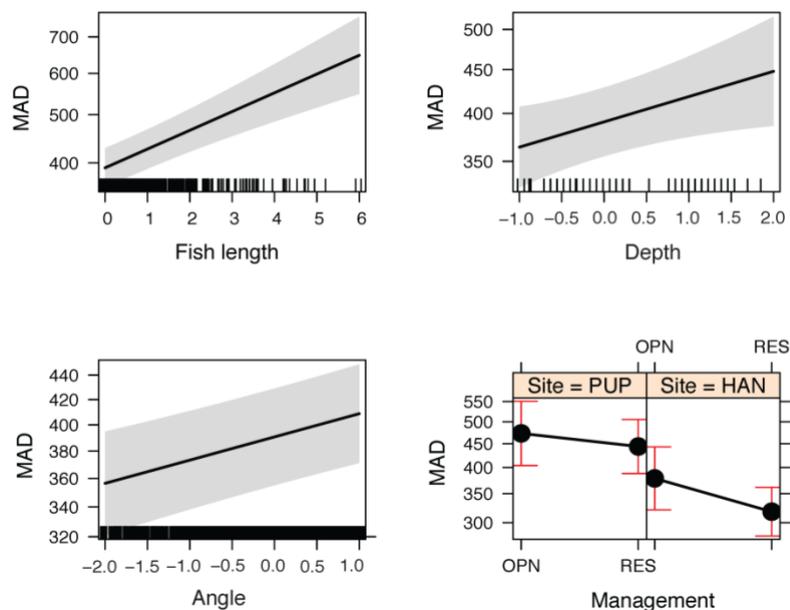
Stereo-DOV belt transects were completed at 25 locations inside the Pūpūkea reserve and 27 locations in adjacent open areas, 7 of which did not contain targeted species. Surveys using the same methods were completed at 35 locations inside Hanauma Bay MLCD and 37 locations in adjacent open areas, 18 of which did not contain targeted species. These resulted in a total of 1,486 observations of 35 coral reef fish species targeted by fishers in Hawai‘i (Supplement 5.1). Reserve locations had higher abundances of targeted species such that the majority of observations occurred at locations protected from fishing. At Pūpūkea there were 475 observations inside the reserve and 272 outside. At Hanauma Bay there were 572 observations inside the reserve and 167 outside. Three schools of greater than 50 individuals were recorded in Hanauma Bay reserve, the two larger of the schools (n=150, 75) consisting of *Acanthurus triostegus* and the third (n=62) made up of *Acanthurus leucopareius*. The largest school (n=55) recorded at Pūpūkea was in the open area and also consisted of *A. leucopareius*. Both marine reserves had significantly higher biomass of targeted fishes ( $F_{1,120}=48.9$ ,  $p<0.001$ ). The ratio of mean targeted fish biomass inside the reserve vs. outside was 4.9 for Hanauma Bay and 1.5 for Pūpūkea.

### Fish wariness (MAD)

Reserve sites had lower MAD, though not significant at  $\alpha=0.05$  when data for both sites were combined (Table 5.2). There was no significant interaction between management and site, though when sites were modeled separately, management was significant at Hanauma Bay ( $F_{1,56}=4.1$ ,  $p=0.046$ ), though not at Pūpūkea ( $F_{1,41}=0.19$ ,  $p=0.6$ ). However, MAD at Pūpūkea was significantly higher overall compared to Hanauma Bay (Table 5.2, Figure 5.2).

**Table 5.2** Linear mixed model results for MAD values for individual fishes, combining both sites. Significant effects shown in bold.

	Sum Sq	Mean Sq	DF	Den DF	F value	P value
Management	0.42	0.42	1	96.8	3.2	0.08
<b>Site</b>	2.36	2.36	1	105.7	18.0	<b>&lt;0.001</b>
<b>Fish length</b>	4.68	4.68	1	897.0	35.7	<b>&lt;0.001</b>
<b>Depth</b>	0.71	0.71	1	97.3	5.4	<b>0.02</b>
<b>Angle</b>	3.06	3.06	1	1417.4	23.3	<b>&lt;0.001</b>
Mgmt x Site	0.08	0.08	1	95.4	0.6	0.44

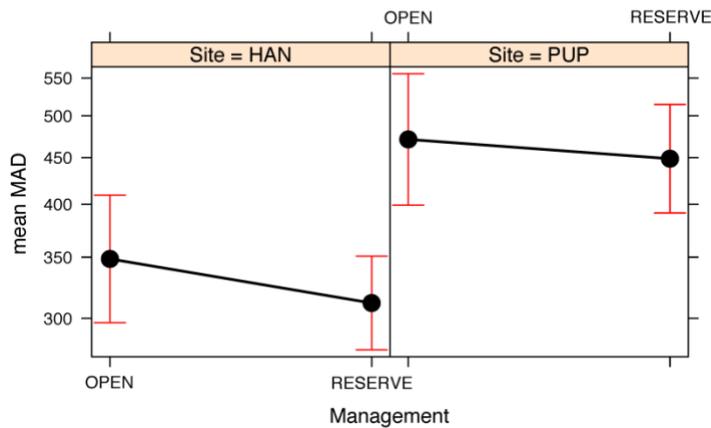


**Figure 5.2** Fixed effects from linear mixed model of MAD values (cm) for individual fishes at both sites combined. All continuous variables were scaled and centered previous to modeling.

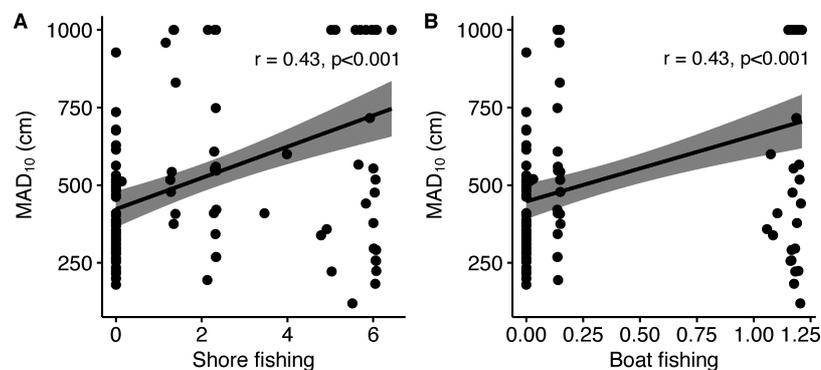
Fish length, depth, and angle of approach were significantly positively related to MAD. However, when each site was modeled separately, only fish length was significant at Pūpūkea ( $F_{1,41}=25.1$ ,  $p<0.001$ ). Mean MAD by transect showed a very similar pattern between sites and management types (Table 5.3, Figure 5.3). Depth was not a significant factor at the transect level (Table 5.3). When including only sites with targeted fishes present, MAD was not correlated with estimated shore ( $p=0.42$ ) or boat ( $p=0.25$ ) fishing pressure. In contrast, MAD<sub>10</sub> was significantly correlated with both shore and boat fishing (Figure 5.4A&B).

