THE MOVEMENTS OF PREDATORY REEF FISHES IN THE MOLOKINI MARINE LIFE CONSERVATION DISTRICT

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

MASTER OF SCIENCE

IN

ZOOLOGY (MARINE BIOLOGY)

MAY 2016

By

Alexander A. Filous

Thesis Committee:

Alan Friedlander, Chairperson

Cindy Hunter

Carl Meyer

Keywords: Acoustic Telemetry, *Triaenodon obesus*, *Carcharhinus amblyrhynchos*, *Caranx ignobilis*, *Caranx melampygus*, *Aprion virescens*, Molokini MLCD

Dedications

I would like to dedicate this work to my mother and father who have always supported my passion for fish, my sister, Aunt Nene, Uncle Gene, the staff at Maui DAR, all my friends, family and the giant trevally (Ulua) of the Hawaiian Islands.

Acknowledgements

I would like to acknowledge the staff at the Maui Division of Aquatic Resources for their invaluable assistance in the field work that made this project possible. These individuals spent countless hours at sea and many late nights fishing in the Molokini MLCD, for us to be able to tag these predators and shed light on their movement patterns in the Maui Nui Complex. Furthermore, I would like to acknowledge my advisor Alan Friedlander for the opportunity to work on this project and his guidance in becoming a fisheries ecologist, Marc Lammers for providing noise data from the Ecological Acoustic Recorder (EAR) located in the MLCD, the staff at the Kahoʻolawe Island Reserve Commission for their assistance in placing an acoustic receiver on Kahoʻolawe and Carl Meyer for sharing fish detection data from his acoustic array on Maui. Finally, I would like to acknowledge the help of my friends (Hal Koike, Kosta Stamoulis, Barrett Wolfe, Paolo Usseglio, Stephen Scherrer and Robert Lennox) who taught me to use R and provided invaluable assistance in analyzing this data set and all my other friends at the Fisheries Ecology Research Laboratory (Mary Donovan, Keith Kamikawa, Jonatha Giddens, Kaylyn McCoy, Eva Schemmel, and Whitney Goodell) who helped me along the way.

Abstract

Predators play a critical role in maintaining the balance of marine ecosystems and are an important component of Hawaii's recreational and commercial fisheries. In light of the increasing pressures on these populations in recent decades across the main Hawaiian Islands from both consumptive and non-consumptive resources use, the study of apex predator movements in marine protected areas has become a research priority. To this aim, we used passive acoustic telemetry to investigate the spatial and temporal movement patterns of five apex predators: bluefin trevally (*Caranx melampygus*), giant trevally (*Caranx ignobilis*), green jobfish (*Aprion virscens*), whitetip reef sharks (*Triaenodon obesus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) at the 31 ha Molokini Marine Life Conservation District (MLCD) off Maui, Hawaii. The Molokini MLCD is the second most visited MLCD in the State of Hawaii with over 300,000 visitors per year. Our results indicate that residency was variable across species, with bluefin trevally exhibiting the highest residency in the MLCD and green jobfish the lowest. Bluefin trevally showed displacement from critical habitats in the MLCD during peak visitation hours. Long distance movements between the Molokini MLCD and the other islands of the Maui Nui Complex were common for grey reef sharks, giant trevally, and green jobfish. These results indicate that despite its small size, the Molokini MLCD provides a high level of protection to resident species such as bluefin trevally. However, this MLCD is less effective at protecting more mobile apex predators such as green jobfish, grey reef sharks, and giant trevally.

Table of Contents

List of Tables

List of Figures

General Introduction

The study of the movements of reef predators has become a research priority in Hawaii's marine ecosystems, these species play a critical role in maintaining the balance of marine ecosystems by imposing a top down effect on lower trophic groups (Baum and Worm 2009, Barnett et al. 2012). Furthermore, predators are critical to the state's recreational and commercial fisheries and have experienced significant declines in the main Hawaiian Islands over the past century (Shomura 2004). In recent decades, Marine Protected Areas (MPAs) have been popularized as an effective tool to protect tropical reef species but the conservation of predators is confounded by a lack of information on the movement patterns of these fishes within their borders.

In Hawaii, the Marine Life Conservation District (MLCD) program was established in 1967 to conserve and replenish marine resources for the purpose of education and human enjoyment and has been successful in maintaining high biomass and diversity of fish assemblages within the borders of Hawaii's MLCDs (Friedlander et al. 2007). Today, there are 11 MLCDs in the main Hawaiian Islands and these locations have some of the most intact populations of reef predators in the region. Friedlander et al. (2007) found that there was a greater abundance (62%) and biomass (52%) of predators inside Hawaii's MLCDs when compared to non-protected localities with similar habitat characteristics. However, despite their effectiveness, questions remain as to how well does this small and fragmented network of MPA around the state protect these highly mobile predators and how is this different between species? To answer these questions, quantitative information on the residency, habitat use and dispersal of these fishes is urgently needed. Passive acoustic telemetry has been widely used to identify patterns in long-term movement, site fidelity, and habitat use of various species of tropical marine fishes. This technology, provides a time and date record of a tagged animals presence within the detection range of an acoustic receiver (Heupel et al. 2006) and allows us to investigate the movements of tagged fish in relation to MPAs.

Furthermore, in addition to fisheries conservation, the increase in biomass and diversity of fish assemblages in these areas provides a major source of attraction in the state of Hawaii's marine tourism industry. Marine ecotourism such as boating, snorkeling and SCUBA diving promotes non consumptive resource use and stimulates local economic enterprise but little information exists on the potential effects of overcrowding on the behavior of marine fishes and management strategies for non-consumptive recreational activities in Hawaii's MLCDs are deficient. The increasing popularity of recreational activities in the state's MLCDs poses the question, is there a relationship between the intensity of anthropogenic use in an ecosystem and the presence of predators?

The abundant fish life, scenic beauty and calm clear water inside of the Molokini MLCD make it an ideal location for recreational snorkeling and SCUBA diving and consequently it is the second most visited MPA in the state. Currently, there are 41 commercial vessels permitted to run snorkel and dive tours to the Molokini MLCD and the annual economic benefit of recreational activities in the Molokini MLCD is estimated at 20 million dollars (Van Beukering and Cesar 2004, Needham et al. 2011). In response to the increased popularity of Molokini and a desire to maintain the healthy marine ecosystem, the State of Hawaii's Division of Aquatic Resources revised the MLCD commercial permitting system in 2009 and instituted a requirement for commercial operators to keep logs on the number of passengers, mooring location, and time. These records indicate that in 2012, an average of 29 vessels per day used the park and a total of 330,000 people visited the MLCD. This combination of an intact predator assemblage and high anthropogenic use (which can be accurately measured through mandatory commercial logbooks) provides a unique opportunity to study the movement patterns of predators in the main Hawaiian Islands and investigate the relationship between predatory assemblages inside the MLCD and intensity of anthropogenic use.

In this research, we used passive acoustic telemetry to examine the long-term spatial and temporal movement patterns of several species of reef predators including bluefin trevally (*Caranx melampygus*), giant trevally (*Caranx ignobilis*), green jobfish (*Aprion virscens*), whitetip reef sharks (*Triaenodon obesus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) at the Molokini MLCD. The results of this research are addressed in the following two chapters of this thesis. In chapter one, we describe the residency, habitat use within the MLCD and dispersal to other locations in the Maui Nui Complex to assess what extent these species are protected by the MLCD. In chapter 2, we address the question of whether predatory fishes are displaced from their preferred habitats by anthropogenic use at the Molokini MLCD.