**Table 5.3** Linear model results of mean MAD by transect, excluding transects where targeted fishes were not observed.. Significant effects shown in bold.

	DF	Sum Sq	Mean Sq	F value	P value
Management	1	0.16	0.16	1.3	0.26
<b>Site</b>	1	3.00	3.00	24.3	<b>&lt;0.001</b>
Depth	1	0.22	0.22	1.8	0.19
Mgmt:Site	1	0.02	0.02	0.2	0.67
Residuals	94	11.62	0.12		



**Figure 5.3** Management x Site effect for linear model of mean MAD (cm) by transect, excluding transects where targeted fishes were not observed.



**Figure 5.4** Comparison of MAD<sub>10</sub> with estimated shore (A) and boat fishing (B). Spearman rank correlation coefficients and associated p-values shown.

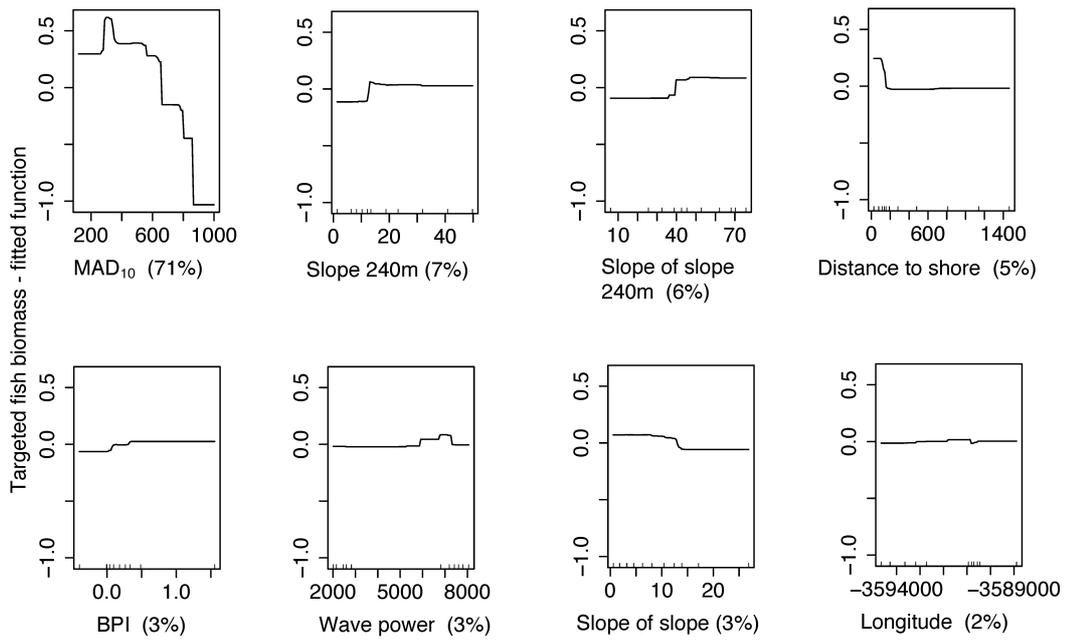
### Species distribution models

Models that included management, but not behavior explained 57% and 10% of the variability in targeted fish biomass for Hanauma Bay and Pūpūkea, respectively (CV PDE, Table 5.4). When MAD was included as a predictor, excluding transects with no targeted fishes, CV PDE increased greatly for Hanauma Bay (+21% CV PDE) and very little for Pūpūkea (+1% CV PDE). For these models, MAD accounted for 82% of explained variation at Hanauma Bay and 80% at Pūpūkea (Supplement 5.2 & Supplement 5.3). When MAD<sub>10</sub> was included as a predictor, CV PDE increased by ~20% for both sites (Table 5.4). For models excluding fish behavior and including presence/absence of targeted fishes, CV PDE increased by 11% for Hanauma Bay and 4% for Pupukea compared to models that included management and not behavior. For models including MAD<sub>10</sub>, this variable accounted for 71% of

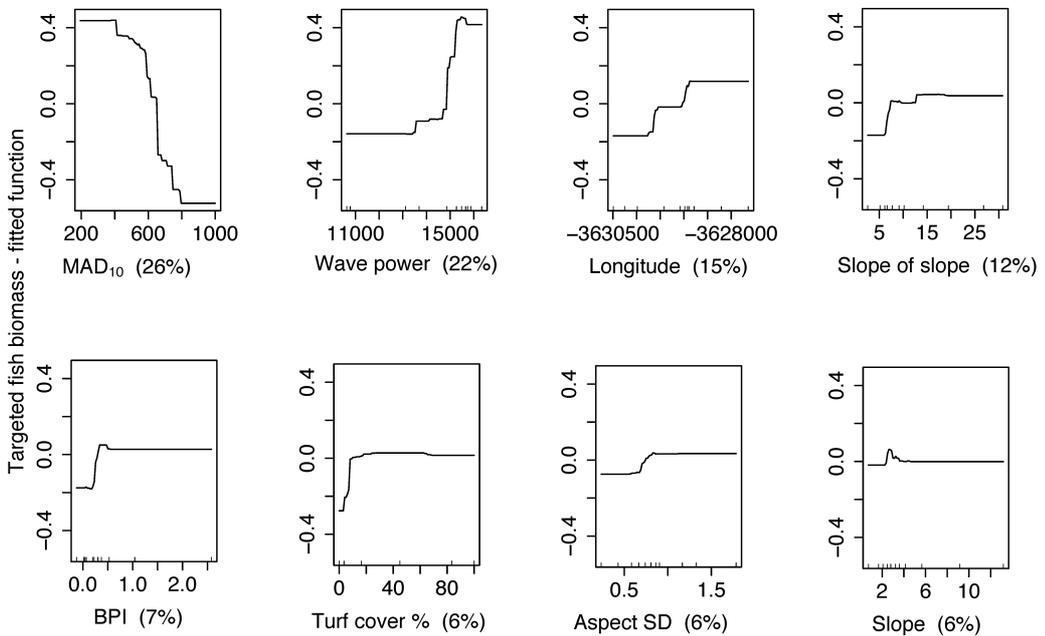
explained variation at Hanauma Bay and 26% of explained variation at Pūpūkea (Figure 5.5 & Figure 5.6). Because including MAD<sub>10</sub> improved model performance at both sites, prediction accuracy was evaluated for these models and was shown to increase with larger values of R<sup>2</sup> and GRCE compared to models which did not include MAD<sub>10</sub> (Table 5.4). Prediction error for all three measures decreased when MAD<sub>10</sub> was added to the models (Table 5.4). For models incorporating behavior, it explained the greatest amount of variability compared to other predictors (Figure 5.5 & Figure 5.6). In models including management status but not behavior, management was not selected as a final predictor.