Chapter 1: Movement patterns of reef predators in a small isolated Marine Protected Area with implications for resource management.

Abstract

Reef predators play a critical role in maintaining the balance of marine ecosystems and are an important component of Hawaii's recreational and commercial fisheries. In light of the increasing demands on these populations across the main Hawaiian Islands, the study of predator movements in marine protected areas has become a research priority. To this aim, we used passive acoustic telemetry to investigate the spatial and temporal movement patterns of five reef predator species: bluefin trevally (*Caranx melampygus*), giant trevally (*Caranx ignobilis*), green jobfish (*Aprion virescens*), whitetip reef sharks (*Triaenodon obesus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) at the 31 ha Molokini Marine Life Conservation District (MLCD) off Maui, Hawaii (Lat: 20.633164°, Lon: -156.496317°) from November 13th 2013 to August 28th 2015. Our results indicate that the predator assemblage in the MLCD was dominated by teleost fishes during the day and sharks at night. Residency was variable across species, with bluefin trevally exhibiting the highest residency in the MLCD, green jobfish the lowest, and long distance movements between the Molokini MLCD and the other islands of the Maui Nui Complex were common for grey reef sharks and giant trevally. These results indicate that despite its small size, the Molokini MLCD provides a high level of protection to resident species such as bluefin trevally. However, this MLCD is less effective at protecting more mobile predators such as green jobfish, grey reef sharks and giant trevally.

I. **Introduction**

Predators play a critical role in maintaining the balance of marine ecosystems by regulating and imposing a top-down effect on lower trophic groups (Baum and Worm 2009). With the evolution of modern fisheries, this trophic group has been subjected to intense fishing pressure and as such, has declined substantially from their historical abundance in many parts of the world's oceans (Jackson et al. 2001; Myers and Worm 2005). Declines in predator populations as a result of overfishing have been shown to alter ecosystem function and, in some cases, lead to cascading effects in the marine environment (Heithaus et al. 2008). These changes as a result of overfishing are well documented in the reefs of the tropical Pacific, with drastic differences in both the fish and benthic assemblages of coral reef ecosystems along an increasing gradient of human use (Friedlander and DeMartini 2002; Sandin et al. 2008; Williams et al. 2015).

Over the past century, the main Hawaiian Islands (MHI) have experienced rapid growth in human population density and demands on coastal fish populations have increased concomitantly, with reciprocal declines in predator biomass (Friedlander and DeMartini 2002; Shomura 2004). The species of predators that are the focus of this research, bluefin trevally (*Caranx melampygus*), giant trevally (*Caranx ignobilis*), green jobfish (*Aprion virescens*), whitetip reef sharks (*Triaenodon obesus*) and grey reef sharks (*Carcharhinus amblyrhynchos*) are a critically important component of Hawaii's costal fisheries resources (McCoy 2015). From 2009 to 2014, the average annual commercial landings of bluefin trevally, giant trevally, and green jobfish in Maui County amounted to 526, 1,469 and 7,362 kg a year respectively and these figures likely underrepresent the level of harvest placed on the populations of these species, as they are a cornerstone of the state's inshore recreational fisheries which are not reported (Williams and Ma 2013). Although sharks are not specifically targeted by commercial and recreational fisheries in Hawaii, these species are common by-catch across the states coastal fisheries (Wetherbee et al. 1997; Whitney et al. 2012). The significance of these predators to the state's fisheries and apparent decline in predator biomass in the MHI in comparison to the relatively pristine northwest Hawaiian Islands (NWHI), has made developing conservation strategies for predators a priority in the region (Friedlander and DeMartini 2002).

In response to declining fisheries resources in Hawaii and around the world, Marine Protected Areas (MPAs) have become an important tool in contemporary fisheries management (Rice et al. 2012; Mesnildrey et al. 2013). These areas protected from fishing, are believed to enhance conservation of the species within them and benefit fisheries through movements of adults and enhanced reproductive output into adjacent areas open to fishing (Gaines et al. 2010; Vandeperre et al. 2011; Harrison et al. 2012; Sakihara et al. 2014; Russ et al. 2015). However, the conservation of predators within MPAs is confounded by the fact that many of these species are highly mobile and often move outside the confines of protected areas (Kramer and Chapman 1999; Le Quesne and Codling 2009; Toonen et al. 2013; Batista et al. 2015). Furthermore, many MPAs are only partially protected and instead of no take reserves spatial zoning restrictions control the harvest of marine life within their borders (Lester and Halpern 2008). In order for MPAs to be effective, they must be large enough to contain the movements of a species throughout the entirety of its life cycle, as fishes often undertake movements away from their typical home ranges for the purpose of reproduction and feeding (Sale et al. 2005; Grüss et al. 2011). In recognition of the need to protect highly mobile fish stocks and the limited information on the movements of many marine fishes, the establishment of large scale marine protected areas (LSMPAs) has intensified in recent years (Toonen et al. 2013; Wilhelm et al. 2014).

In Hawaii, MPAs have become an important tool in the conservation of fishes on both large and small scales (Friedlander et al. 2014). Large-scale MPAs like the Papahānaumokuākea Marine National Monument offer mobile species within them high levels of protection and are often created in remote parts of the world's oceans and therefore, have limited social costs associated with their establishment (Friedlander et al. 2014). However, in contrast to the NWHI, at locations with a human population such as the MHI, LSMPAs are not practical or achievable management options and smaller less contiguous areas are the only application of no-take reserves. The Marine Life Conservation District (MLCD) program was established in 1967 to conserve and replenish marine resources for the purpose of education and human enjoyment and today there are 11 small MLCDs across the state. These areas have been successful in maintaining high biomass and diversity of fish assemblages within their borders (Friedlander et al. 2003; Friedlander et al. 2007a; Friedlander et al. 2007b). The short-term movements of some of these predators have been investigated within small protected areas in the MHI (Holland et al. 1996; Wetherbee et al. 2004; Meyer and Honebrink 2005) and their long-term movements have been investigated in the coral atolls of the NWHI (Meyer et al. 2007a; Meyer et al. 2007b), but little attention has been given to the long-term movements of these predators within the state's MLCDs and the effectiveness of small MPAs for protecting large, mobile predatory fishes in the MHI remains uncertain.

The Molokini Shoals Marine Life Conservation District (MLCD) was established as a protected area in 1977 and despite its small size, maintains one of the highest concentrations of predators in the MHI (Friedlander et al. 2007b). Nevertheless, this and many of the other MLCDs across the state were developed without an understanding of the movement and behavior of the species within them and information on the residency and habitat use of predators is an essential prerequisite to understanding the effectiveness of these protected areas in accomplishing conservation objectives (Kramer and Chapman 1999; Chateau and Wantiez 2009). In this study, we applied acoustic telemetry to examine the movements of the MLCD's five dominant predators and investigated spatial and temporal patterns in residency, within and among species to assess the extent to which these species are protected by this small and isolated MPA.

II. Methods

Study site

Molokini Shoals MLCD is a small (31 ha) crescent-shaped volcanic islet in the Maui Nui Complex, which consists of the four Hawaiian Islands; Maui, Molokai, Lanai, and Kahoʻolawe interconnected by a relatively shallow sea floor that descends to a maximum depth of 500 m (Price and Elliott-fisk 2004). The Molokini MLCD is located in the Alalakeiki Channel between the islands of Maui and Kahoʻolawe and the nearest straight line distances between these two land masses is 5 and 7 km, respectively. The inside of Molokini's crater is characterized by a shallow coral reef (<30 m) protected from major ocean swells and the backside of the islet forms a steep vertical wall that descends to approximately 100 m. The depth of the surrounding waters in the Alalakeiki Channel can reach 140 m. The Molokini Shoals MLCD is comprised of two management zones, subzone A and subzone B. Subzone A includes the inside of the crater bounded by a line extending from the end of the submerged coral ridge on the west side of the crater to the east side of the crater (Figure 1.1). The harvest of marine life is prohibited in subzone A and the majority of boating and recreational activities occur in this region. Subzone B extends 100 m seaward of subzone A and encompasses the entire perimeter of the islet; the harvest of fish with trolling gear is allowed in subzone B (CAP 2014).