**Table 5.4** BRT model evaluation comparison for models including management (Mgmt) and management and behavior (MAD<sub>10</sub>). Accuracy metrics include cross validated percent deviance explained (CV PDE), r-squared (R<sup>2</sup>), and gaussian rank correlation estimate (GRCE). Error metrics include cross-validated standard error (CV SE), root mean square error (RMSE) and symmetric mean absolute percent error (SMAPE).

	Hanauma Bay		Pūpūkea	
	Mgmt	Mgmt + MAD <sub>10</sub>	Mgmt	Mgmt + MAD <sub>10</sub>
<b>Accuracy</b>				
CV PDE	56.8	72.5	10.4	32.6
R <sup>2</sup>	0.37	0.58	0.27	0.57
GRCE	0.81	0.87	0.67	0.81
<b>Error</b>				
CV SE	7.6	5.7	19.4	10.0
RMSE	26.6	25.1	40.7	30.7
SMAPE	1.02	0.91	1.03	0.95



**Figure 5.5** Partial dependence plots for Hanauma Bay BRT model of targeted fish biomass including targeted fish behavior – MAD<sub>10</sub>.



**Figure 5.6** Partial dependence plots for Pūpūkea BRT model including targeted fish behavior – MAD<sub>10</sub>.

## **Discussion**

### Management and site differences in fish wariness

MAD was lower inside reserves compared to open areas for both sites, although this difference was only significant at Hanauma Bay. This is consistent with the hypothesis that MAD is a proxy of fish wariness that increases with fishing pressure. These results correspond to those of Lindfield et al. (2014a) who compared the MAD of targeted acanthurids and scarids between reserves and fished areas in Guam, and Goetze et al. (2017) who measured the MAD of targeted species before and after harvest events in periodically harvested closures in Fiji.

MAD was significantly higher on average at Pūpūkea on the north shore of O'ahu, compared to Hanauma Bay on the south shore. A likely explanation is that spearfishing pressure was higher there. Surveys were conducted in the summer months when the wave conditions allow for diving/spearfishing and the shoreline at Pūpūkea is very accessible with multiple access points. Spear fishers can swim in from either boundary, or simply enter the reserve directly. Illegal spearfishing is a regular occurrence (Stamoulis and Friedlander 2013). This likely accounts for the non-significant difference in MAD at the Pūpūkea reserve compared to adjacent open areas. In contrast, shoreline access to the Hanauma Bay reserve is highly regulated. The reserve is monitored on a daily basis and it is unlikely that any spearfishing (poaching) occurs, with the possible exception of divers crossing the seaward boundary from boats. This likely contributed to the larger relative difference in MAD effect size between reserve and open areas compared to Pūpūkea, as well as the larger relative difference in targeted fish biomass.

### Effects of other variables on fish wariness

Fish body length had a positive relationship with MAD as shown in previous studies (Lindfield et al. 2014a, Goetze et al. 2017). Optimal fitness theory predicts that as reproductive value increases, risk-taking should decrease (Clark 1994). Previous studies using flight initiation distance (FID) as a measure of fish wariness also showed a positive relationship with body length (Gotanda et al. 2009, Januchowski-Hartley et al. 2011, 2015, Bergseth et al. 2016). Approach angle ranged from 0-25° and had a significant positive relationship with MAD at Hanauma Bay, but not

Pūpūkea. This is likely a result of the methodology as opposed to a behavioral response. Fishes measured at a more oblique (higher) angle are farther from the transect, and are consequently less likely to be approached closely compared to fishes closer to the transect. In contrast to our results from Hanauma Bay, Goetze et al. (2017) did not find a relationship between MAD and approach angle.

Depth had a positive relationship with MAD. This is contrary to previous findings (Chapter 3) which showed depth to have a negative relationship with FID. This result is likely context dependent and the positive influence of depth is a result of low MAD in shallow areas of the marine reserves surveyed in this study. Both Hanauma Bay and Pūpūkea receive a large number of visitors who come to enjoy the abundant marine life. The majority of tourists tend to remain in shallow areas, thus targeted fishes in these marine reserves are likely habituated to non-aggressive human interactions, leading to reduced MAD in shallow areas. In the previous study, the marine reserve surveyed has restricted access and does not receive many visitors.

#### MAD as predictor for species distribution models

Mean MAD showed no correlation with estimated fishing pressure when only transects containing targeted species were included. This is likely because the fishing pressure maps are coarse estimates based on weighting factors related to accessibility of fishers at the scale of the entire MHI (Chapter 3) and not designed to represent fine-scale patterns. However, when the maximum value was substituted for transects that did not contain target species, MAD<sub>10</sub> showed a positive correlation with estimated fishing pressure. Because high fishing pressure is associated with increased wariness and low biomass of targeted species, it is logical to assume maximum MAD where there is minimum biomass. The resulting pattern is consistent with the MAD linear mixed model results at Hanauma Bay in this study and with the two previous studies that used this metric (Lindfield et al. 2014a, Goetze et al. 2017).

Including MAD<sub>10</sub> as a predictor for SDMs greatly improved model fits and predictive performance. In contrast, management type was not selected as a final predictor for any models. Furthermore, models including MAD<sub>10</sub> performed better than models including presence/absence of targeted fishes indicating that the increases in performance were not only due to accounting for zeros in the response

variable. Partial dependence plots indicated a strongly negative relationship between MAD<sub>10</sub> and targeted fish biomass. BRT models incorporating mean MAD without setting a maximum value for transects with no targeted species improved the model fit for Hanauma Bay, but not for Pūpūkea. BRTs handle missing predictor values by using a surrogate variable which best agrees with the original splitting variable (Breiman et al. 1984, De'ath and Fabricius 2000). These models appeared to over fit the training data with MAD accounting for > 80% of total variation for both sites. In addition, partial dependence plots showed relationships of MAD with biomass that did not have a consistent pattern and were non-directional. The large proportion of missing values and the fact that habitat variables were not well correlated with MAD ( $\rho < 0.3$ ) and do not provide good surrogates may explain why these models did not perform well. Therefore, when sampling along a steep gradient of fishing pressure, such as across MPA boundaries, with relatively small sample sizes; setting MAD to the maximum value for surveys with no targeted fishes present appears necessary to provide a proxy of fishing pressure and inform SDMs.

When MAD was modeled separately for each site, only fish body length was a significant factor for both sites. Because the response variable for SDMs was targeted fish biomass which integrates fish length, it was not necessary to correct for length in transect-level estimates of mean MAD. Furthermore, patterns of mean MAD across sites and management types were nearly identical to those shown by models accounting for fish body length and approach angle. Based on these results, MAD<sub>10</sub> of targeted species at the transect level appears to be a robust proxy of fish wariness when used in SDMs of targeted fish biomass.

In order to validate these results, future research should focus on comparing empirical measures of spearfishing pressure with MAD of targeted species to better quantify this relationship. A drawback of using MAD as a predictor for SDMs is that it's not possible to make predictions to locations for which MAD data is not available. Further research should focus on creating spatially explicit estimates of fishing pressure such as those created in Chapter 3. Estimated fishing pressure could be used directly as a predictor for SDMs. A better understanding of the relationship of MAD and fishing pressure could help inform this work by providing a proxy for fishing which could be used to ground-truth models of fishing pressure.

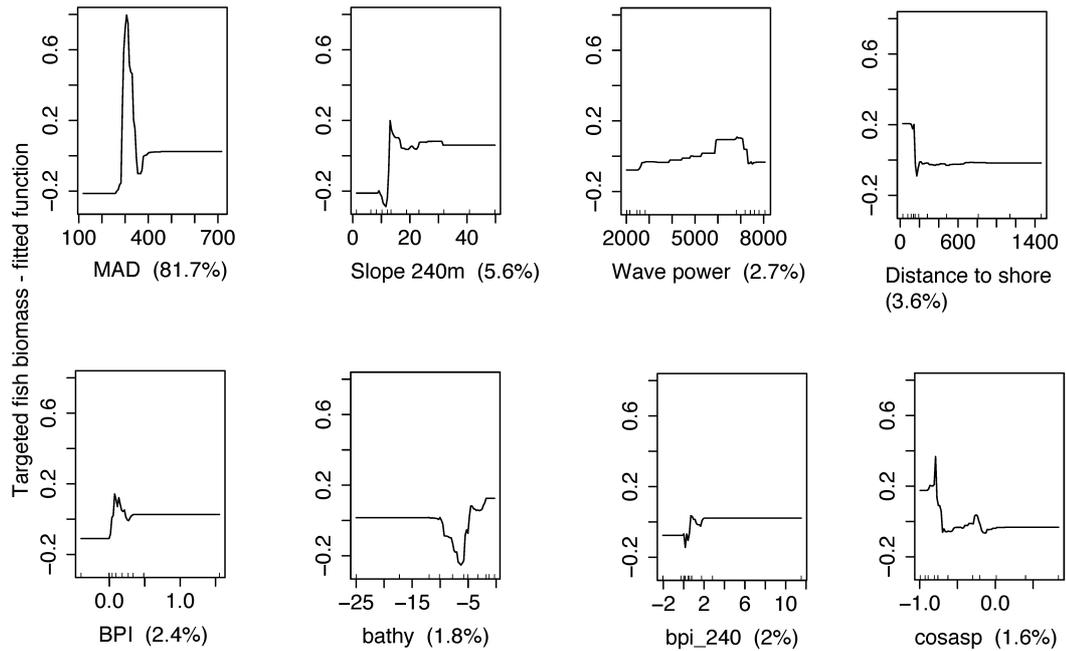
Another possibility is integrating MAD directly into measures of fish assemblage characteristics used to calibrate SDMs. An existing survey method, distance-based sampling, records the distance from the observer, or transect center line, to the fish at the time of observation, thereby incorporating a measure of fish behavior (Buckland et al. 2005, Thomas et al. 2006). A detection function, representing the probability of detection as a function of distance from the line can be modeled, allowing estimation of the proportion of fish missed within the surveyed area, resulting in density estimates (Buckland et al. 2005, Thomas et al. 2006). In this case, detection functions could be generated using data from locations with no fishing pressure and should thus correct for altered fish behavior when applied in areas where fishing occurs, thus generating more accurate density estimates for use in SDMs.

In this study, it is unclear what portion of the variance explained by MAD in SDMs is due to survey bias from fish behavior or the direct effects of fishing pressure, for which MAD provides a proxy. However, because the directionality of these influences on targeted fish biomass is the same, it is irrelevant to SDM performance. If behavioral differences were incorporated into density estimates, as may be possible using distance sampling, then the variability attributed to MAD in SDMs could then be attributed solely to fishing effects. Based on the results from this and two previous studies (Lindfield et al. 2014a, Goetze et al. 2017), MAD appears to provide a proxy for fishing pressure. We've shown that including mean MAD as a predictor in SDMs greatly improves model accuracy. Future research should seek to improve spatially explicit estimates of fishing pressure, for which MAD could provide a valuable reference, to improve accuracy of SDM predictions in un-sampled areas.