Acoustic array design

A VR2W passive acoustic monitoring array was used to track the movements of tagged predators in the Molokini MLCD from November 13th 2013 to August 28th 2015. Seven VR2W acoustic receivers (308 mm long x 73 mm diameter, Vemco, Halifax, Nova Scotia) were deployed in strategic locations that enabled the observation of fish movements within the MLCD. In locations with sandy substrate, the VR2W receivers were secured to the bottom with sand screws (2 m long x 10 cm diameter) and attached to a 2 m section of 2 cm diameter polypropylene rope suspended by a small crab float (35 cm long x 15 cm diameter). At receiver sites where the seabed consisted of hard substrate, the moorings were secured to the bottom by passing a section of 6 mm stainless steel wire rope covered by hydraulic hose through natural benthic features and fastened with two stainless steel wire crimps. Three receivers were moored inside subzone A and four were positioned along the back wall of the crater in subzone B (Figure 1.1). The substrate depth of Molokini crater is variable and in subzone A, receivers 1 (R1) and 2 (R2) were placed in 14 m of water, while receiver 3 (R3) was 27 m deep. Range testing indicates that R3 and the four receivers located in subzone B were capable of detecting V13 acoustic transmitters up to 100 m deep. In addition to the receivers located in the MLCD, 18 additional receivers were in place around the islands of Maui and Kahoʻolawe as part of another study, which allowed us to document large-scale movements between these islands and the Molokini MLCD.

Fish capture and transmitter deployment

To deploy acoustic tags, bluefin trevally (n=15), giant trevally (n=16), green jobfish (n=10), whitetip reef shark (n=13), and grey reef shark (n=5) were captured with hook and line. Captured sharks were tail roped and restrained alongside the research vessel where they were inverted and induced into tonic immobility (Henningsen 1994). Teleost fishes were brought on board the research vessel and placed supine in a padded V board with a hose circulating sea water over their gills. Once cataleptic, the specimens were measured, sexed (sharks only) and tagged with Vemco V-13 coded transmitters (13 mm diameter, 45 mm long, Vemco, Halifax, Nova Scotia). Tags were programmed to transmit an individual identification number via a 69 kHz pulse, every 80 to 160 seconds (120 seconds nominal delay) for up to 1019 days. The transmitters were surgically implanted into the body cavity of each animal through a 2 cm incision in the abdominal wall and closed with an interrupted nylon suture (Holland et al. 1999; Meyer and Honebrink 2005). After surgery, sharks and large teleost fishes (>110 cm FL) were tagged with an M-type conventional ID tag, smaller teleost fishes (<110 cm FL) were tagged with 10-cm plastic dart tags (Hallprint, South Australia) before being released. These methods were reviewed and approved by the University of Hawaii's Institutional Animal Care and Use Committee, IACUC protocol number 13-1712.

Range testing

Short-term range testing of our acoustic array was conducted throughout the MLCD by towing a V13 range test tag with 10 second fixed delay from a vessel and simultaneously tracking the GPS location with a VR-100 acoustic receiver. The timing of tag detections by VR2W acoustic receivers was linked to the timing of tag detections by the VR-100 and the corresponding GPS coordinates. The location of each tag detection was plotted in a Geographic Information System (GIS) to generate a map of tag detections in the array. The maximum horizontal detection ranges of each VR2W were determined by measuring the straight line distance from receiver to the farthest point of tag detection.

To evaluate potential bias in fish detection patterns in our VR2W array from both natural and human acoustic interference (Payne et al. 2010), we conducted 48 hour range tests across the diel cycle by placing four V13 range test tags 4 m off the bottom, at staggered intervals from the VR2W's located in subzone A. This allowed us to test receiver performance at a range of distances from 0 to 280 m for receivers located in subzone A. The total number of detections received in a given hour was divided by the total expected number of transmissions to calculate the percentage of successful detections at each distance. To obtain estimates of percent detections at a given distance across the diel cycle, data were binned into day and night, categories based on the hours 19:00 to 7:00 and a binomial general additive model (GAM) was fitted to the data. The maximum receiver range was defined as the distance at which only 5% of transmissions were detected.

Spatial and temporal movement data analysis

Scatter plots

To identify patterns in predator behavior and long-distance movements from the MLCD, diel scatter plots with day and night shading were generated of detections at the seven receivers stationed at Molokini crater and the 18 additional receivers at Maui and Kaho‘olawe for each transmitter equipped fish.

Spatial use of the MLCD and overlap between species

To evaluate spatial distribution of predator habitat use within the Molokini MLCD, the total number of detections at each receiver was calculated for every transmitter-equipped fish. These values were then normalized by calculating an index of receiver use, whereby the number of an individual’s detections at a given receiver was divided by the total number of detections from that individual. These values were then averaged for each species. To describe the overlap in receiver use for all five species, we used EcoSimR’s Pianka’s index to evaluate pairwise overlap in receiver use (Gotelli and Ellison 2013). The mean receiver use index of each species was used to represent receiver utilization and the Pianka’s index was then calculated for all 10 combinations of the five species.

$$O_{12} = O_{21} = \frac{\sum_{i=1}^{n} p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^{n} p_{2i} \sum_{i=1}^{n} p_{1i}}}$$

Where p_{1i} = species one receiver utilization, p_{2i} = species two receiver utilization, (O_{12}) = species one overlap, (O_{21}) = species two overlap. The degree in receiver overlap is represented on a scale of 0 to 1 with a value of 0 indicating no overlap in space use and 1 indicating completely identical overlap in receiver use.

Residency and dispersal

Overall residency in the Molokini MLCD was determined for individual fishes by calculating an index of residency, defined as the number of days each transmitter-equipped fish was detected within the Molokini MLCD array divided by the number of days elapsed since first tagging and the end of the study. A fish was determined to be present at the MLCD on a given day if it was detected at least once over the duration of a 24 hour period. Fish were then assigned into three residency groups: defined as low (< 33%), moderate (33 - 66%) and high (> 66%), based on the results of these residency values (Tinhan et al. 2014). For all transmitter-equipped fishes recaptured and harvested by fishers, the dates elapsed since initial tagging were truncated to the date of capture in the calculation of residency.

To examine post tagging dispersal rates, we determined the proportion of tagged individuals present at the MLCD by species and pooled these proportions based on the days elapsed since initial tagging. A 30 day moving average was calculated and these values where plotted against the number of days elapsed since initial tagging (Wolfe and Lowe 2015). We then compared residency across species by calculating a mean residency index for each species and testing the mean values for each species group with a 1-way analysis of variance. The location of the significant difference between species groups was then identified using Tukey's honestly significant difference (HSD) test. For green jobfish, only individuals larger than 42.5 cm, the empirical length at sexual maturity, were included in this portion of the analysis (Everson et al. 1989). Finally, the relationship between fish size and residency time in the MLCD was investigated for all five species using general linear models (GLMs). The independent variables in the models were fish size (FL), and time at large (days elapsed since initial tagging), with the residency index the dependent variable. For whitetip and grey reef sharks, sex was also added as an independent variable in the model.