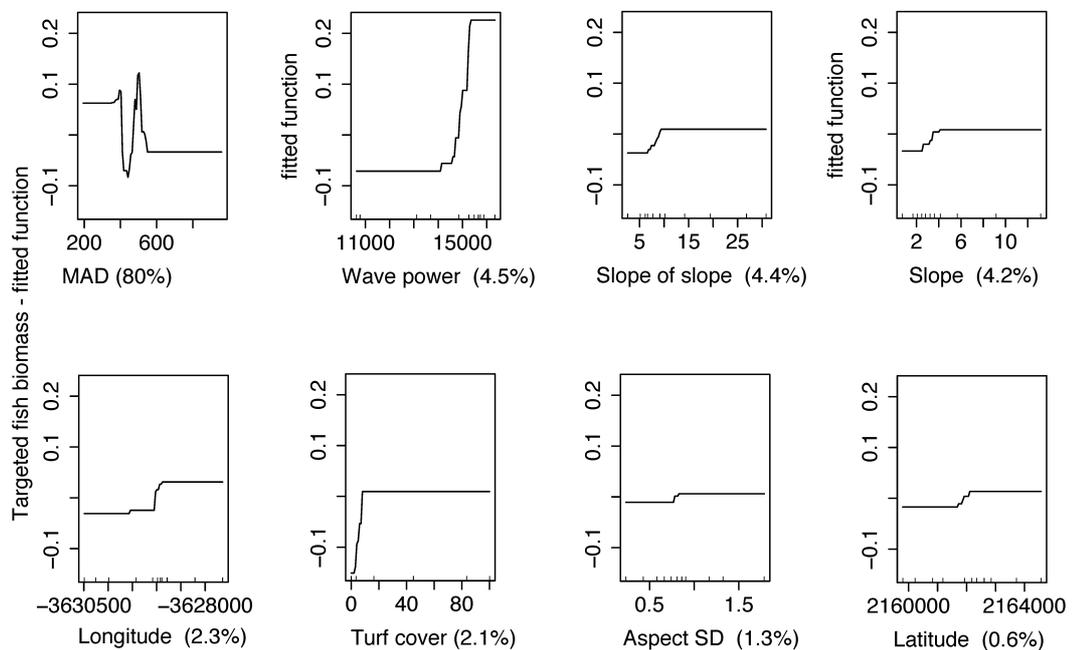
## Supplementary Material

**Supplement 5.1** List of targeted species recorded on stereo-DOV surveys.

<b>Family</b>	<b>Species</b>
Acanthuridae	<i>Acanthurus achilles</i> <i>Acanthurus blochii</i> <i>Acanthurus dussumieri</i> <i>Acanthurus guttatus</i> <i>Acanthurus leucopareius</i> <i>Acanthurus nigroris</i> <i>Acanthurus olivaceus</i> <i>Acanthurus triostegus</i> <i>Acanthurus xanthopterus</i> <i>Ctenochaetus strigosus</i> <i>Naso lituratus</i> <i>Naso unicornis</i> <i>Zebrasoma veliferum</i>
Carangidae	<i>Carangoides ferdau</i> <i>Carangoides orthogrammus</i> <i>Caranx melampygus</i>
Kyphosidae	<i>Kyphosus sp</i>
Labridae	<i>Anampses cuvier</i> <i>Bodianus bilunulatus</i>
Lethrinidae	<i>Monotaxis grandoculis</i>
Lutjanidae	<i>Lutjanus fulvus</i> <i>Lutjanus kasmira</i>
Mullidae	<i>Mulloidichthys flavolineatus</i> <i>Mulloidichthys vanicolensis</i> <i>Parupeneus cyclostomus</i> <i>Parupeneus insularis</i> <i>Parupeneus multifasciatus</i> <i>Parupeneus pleurostigma</i>
Scaridae	<i>Calotomus carolinus</i> <i>Chlorurus perspicillatus</i> <i>Chlorurus sordidus</i> <i>Scarus psittacus</i> <i>Scarus rubroviolaceus</i>
Serranidae	<i>Cephalopholis argus</i>



**Supplement 5.2** Partial dependence plots for Hanauma Bay BRT model including targeted fish behavior – MAD excluding sites with no targeted species.

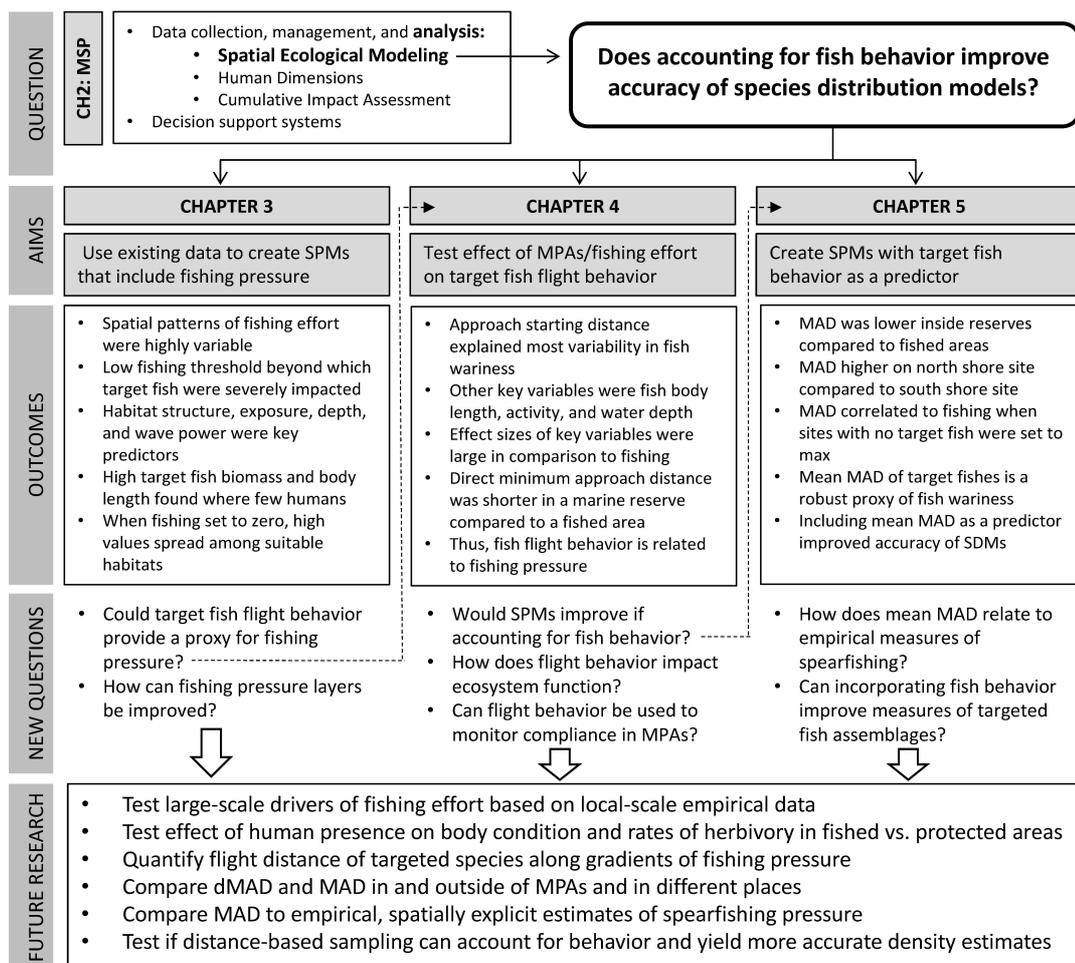


**Supplement 5.3** Partial dependence plots for Pūpūkea BRT model including targeted fish behavior – MAD excluding sites with no targeted species.

## **CHAPTER 6 – General Discussion**

### **Summary of findings**

This thesis begins by reviewing the data and analyses necessary to support marine spatial planning (MSP) and focuses on improving one key component; spatial ecological modeling. I demonstrate the utility of incorporating fishing pressure into species distribution models (SDMs) of targeted reef fishes (a specific application of spatial ecological modeling) and how these models can be applied to prioritize areas for fisheries management. I then focus on targeted fish behavioral response to divers as related to fishing pressure and how it can be used to improve accuracy of SDMs when detailed fishing information is not available. In this general discussion I summarize the main findings, discuss implications for management and conservation, and present new research avenues to improve the science of species distribution modeling of targeted fishes and support marine spatial management and planning (Figure 6.1).



**Figure 6.1** Flow chart summarizing key outcomes, questions, and future research directions.

**Chapter two** reviews the data and tools needed to operationalize MSP, which is a complex and data intensive process combining geographic information science (GISc), environmental management, and land use planning. Advances in technology and computing have enabled us to gather and analyze information about our environment at an unprecedented scale and resolution. We apply GISc to manage and interpret spatial data, and spatial analysis is crucial to MSP. Key steps in the MSP process are 1) define present conditions through data collection; 2) analyze present conditions using spatial ecological modeling, human use analysis, and cumulative impact assessment; and 3) project future conditions using decision support tools. To a large extent the success of a MSP program relies on the amount and quality of the data available for synthesis and the capacity to analyze it (Ehler and Douvère 2009). It is important to consider that the scope and scale of the data assembled for MSP should match the scope of the planning area and the scale of the

planning units. Data management is nearly as important as the data themselves and can be facilitated through the use of geodatabases. Analytical methods such as spatial ecological modeling, human use analysis, and cumulative impact assessment allow for the summarization and integration of a range of datasets representing planning components, enabling efficient comparisons and a holistic view of present conditions. Species distribution modeling and predictive mapping provide cost-effective, quantitative and spatially explicit information necessary for MSP. SDMs can allow scientists and resource managers to conduct large-scale ecological assessments, better understand species-habitat associations, and inform management strategies (Mellin et al. 2010, Shucksmith and Kelly 2014). Decision support systems provide visualization and evaluation of alternate management measures that is crucial to the MSP process. A number of such tools are available and the capabilities of a selected platform should be matched to the needs and scope of an MSP project.

**Chapter three** is the first study of its kind to develop regional-scale SDMs that integrate spatially explicit estimates of fishing pressure. SDMs of targeted fish biomass and body length showed that spatial patterns of fishing effort were highly variable and demonstrated a low fishing threshold beyond which targeted fishes were severely impacted. The highest intensity of shore and boat fishing was generally estimated to be near highly populated areas. Targeted fish biomass and body length declined rapidly within the first 10% of both shore and boat fishing effort. The seascape models also revealed habitat structure, depth, exposure, and wave power as key predictors which defined productive habitats for coral reef fishery species. These variables all showed positive relationships for both targeted fish indicators. Under current fishing levels, high target fish biomass and body length were found in remote areas with few humans. Under a theoretical scenario where fishing pressure was removed, predicted distributions of high target fish biomass and body length expanded throughout suitable habitats. Predicted mean values of these fishery indicators by island increased significantly when the influence of fishing pressure was removed. Areas with the highest recovery potential for targeted fish biomass and body length were identified on each island in productive habitats with currently high fishing pressure. High recovery potential for targeted fish biomass and body length were typically found in the same areas, though often with little direct spatial overlap.

**Chapter four** evaluated the effect of marine protection and other variables on direct measures of targeted fish flight behavior and showed that approach starting distance explained the most variability in fish wariness. Other key variables were fish length, activity, and depth. When including these co-variables in models of flight initiation distance (FID) and direct minimum approach distance (dMAD) of targeted reef fishes, I found significant differences between a marine reserve and a heavily fished area for dMAD, but not for FID. While patterns of dMAD were very similar to FID, I found dMAD to be less dependent on starting distance. Relative effect sizes of starting distance and, to a lesser extent other co-variables were large in comparison to management type (fishing pressure). I found no significant differences in FID or dMAD between reef fish families, however, emperors (Lethrinidae – represented by a single species in this study) had the largest mean effect size suggesting that it could be a potential indicator species for spear fishing pressure in Hawai‘i. In addition, I show that escape response behaviors of parrotfishes (Scaridae) and goatfishes (Mullidae) support the dMAD results. These findings highlight important methodological considerations for direct measurements of fish flight behavior and show that dMAD is related to fishing pressure but is primarily driven by other key variables which must be accounted for.

**Chapter five** builds upon the previous two chapters by testing the relationship of an indirect measure of fish wariness (minimum approach distance - MAD) with management/fishing pressure and applying it as a predictor in SDMs of target fish biomass to determine if it improves model accuracy. While MAD varied between sites, it was lower inside reserves compared to adjacent fished areas reflecting the expected pattern of fish wariness; targeted fishes were less wary inside reserves. Mean MAD of targeted fishes at the transect level also matched this pattern and was used as a predictor in SDMs of targeted fish biomass, though was not correlated with estimated fishing pressure from maps developed in Chapter three. Including MAD as a predictor, without replacing missing values (due to no targeted fishes present), improved model accuracy for one of two sites. However, resulted in model over fitting. Alternatively, MAD was set to the maximum value of 10 m (MAD<sub>10</sub>) for transects with no targeted fishes. It then correlated to estimated fishing pressure. Incorporating MAD<sub>10</sub> as a predictor in SDMs greatly improved accuracy for both sites and MAD<sub>10</sub> had a negative relationship with targeted fish biomass, similar to

fishing. Therefore, when sampling along a large gradient of fishing pressure (such as across reserve boundaries), setting MAD to the maximum value for surveys with no targeted fishes provides a proxy for fishing that can inform SDMs.

### **Thesis limitations**

The SDMs developed in Chapter three made best use of the available data. However, there were a few gaps in the spatial coverage of the response dataset of fish surveys that could have influenced the model calibrations. There were also gaps in the bathymetry-derived habitat datasets that limited the extent of the predicted maps and subsequent prioritization analysis. In addition, some of the predictor datasets were produced at different resolutions which may have influenced model fitting. A critical component of SDMs of targeted fishes is accounting for fishing pressure patterns. The fishing effort layers developed in Chapter three represent the most spatially comprehensive, high resolution, and broad-scale products yet created to quantify spatial patterns of coral reef fishery effort. However, a few simplifying assumptions were made to produce them, such as fishers are more likely to frequent accessible areas, more likely to fish close to home, and that number of fishers are proportional to total population. For this reason, these fishing effort maps may have captured additional aspects related to accessibility and proximity to humans, such as land-based source pollution. While shown to be effective at a regional scale, these fishing pressure maps are likely to be less accurate and useful at finer scales, necessitating further development for those types of applications.

The prioritization analysis in Chapter three was largely dependent on the estimated patterns of fishing effort as it compared modeled patterns of targeted fish assemblage indicators under present fishing effort to those predicted when fishing effort was removed. This means the uncertainty inherent in the fishing effort layers was transferred to the prioritization analysis. The response variables for the SDMs were derived from pooling all targeted coral reef fish species, likely obscuring species-specific patterns. These species represent a range of trophic guilds, life history traits, and vulnerability to fishing. The differences in terms of life-span and age of maturity will influence timelines of recovery among species. Finally, this prioritization

approach did not incorporate larval connectivity which is important to consider when selecting areas to manage for fisheries replenishment.

Chapter four compared direct measures of fish wariness (FID and dMAD) between areas with different levels of fishing pressure to determine if patterns corresponded to those shown by previous work in other places and validate the use of fish behavior as a proxy for fishing pressure in Hawai‘i. Chapter five compared an indirect measure of fish wariness (MAD) between reserve and fished areas to support its use as a predictor in SDMs of targeted fish biomass. However, direct and indirect measures of fish wariness were not compared.

The evaluation of MAD as a predictor for SDMs of targeted fishes in Chapter five represents the primary objective of this thesis. I apply the comparison of SDMs, with and without including MAD as a predictor, at two separate sites containing both reserve and fished areas. The purpose of dividing the sampling effort between these two sites with different habitat, environmental, and human use characteristics was to replicate the comparison to provide a more robust test of the effect of incorporating fish behavior in SDMs of targeted fish biomass. This resulted in relatively low sample sizes for each site which were adequate to develop SDMs and had a high prevalence of locations with zero biomass. This presented a problem because it was not possible to measure fish behavior at these locations, and the SDMs failed when excluding those data. I addressed this issue by developing SDMs both with missing values for MAD and by substituting maximum MAD values for those locations. This is a justifiable, yet novel approach and larger sample sizes would have helped to further explore and validate it.