Long-distance movements from the MLCD

The extent of long-distance movements from the MLCD was calculated for all the fishes for which we had detections at receivers located in the Maui Nui Complex by measuring the minimum linear distance traveled between the MLCD and location of VR2W detection, or the locations of fish recaptured in fisheries interactions (Meyer et al. 2007a; Meyer et al. 2007b). The average time to cross Alalakeiki Channel was calculated for all last detections at the MLCD and first detections at receivers stationed around Maui or Kahoʻolawe that occurred in less than 24 h.

III. Results

Detection ranges of VR2Ws in the acoustic array

Maximum instantaneous detection ranges in the VR2W acoustic array ranged from 160 to 270 m with an average of 227 m (± 39 SD). The binomial general additive models of detection efficiency generated from the results of the 48 hour range test were significant for both the day (R^2 = 0.93, P < 0.001) and night models (R^2 = 0.98, P < 0.001). The predictions estimated from these models indicate that the maximum range during the day was 203 m and 72 m at night (Figure 1.2a and b).

Spatial and temporal movement patterns of each species in the Molokini MLCD

Bluefin trevally (Caranx melampygus)

All fifteen bluefin trevally were detected within the array, with detection spans ranging from 111 to 585 days (Table 1.1). Bluefin trevally were primarily active within the MLCD during daylight hours. At night, individuals either: (1) moved out of detection range, (2) were less frequently detected, or (3) shifted habitat use between the inner crater and the back wall, suggesting that bluefin trevally moved to deeper water at night or the reduction of detection range from 203 m to 72 m, made them less detectable at night (Figure 1.3a). The residency times of this species ranged between 23 -100% of days monitored ($\bar{x}$ = 77%, ± 28 SD). The majority (n = 11, 68%) of bluefin trevally exhibited high residency times. However, one 64 cm bluefin trevally (CAME1) was tagged in the

MLCD on December 9th 2013 and remained undetected until January 16th 2015, where it was first detected by a VR2W located off south Maui, 5 km away from the MLCD. Approximately 13 hours later, this fish was again detected in the Molokini MLCD, where it persisted for the duration of the study.

Giant trevally (Caranx ignobilis)

All 16 giant trevally were detected within the array, with detection periods spanning from 94 to 605 days (Table 1.1). The majority of detections from this species occurred during daylight hours and at receivers located in close proximity to deep water (Figure 1.3b), in subzone B (84%) and at the deep receiver R3 (15%) on the inside of Molokini in subzone A (Figure 1.4b). The residency times of giant trevally to the MLCD ranged from 3 to 100% ($\bar{x}$ = 52%, ± 31 SD). Fish size and time at large were significantly related to giant trevally residency at the MLCD, with smaller giant trevally being detected on a higher proportion of days than larger fish ($F_{2, 13} = 20.78$, $P < 0.001$). Giant trevally frequently made large-scale movements ranging from 5 to 11 km between the MLCD and receivers located throughout the Maui Nui complex. The locations of these movements from the MLCD to Maui or Kahoʻolawe were documented in eight (50%) of the giant trevally and two patterns of large-scale movements are present in our data (Figure 1.7). The first pattern is long-term movements indicative of home range shifts; while the second is short term cyclical movements indicative of spawning behavior (Figure 1.3b). These short-term cyclical patterns in giant trevally residency at the MLCD were exhibited by the majority of individuals, and we were able to document the locations of these movements away from the MLCD for five of these fish during the septentrional summer of 2015 (Figure 1.3b, i.e., CAIG13, CAIG14, CAIG16). These trans-channel movements were completed by giant trevally in the time span several hours ($\bar{x}$ = 8.24 ± 3.06 SD).

Green jobfish (Aprion virescens)

Nine of the 10 (90%) green jobfish we tagged were detected within the array with detection periods ranging from 6 to 605 days (Table 1.1), and the one undetected green jobfish, APVI4 was recaptured after 293 days at large 15km from the MLCD off south Maui. At the MLCD green jobfish were detected during daylight hours, with arrival and departure from the VR2W array synchronized with sunrise and sunset times over the course of the study (Figure 1.3c). The majority of reproductive sized green jobfish detections at the Molokini MLCD (59%) occurred at the deep receiver (R3) in subzone A (Figure 1.4c). Green jobfish exhibited low residency and transient behavior to the MLCD with 4 out of 10 fish spending short time periods (<10 days) at the MLCD or leaving for extended periods of time and only 2 (20%) individuals exhibited high residency. The green job fish APVI8 was the only individual to exhibit an exceptionally high degree of residency to the MLCD, being detected on 96% of the days elapsed since initial tagging. Based on its length (40 cm FL), this fish was the only immature jobfish tagged. With this outlier removed, the mean residency for reproductively mature green jobfish was 23% (± 27 SD). Six of the 13 (46%) green jobfish tagged with conventional dart tags were recaptured in fisheries interactions outside of the protected area, one of which (APVI2) was recaptured on two separate occasions. Half of these recaptures occurred at distances of less than one km from the MLCD, just outside of the protected area in subzone B, whereas the other half were recaptured on Maui and Kahoʻolawe from 2.5 to 30 km from the MLCD (Figure 1.8).

Whitetip reef shark (Triaenodon obesus)

All of the 13 acoustically tagged whitetip reef sharks were detected within the MLCD array, with detection spans from 163 to 642 days (Table 1.1). Whitetip reef sharks were generally active in subzone A at night and were either undetected at the MLCD during daylight hours or moved to subzone B where they were detected by the receivers located on Molokini's back wall (Figure 1.3d). Individual whitetip reef sharks were often present in subzone B throughout the diel cycle (Figure 1.3d, e.g., TROB4, TROB7). The residency times of this species ranged from 21 to 88% ($\bar{x}$= 48%, ± 48 SD). Four (31%) of the whitetip reef sharks that exhibited low residency were tagged in 2013 and these sharks either left the study site permanently after exhibiting site attachment to the MLCD during the winter of 2014 or returned after an extended absence from the MLCD (202 days).

Grey reef shark (Carcharhinus amblyrhynchos)

All five grey reef sharks were detected within the MLCD array, with detection periods spanning from 11 to 625 days. The majority (84%) of detections from this species occurred in subzone B (Figure 1.4e) with no clear pattern in diel use (Figure 1.3e). The residency times of this species ranged from 5 to 95%% ($\bar{x}$ = 36 %, ± 35 SD) and long-distance movements of 7 km to the VR2W receiver stationed at Kahoʻolawe were documented for four out of the five grey reef sharks we tagged in this study (Figure 1.3e). These movements were regular for three of the four individuals detected in this location, and round trip movements of 14 km between the MLCD and Kahoʻolawe often occurred multiple times over the course of the same day (Figure 1.3e, CAAM4).

Comparisons in residency and habitat use of the MLCD across species

Of the five species of predators we examined, bluefin trevally exhibited the lowest dispersal rates from the MLCD (Figure 1.5). The mean residency index was significantly different between species (F_4 = 5.48, P < 0.001; Table 1.2). Bluefin trevally had the highest site fidelity to the MLCD while green jobfish exhibited the lowest (Figure 1.6). These two species were the only ones to show significant differences in residency (Table 1.2).