### **Implications for management and conservation**

As oceans spaces become more crowded, MSP has become necessary to support current and future uses of ocean and coastal ecosystems while minimizing conflicts to maintain the delivery of valuable ecosystem services for future generations (Douvere 2008). GISc has provided tools to manage and analyze data for MSP and geodatabases should be used to maintain integrity of spatial data in a consistent and accurate manner. Analytical methods such as spatial ecological modeling and

cumulative impact assessments allow for summarization and integration of datasets representing planning components, enabling efficient comparison and comprehensive representations of the current state of marine spaces. Decision support systems can create alternative spatial management scenarios and evaluate trade-offs for the consideration of stakeholders. It is in the interest of MSP practitioners and stakeholders to incorporate these methods and tools in their decision-making process.

The maps of fishing effort developed in Chapter three have utility for management because they represent a set of key human uses and subsequent impacts in marine spaces, as well as the activities of an important and often vocal stakeholder group (Salas and Gaertner 2004). My results support previous work in showing that the greatest impacts to fishery resources occur at low fishing levels (Jennings and Polunin 1996, Jennings and Kaiser 1998). There are few such examples in the literature showing this relationship for coral reef fisheries and it highlights the importance of no-take MPAs and suggests that fishing effort in rotational closures should be carefully managed. I used mean biomass and body size of the targeted fish assemblage as response variables for the SDMs. Both are thought to represent the relative abundance of large and small individuals (Shin et al. 2005). However, my results suggest they are not interchangeable and instead complementary because they capture different aspects of the fished assemblage. While higher average length always reflects greater abundance of large individuals, high biomass can also result from high abundance of small individuals. Fisheries managers are in need of simple yet meaningful metrics to guide management actions (Nash and Graham 2016) and it is important to consider both fished assemblage biomass and size distribution because large individuals represent high-value species and high reproductive capacity (Birkeland and Dayton 2005).

The regional scale SDMs from Chapter three revealed that high wind and wave exposure were related to high target fish biomass and size, suggesting that they create natural refuges from fishing pressure which should be accounted for in planning and management efforts. The prioritization analysis identified areas where management actions will be most effective in restoring coral reef fisheries. This was a result of comparing spatial distributions of fishery indicators under current fishing levels, with those predicted if fishing pressure were removed. Each of these predicted

maps also has utility for management. Spatial patterns of fishery indicators identified areas that presently support healthy fish assemblages. Managing fishing in these areas would ensure that they continue to replenish adjacent fisheries, through larval export and spillover (Harrison et al. 2012, Stamoulis and Friedlander 2013).

Predicted maps of targeted fish distributions with fishing pressure removed identified habitats capable of supporting high biomass and larger fishes, which can be used to characterize these essential habitats for coral reef fisheries. Finally, the approach I developed is flexible so that it can be applied anywhere that demersal fish populations are targeted, and any response variable derived from fish survey data can be modeled depending on the research or management question.

My Chapter four research revealed differences in fish wariness between areas with different levels of fishing pressure and identified a potential indicator species for spear fishing pressure in Hawai‘i. A better understanding of fish diver avoidance behavior (wariness) has a number of applications for management and conservation. Fish wariness has been shown to be more sensitive to changes in management than traditionally used measures of fish assemblages (Goetze et al. 2017) and is a potential indicator of spear fishing pressure that could be used as a tool to measure and monitor compliance in marine reserves (Bergseth et al. 2015).

Chapter five improves SDMs through incorporating fish flight behavior as a detailed proxy for fishing pressure which is appropriate for local-scale models. Predictive mapping based on SDMs expands on field survey efforts that are expensive and spatially limited and produces continuous spatial information at the scope and scale required for management and MSP. Improving the accuracy of SDMs will decrease uncertainty in the predicted maps and increase the usefulness of these important management tools.

### **New research avenues**

This thesis examined questions related to spatial patterns of fishing, reef fish behavioral responses to humans, and implications for SDMs of targeted reef fishes. These topics are not well studied, and the findings lead to additional questions and needs for future research. Future studies aimed at improving fishing effort maps,

which have important applications for management, should focus on testing large-scale drivers of fishing effort based on local-scale empirical data. Such efforts would require standardized methods for collecting fishing effort data with broader spatial coverage such as recommended by Delaney et al. (2017). Establishing spatial relationships of fishing effort and large-scale drivers such as human population, economic status, accessibility, and environmental variables would allow for more precise modeling of these patterns and lead to more accurate fishing pressure maps to support management directly and through informing SDMs. In addition, building off the results of the prioritization analysis in Chapter three, areas shown to support large reproductive size fishes should be matched with information on source areas for reef fish larvae to inform spatial management and support reef fisheries.

The investigation of fish flight behavior in Chapter four explored potential implications for visual fish surveys and raised new questions about how fish wariness may impact body condition and ecosystem functions of targeted fishes. Body condition has been shown to be lower at sites with higher predator abundance (Walsh et al. 2012). To address the question of whether body condition is lower in the presence of human predators, mean body mass adjusted for length could be compared in reserve versus fished areas. Targeted fishes often include herbivores, which promote coral reef resilience by consuming algae and clearing space for coral settlement (Ledlie et al. 2007). Behavior shifts due to high fishing pressure may influence foraging patterns and feeding rates of herbivorous fishes, disrupting ecosystem functions critical to coral reef health (Madin et al. 2010, 2011). The effect of altered behavior due to fishing on the functional roles of targeted herbivores could be measured by comparing feeding rates and spatial patterns in fished versus protected areas. Measures of fish flight behavior have been proposed as a potential indicator of spearfishing pressure that could be used to monitor compliance in marine reserves (Bergseth et al. 2015). To address this question, measures of fish wariness should be quantified along gradients of spear fishing effort. Ideally, flight behavior and spear fishing effort would be measured at the same locations during the same time periods enabling direct comparisons. This would enable characterization of the relationship between spearing and fish wariness specific to different locations and species, ultimately allowing for estimates of spearing pressure based only on the

behavior of indicator species. This method could then be used to easily and cost-effectively monitor compliance in marine reserves, among other applications.

MAD is an indirect measure of fish wariness which was shown to be higher in fished areas. In order to further validate MAD as a proxy for fishing pressure, it should be compared with a direct measure of fish wariness (dMAD) across marine reserve boundaries and in different places. Fish wariness is likely to be influenced by levels of spear fishing pressure and perceived value of targeted species (often related to maximum size) and will vary among places (Nunes et al. 2018). Both MAD and dMAD should be measured at the same locations during the same times to provide a robust comparison and limit potential confounding variables. A next step would be to compare MAD to empirical, spatially explicit estimates of spear fishing effort. I show that including MAD as a predictor improves the accuracy of SDMs of targeted fish biomass, however, it is not possible to make predictions to unsampled locations where MAD data is not available. Instead, estimated fishing pressure could be used directly as a predictor for SDMs. A better understanding of the relationship of MAD and spearing pressure could help inform development of more detailed fishing effort maps by providing a proxy for fishing which could be used to ground-truth estimated fishing patterns. Another possibility is integrating MAD directly into measures of fish assemblage characteristics used as response variables for SDMs. An existing survey method, distance-based sampling (Buckland et al. 2005), incorporates distances between observers and fishes into density estimates based on species-specific detection functions. Detection functions could be generated using data from locations with no fishing pressure and should correct for altered fish behavior when applied in areas where fishing occurs, thus generating more accurate density estimates for use in SDMs. However, accuracy of predictions in unsampled areas with unknown levels of fishing pressure may still be questionable and research is needed to determine the viability of this method.

## **Conclusions**

Comprehensive and spatially explicit information on fishing patterns and marine species distributions are necessary to inform ecosystem-based management and MSP. SDMs can be used to study habitat and environmental associations as well as

impacts from human activities. Chapter three applied SDMs to identify marine areas with the highest recovery potential for coastal fisheries to prioritize these areas for management. This analysis incorporated spatially explicit estimates of fishing pressure to predict recovery if fishing pressure were to be removed. This is a novel and transferable approach which holds great promise for managing coastal fisheries worldwide.

Fishing pressure patterns are critical inputs for modeling distributions of fishery resources and more research should focus on mapping these patterns. Chapter three developed maps of recreational fishing effort from island-scale estimates which were distributed into nearshore areas based on accessibility to fishers. While patterns of fishing effort for pelagic fisheries are relatively well defined based on strict reporting requirements and the availability of VMS data, little information exists for coastal fisheries for which recreational fishing makes up a large component. This information is critical for management of these nearshore fisheries which seeks to understand the relationships between resource abundance and extraction and account for stakeholder interests.

Diver avoidance behavior or fish wariness provides a proxy for spear fishing effort that could potentially be used to refine and ground-truth maps of fishing pressure. Fish flight behavior holds promise for management applications such as measuring compliance in marine reserves, and measures of fish wariness can improve accuracy of SDMs when used as a predictor of targeted fish biomass. Chapter four advances the field of flight behavior research of marine fishes, providing critical guidance for future studies. Chapter five applies measures of fish behavior to inform SDMs of targeted fishes. Together this research promotes a better understanding of fish behavioral responses to human predation that could be used to refine measures of fish assemblages and SDMs, leading to improved ecosystem-based management of coastal fisheries.

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To Whom It May Concern,

I, Kostantinos Stamoulis, designed the study and wrote the manuscript, and with the assistance of my co-author, conceived and executed the analyses and figures and edited the manuscript for the following publication:

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Date: 4 April 2018

I, as Co-author, endorse this level of contribution by the candidate indicated above is appropriate.

Jade Delevaux



Date: 4-Apr-2018

To Whom It May Concern,

I, Kostantinos Stamoulis; designed the study, contributed to predictor generation, conceived and executed the data analyses, and wrote and edited the manuscript for the following publication:

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Date: 4 April 2018

I, as Co-author, endorse this level of contribution by the candidate indicated above is appropriate.

Jade Delevaux		Date: <u>6-Apr-2018</u>
Ivor Williams	<hr/> <small>Digitally signed by WILLIAMS.IVOR.DOUGLAS.1387537720 DN: cn=US, ou=U.S. Government, ou=DoD, ou=PI, ou=OTHER, cn=WILLIAMS.IVOR.DOUGLAS.1387537720 Date: 2018.04.04 13:13:41 -10'00'</small>	Date: <u>4-Apr-2018</u>
Matthew Poti	<hr/> <small>Digitally signed by POTI.MATTHEW.DAVID.1398827224 4 Date: 2018.04.05 09:52:59 -04'00'</small>	Date: <u>5-Apr-2018</u>
Joey Lecky	<hr/> <small>Digitally signed by LECKY.JOSEPH.HENSLEY.139494900 4900 Date: 2018.04.04 19:01:41 -10'00'</small>	Date: <u>4-Apr-2018</u>
Bryan Costa	<hr/> <small>Digitally signed by COSTA.BRYAN.MATTHEW.1383870441 0441 Date: 2018.04.05 08:32:19 -07'00'</small>	Date: <u>5-Apr-2018</u>
Matthew Kendall	<hr/> <small>Digitally signed by KENDALL.MATTHEW.S.1365859520 0 Date: 2018.04.05 07:42:20 -04'00'</small>	Date: <u>5-Apr-2018</u>
Simon Pittman	<hr/> <small>Digitally signed by Simon J Pittman Date: 2018.04.06 14:00:24 +01'00'</small>	Date: <u>6-Apr-2018</u>
Mary Donovan	<hr/> <small>Digitally signed by Mary Donovan DN: cn=Mary Donovan, o, ou, email=mdono@hawaii.edu, c=US Date: 2018.04.04 13:20:31 -10'00'</small>	Date: <u>4-Apr-2018</u>
Lisa Wedding	<hr/> <small>Digitally signed by Lisa Wedding Date: 2018.04.05 10:57:58 -07'00'</small>	Date: <u>5-Apr-2018</u>
Alan Friedlander		Date: <u>5-Apr-2018</u>

To Whom It May Concern,

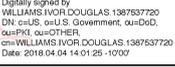
I, Kostantinos Stamoulis; designed the study, collected the data, executed the data analyses, and wrote and edited the manuscript for the following paper submitted for publication:

Stamoulis, K. A., E. S. Harvey, A. M. Friedlander, I. D. Williams, K. C. Weng, C. Wiggins, G. W. Wagner, and E. J. Conklin. In Review. Flight behavior of targeted fishes depends on fishing and other key variables. Ecological Indicators.



Date: 4 April 2018

I, as Co-author, endorse this level of contribution by the candidate indicated above is appropriate.

Euan Harvey	 <small>Digitally signed by Euan Harvey Date: 2018.04.05 19:25:38 +08'00'</small>	Date: <u>5-Apr-2018</u>
Alan Friedlander		Date: <u>5-Apr-2018</u>
Ivor Williams	<small>WILLIAMS.IVOR.DO UGLAS.1387537720</small>  <small>Digitally signed by WILLIAMS.IVOR.DOUGLAS.1387537720 DN: cn=US, o=U.S. Government, ou=DoD, ou=PMI, ou=OTHER, cn=WILLIAMS.IVOR.DOUGLAS.1387537720 Date: 2018.04.04 14:01:25 -10'00'</small>	Date: <u>4-Apr-2018</u>
Kevin Weng		Date: <u>5-Apr-2018</u>
Chad Wiggins		Date: <u>5-Apr-2018</u>
Gary Wagner		Date: <u>5-Apr-2018</u>
Eric Conklin	 <small>Digitally signed by Eric Conklin Date: 2018.04.05 16:24:12 -10'00'</small>	Date: <u>5-Apr-2018</u>