Predators in the Molokini MLCD exhibited moderate to high overlap in habitat use. Eight of the 10 species pairs had Pianka index scores between 0.71 and 0.81 (Table1.3). Giant trevally and grey reef sharks had the highest degree of overlap (*0* = 0.92), primarily at Molokini' s back wall in subzone B, with 84% and 74% of the mean receiver use, respectively. In contrast, the species that differed the most in their habitat use were bluefin trevally and giant trevally (*0* = 0.60). The low overlap in receiver used for these species is driven by the relatively low number of giant trevally detections at receivers R1 and R2 in subzone A, with the total mean receiver use at these two VR2W's pooled being 32% for bluefin trevally and 1 % for giant trevally (Figure 1.4a,b).

IV. Discussion

Residency is a measure of how much time an individual spends in a particular location and is influenced by a variety of factors including environmental conditions and habitat requirements of a given species (Speed et al. 2010). In the context of this study, residency indices provide an indication of how much time a species remains within the protected waters of a small isolated MPA. Acoustic monitoring technology has the potential to introduce bias into our estimates of residency rates. Problems associated with acoustic tagging include transmitter failure, transmitter shedding, and mortality associated with tagging (Meyer and Honebrink 2005; Meyer et al. 2010). However, our results suggest that bias from these sources was negligible, as 90% of tagged fish had detections spans exceeding 90 days and in many cases individuals that exhibited prolonged absences from the MLCD were subsequently redetected. Furthermore, the one transmitter equipped fish that was undetected in the array (APVI4) was recaptured, 15 km from the MLCD and at the time of capture this individual's tag was present in the fish and functional. Nevertheless, there is as potential for bias in our estimate of residency rates due to these sources (Meyer and Honebrink 2005). Our findings show that these predators exhibit spatial and temporal habitat partitioning, variable residency, and long-distance movements. An understanding of these species-specific movement patterns is an important consideration when evaluating the effectiveness of an MPA in conserving this diverse assemblage of fishes (Kramer and Chapman 1999; Meyer et al. 2010; Hooker et al. 2011).

Temporal and spatial use of the MLCD

Range testing indicated that ambient acoustic noise reduced the detection range of our VR2W receivers during nocturnal hours. This increase in ambient noise is generated by nocturnally active snapping shrimp and is a real limitation to studying the diel movements of reef-associated fishes with acoustic telemetry (Heupel et al. 2006; Payne et al. 2010; Kessel and Simpfendorfer 2013). The difference in detection range between day and night prevents us from definitively concluding whether the diel patterns we observed are a result of habitat shifts for green jobfish and giant trevally. Both of these species appeared to be more active in the MLCD during daylight hours and disappeared from our array at night. However, due to the fact that these species were not detected at separate locations during these nightly absences, it is unclear to what extent these absences are a result of movements out of the MLCD or reduced detection efficiency in our VR2W array.

Whitetip reef sharks and bluefin trevally exhibited several patterns in habitat utilization that suggest temporal changes in the predator assemblage of the MLCD occur across the diel cycle. Whitetip reef sharks showed no strong diel patterns of detection in subzone B, however in subzone A despite the reduction in detection range, whitetip reef sharks dramatically increased their use of this habitat during nocturnal hours. Previous authors have noted increased activity in whitetip reef sharks at night (Randall 1977; Whitney et al. 2007; Fitzpatrick et al. 2011) and our results are consistent with these findings. Two behaviors could be responsible for the variation we observed in the diel detection patterns of whitetip reef sharks in the two management zones of the MLCD. The majority of the reef habitat in subzone A is characterized by a gentle slope between 5 to 30 m deep. Whitetip reef sharks could be vertically migrating into the shallow reef of subzone A to hunt sleeping reef fish at night, and move deeper outside of detection range of our array during the day. In contrast, the back side of Molokini is characterized by a vertical wall that descends from 0 to 100 m. Range testing indicates that an acoustic transmitter can be detected thought the entire water column and as a result, a vertically migrating whitetip reef shark can be detected in subzone B throughout the diel cycle regardless of its depth. Alternatively, another explanation for the absence of whitetip reef shark detections in subzone A during daylight hours could be attributed to sharks resting in small caves or under a ledges with high relief, which would result in terrain shielding of acoustic transmitter signals.

In contrast, bluefin trevally were the principal reef predator in subzone A of the MLCD during the day but often moved to deeper water in subzone B of the Molokini MLCD at night. These findings are consistent with previous research, which suggests that bluefin trevally shift habitat use between day and night, Meyer and Honebrink (2005) documented regular habitat shifts, with one individual exhibiting repeated back and forth movement of 1.1 - 2.8 km between shallow-day and deep-night habitats. Furthermore, active tracking of 5 bluefin trevally in Kaneohe Bay, Oahu indicated that at night, bluefin trevally abandoned their typical day time habitats and moved to the same discrete location in a deep portion of Kaneohe Bay, where they remained quiescent and exhibited restricted movements until dawn (Holland et al. 1996).

Spatially, giant trevally and grey reef sharks had the highest degree of overlap resulting from their use of a steep vertical drop off and strong currents in subzone B. In contrast, giant and bluefin trevally showed the lowest overlap in habitat use, and giant trevally rarely utilized the inner regions of subzone A, this may be a result of interspecific resource partitioning between two similar species as there is relatively little overlap in the diet of these two species (Meyer et al. 2000).

Residency and long distance movements

Continuous reef habitat is thought to a prerequisite for the movement and dispersal of many species of reef associated fishes (Chapman and Kramer 2000; Lowe et al. 2003; Meyer et al. 2010). Although the Molokini MLCD is isolated from other islands in the Maui Nui Complex, the depth of the surrounding waters is generally less than 140m and is relatively shallow in comparison to the other inter-island channels of the MHI. The repeated movements of predators across the Alalakeiki channel may have been facilitated by mesophotic reef which, could serve as contiguous habitat for species that are not limited by their maximum depth tolerance. Whether these individuals follow the seabed and use this habitat while crossing between islands is unknown, but our results indicate that with the exception of bluefin trevally, these species regularly transit a more significant barrier than continuous costal reef and the Molokini MLCD may not be truly isolated from the other islands of Maui Nui.

In our study, bluefin trevally exhibited the highest residency to the Molokini MLCD and the detection spans of bluefin trevally observed were considerably longer than those of acoustically monitored bluefin trevally on the island of Hawaii (Meyer and Honebrink 2005). The differences between the degree of residency and dispersal observed between these two studies may be attributed to the fact that in compassion to Molokini's location in the center of the Alalakeiki channel, no significant barriers to dispersal exist along the continuous shallow reef coastline on the island of Hawaii. However, the round trip movement of over 10 km, made by CAME1 indicates that although uncommon in our data, this species is capable of crossing channels of this depth and scale.

In comparison to bluefin trevally, giant trevally forays away from the MLCD were frequent and longer in duration. Previous research indicates that giant trevally are capable of making regular long-distance movements up to 19 km within individual islands (Wetherbee et al. 2004; Meyer et al. 2007a). In the present study, we documented regular round trip movements of giant trevally across the Alalakeiki channel between the Molokini MLCD and receiver locations at south Maui and Kaho‘olawe. The majority of these movements and long-term absences of giant trevally previously resident at the MLCD occurred during the summer, suggesting that these movements may be related to spawning. Giant trevally spawning has been documented during the septentrional summer in the NWHI (Sudekum et al. 1991), where this species was shown to repeatedly travel long distances to form spawning aggregations in areas with swift current and access to deep water (Meyer et al. 2007a).

The residency of whitetip reef sharks to the Molokini MLCD is consistent with the pattern of site attachment and home range shift proposed by Whitney et al. (2012). Four out of nine white tips we tagged in 2013 exhibited evidence of a home range shift and left Molokini for the duration of the monitoring period. We were unable to document the extent of these movements from the MLCD, however one of the individuals tagged in our study (TROB7) returned to the MLCD after an absence of 202 days suggesting that this species exhibits philopatry and can reestablish residence after extended periods of absence.

Prior to this research, the only available data on the abundance and distribution of grey reef sharks in the MHI dates back to the state sponsored shark control programs of the 1960-1970's where catch rates indicate that grey reef sharks are restricted in their distribution, being frequently captured only in Molokini, Niihau, and Ka‘ula Rock (Wetherbee et al. 1997)**.** Although Molokini is considered to be a one of the few locations in the MHI where this species can be regularly encountered, the overall residency of grey reef sharks to the MLCD is low in comparison to the other species we tagged. The sporadic but regular detections of four of the five grey reef sharks at the VR2W off Kaho‘olawe suggest that this island is an important habitat for grey reef sharks in Hawaii. In contrast to our results, several studies have shown grey reef sharks exhibit high residency to isolated sea mounts and atolls (Field et al. 2010; Barnett et al. 2012). The low residency we observed in grey reef sharks to the Molokini MLCD is consistent with Heupel et al. (2010), who concluded that site fidelity to discrete patch reefs in the Great Barrier Reef (GBR) was limited, as the sharks tagged in their study regularly moved between patch reefs of the GBR. Barnett et al. (2012) suggested that the discrepancies in residency between these studies are likely a function of distance between grey reef habitats. Both the Rowley Shoals and Osprey Reef are isolated atolls separated from other continental reef habitats by distances of 250 km and 125 km, respectively; while the patch reef system on the GBR represents 2400 km of continuous grey reef habitat and poses few obstacles to dispersal. Our results support this theory, in that the reefs of the Maui Nui Complex are separated by channels on a scale of 5 to 15 km and given the mobility of this species it is likely that this part of the MHI represents continuous grey reef habitat and as such, the low residency but philopatry to the Molokini MLCD may be a result of grey reef sharks using the larger area as part of their home range, suggesting that the Molokini MLCD is a small but important habitat for this species.

Implications for management

Despite the comparatively high fish biomass within its borders of Hawaii’s MLCDs, the MLCD program was established to support conservation of the marine resources within their borders and education, not replenish fish stocks (Friedlander et al. 2007b). Nevertheless, our research indicates that bluefin trevally are well protected by this small MPA, and given that bluefin trevally size was not significantly related to residency, the protected status of this isolated population has the potential to enhance reproductive output to neighboring populations in other parts of the Maui Nui complex. These results provide long-term evidence to support the previous conclusions made by Holland et al. (1996) that small MPAs can be effective in the conservation of this species.

The benefits of the Molokini MLCD are varied for the other more mobile species we studied. The regular movements of both giant trevally and grey reef sharks between the Molokini MLCD, Kahoʻolawe and Maui suggest that Molokini is an important corridor for fish movement in the Maui Nui complex. Kahoʻolawe is the largest protected area in the MHI and the protected status of the Molokini MLCD likely enhances the conservation of fish that use this corridor between islands. Giant trevally appear to be offered a moderate level of protection by the MLCD, in that they exhibit relatively high residency, but undertake regular large scale movements to areas outside of the MLCD where they are susceptible to harvest. The significant relationship between giant trevally size and residency suggests that larger fish are more likely to spend less time within the confines of the MLCD and as mentioned above, these large-scale movements to unprotected areas on south Maui could be associated with spawning behavior. If so, giant trevally that are normally protected by the MLCD are vulnerable during spawning events. Furthermore, at a smaller scale, giant trevally are almost exclusively active in subzone B where the harvest of marine fishes is allowed by trolling suggesting that this species is potentially vulnerable to fisheries interactions while resident at the MLCD.

In contrast, the low residency, large scale movements, and high recapture rate of green jobfish tagged at the Molokini MLCD indicates this species is provided little protection by this small isolated MLCD. Though unsubstantiated, the diel pattern green jobfish behavior suggests that when resident these fish leave the protected area on a daily basis, and although we were unable to empirically document the extent of these nightly movements, half of all the green jobfish recaptured in fisheries interactions occurred within one km of the MLCD at night, while others up to 30 km. The high residency of juvenile green jobfish suggests that despite the fact that the MLCD provides little protection to reproductively mature individuals it could be an important nursery habitat that provides protection to green jobfish during the initial stages of this species' life cycle. Our results are consistent with the wide ranging movements of this species that were documented in the coral atolls of the NWHI, indicating that large MPAs on the scale of islands or Maui Nui would be required to protect populations of green jobfish in a pristine state (Meyer et al. 2007b).

Overall, this research suggests that with the exception of bluefin trevally, if fisheries replenishment is a desired outcome, future MPA design in the state of Hawaii would need to consider making reserves large to protect reef predator spawning stocks. At present, MLCDs constitute .03% of the available coastline in the MHI and it has been suggested that a minimum of 20-30% of the MHI should be protected before fisheries benefits such as larval export and spillover of adults can be realized (Friedlander et al. 2007b). However, creating large scale completely protected areas is not practical in the MHI, where fishing is a valued part of the culture and restrictions are often heavily contested (Shomura 2004). Alternatively, a multipronged approach that includes the creation of a large network of small MPAs which incorporate the critical habitats of these species could enhance fisheries conservation. In the case of giant trevally, future research could identify the locations of spawning aggregations in the MHI and a network of small MPAs that target the locations of these predictable movements could enhance the conservation power of small MPAs such as the Molokini MLCD (Meyer et al. 2007a). Furthermore, the fact that larger giant trevally were more mobile and were presumably leaving the MLCD during the summer for spawning events indicates that seasonal harvest restrictions or slot limits could provide additional protection to this species.

The conservation of reef predators is a priority for the maintenance of ecosystem function and the long-term sustainability of fisheries in the MHI. Although this research sheds light on habitat use and residency in the Molokini MLCD, this research indicates that adult population connectivity for mobile species such as green jobfish and giant trevally occurs across the Maui Nui complex and the exploitation of the populations of these species should be managed at this trans-island wide scale. To this aim, a larger network of small MPAs could be effective in conserving of predators but additional research is needed to identify the extent of nightly habitat shifts for these species and locations of spawning aggregations in the Maui Nui Complex so that future marine spatial planning of MPAs can incorporate these high value habitats.

V. Tables

Table 1.1: Summary detection data for 59 predators tagged in the Molokini MLCD (CAME = bluefin trevally, GAIG = giant trevally, TROB = whitetip reef shark, APVI = green jobfish, CAAM = grey reef shark).

Species	N	x̄ FL (cm)	Detection span (days)			Total detections			Residency (%)		
			Min	Max	Median	Min	Max	Median	Min	Max	x̄
CAME	15	54 ± 13	111	585	470	868	28143	7165	23	100	77 ± 28
CAIG	16	91 ± 17	94	605	294	38	22815	4610	3	100	52 ± 31
APVI	10	67 ± 12	0	605	113.5	0	24129	278	0	96	30 ± 35
TROB	13	87 ± 14	163	642	530	1129	4878	2121	22	89	48 ± 48
CAAM	5	116 ± 25	11	625	288	1087	9528	2431	5	94	36 ± 35

Table 1.2: Residency index for each species. Values are means and standard deviation in parentheses. Residency was a significant difference between the species ($F_4 = 5.48$, $P < 0.001$). Tukey's HSD tests were used for unplanned multiple comparisons among species. Species with the same letter are not significantly different ($\alpha = 0.05$).

Species	Residency	Multiple comparisons
Caranx melampygus	0.78 (0.28)	AB
Caranx ignobilis	0.52 (0.31)	BC
Triaenodon obesus	0.48 (0.23)	BC
Carcharhinus amblyrhynchos	0.36 (0.36)	BC
Aprion virescens	0.23 (0.28)	C

Table 1.3: The results of the Pianka index of pairwise overlap in mean receiver use between the ten species combinations at the MLCD.

Species 1	Species 2	Pianka (*O*)
C. amblyrhynchos	*C. ignobilis*	0.92
C. amblyrhynchos	*T. obesus*	0.81
C. amblyrhynchos	*C. melampygus*	0.8
C. melampygus	*T. obesus*	0.79
A. virescens	*T. obesus*	0.78
C. ignobilis	*T. obesus*	0.78
A. virescens	*C. amblyrhynchos*	0.77
A. virescens	*C. melampygus*	0.76
A. virescens	*C. ignobilis*	0.71
C. ignobilis	*C. melampygus*	0.6

VI. Figures

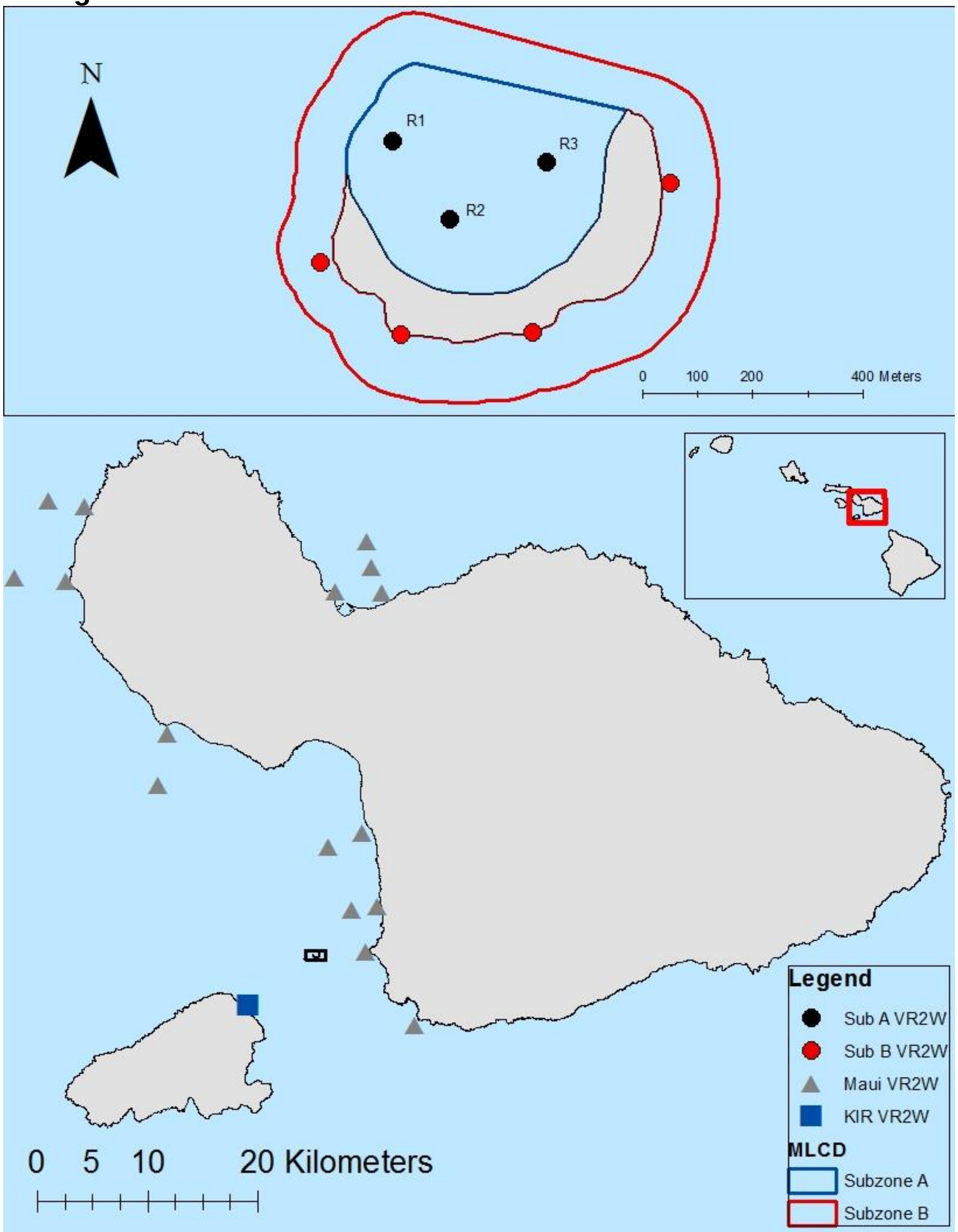

Figure 1.1: The Molokini MLCD acoustic array, and VR2W receiver locations on Maui and Kahoʻolawe (KIR). Red lines indicate subzone demarcation at the MLCD; black dots indicate locations of subzone A receivers, red dots represent subzone B receivers, grey triangles indicate the location of receivers on Maui and the blue square indicates the receiver at the KIR.

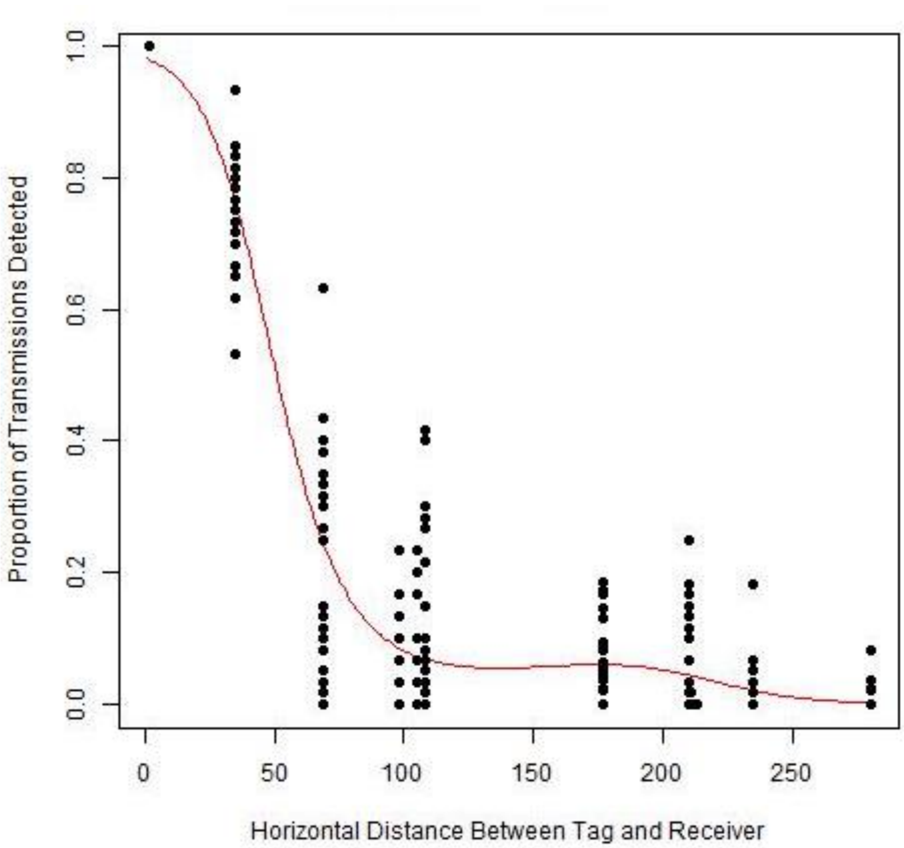

Figure 1.2a: The proportion of transmissions successfully detected, from range test tags placed at varying distances from VR2W acoustic receivers in subzone A during day light hours(8:00 - 18:00), with the predicted fit of the binomial general additive model overlaid on the data (R^2=.93, P- value = <.0001).

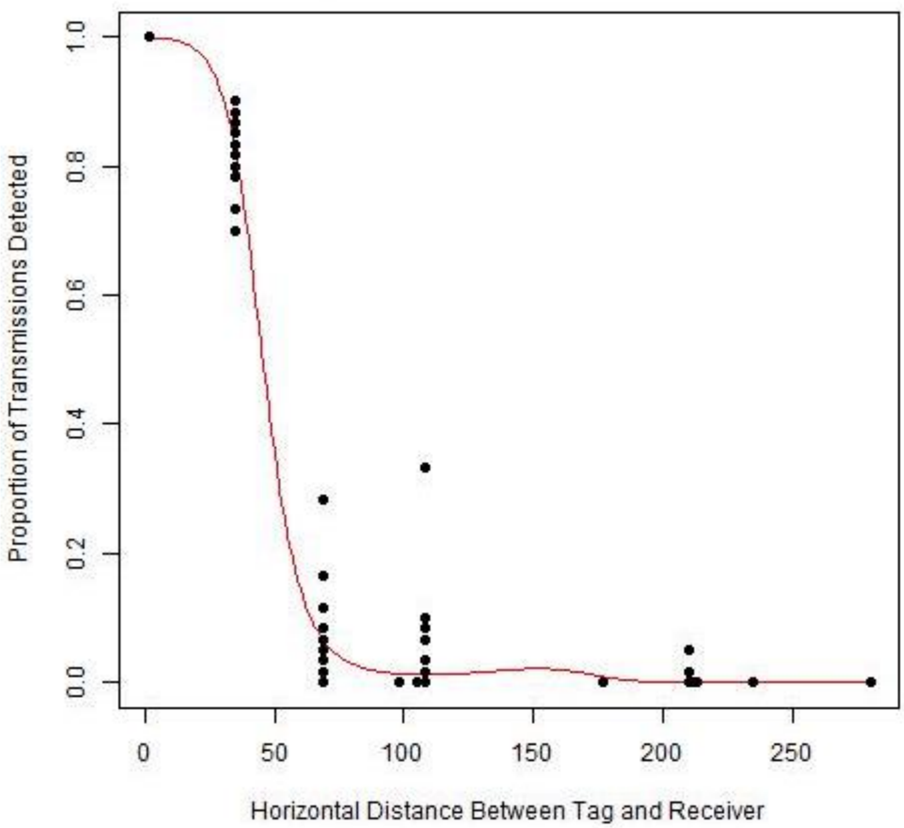

Figure 1.2b: The proportion of transmissions successfully detected, from range test tags placed at varying distances from VR2W acoustic receivers in subzone A during nocturnal hours(19:00 - 7:00), with the predicted fit of the binomial general additive module overlaid on the data (R^2=.98, P- value = <.0001).

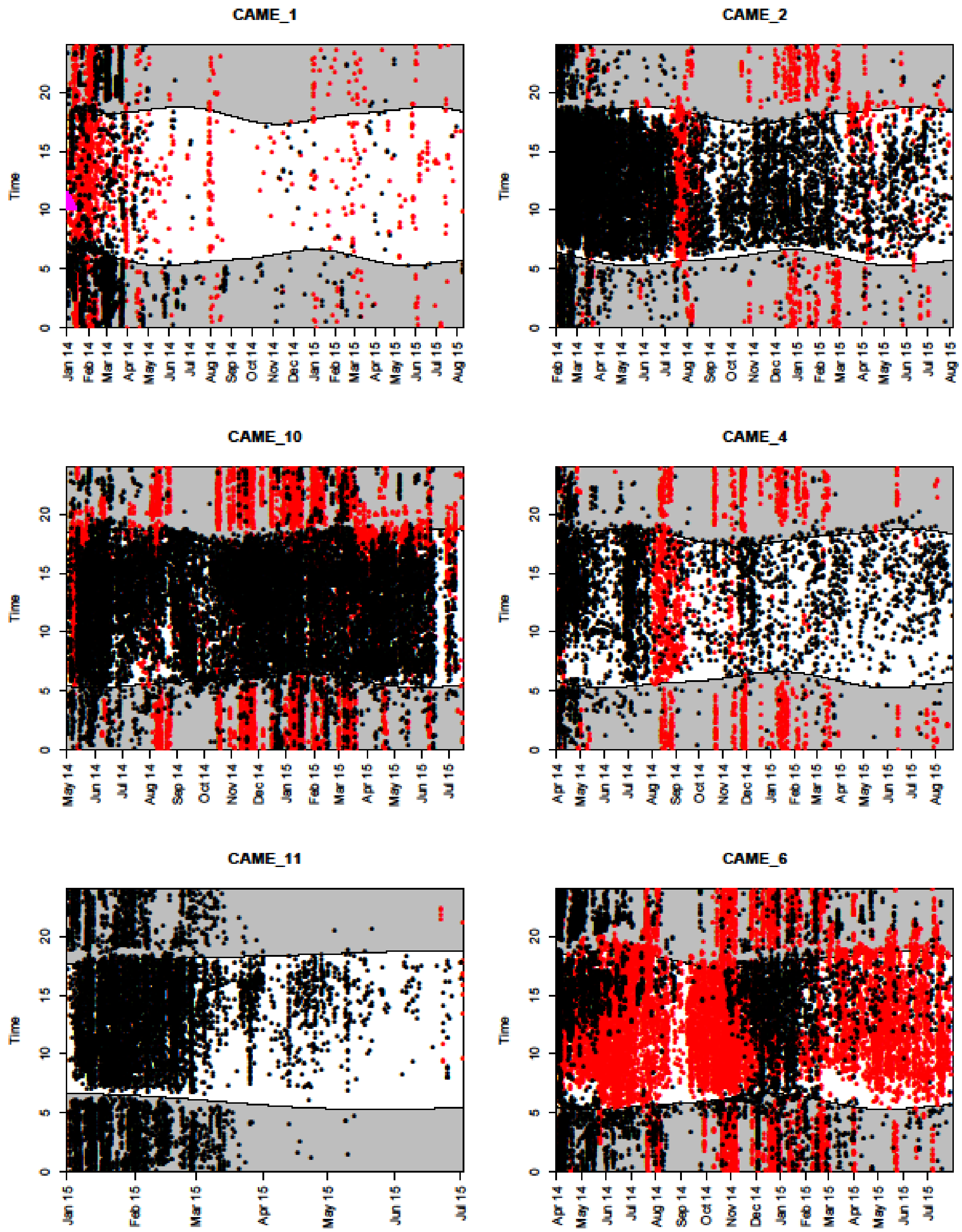

Figure 1.3a: Examples of diel scatter plots bluefin trevally. Black dots indicate detections in subzone A of the Molokini MLCD, red dots indicate detections in subzone B, squares indicate detections at Kaho‘olawe, and triangles indicate detections on Maui, with colors corresponding to individual VR2W’s. Day and night shading is overlaid on the scatter plots based on the timing of sunrise and sunset over the duration of the monitoring period (note differing scales on the x-axis).

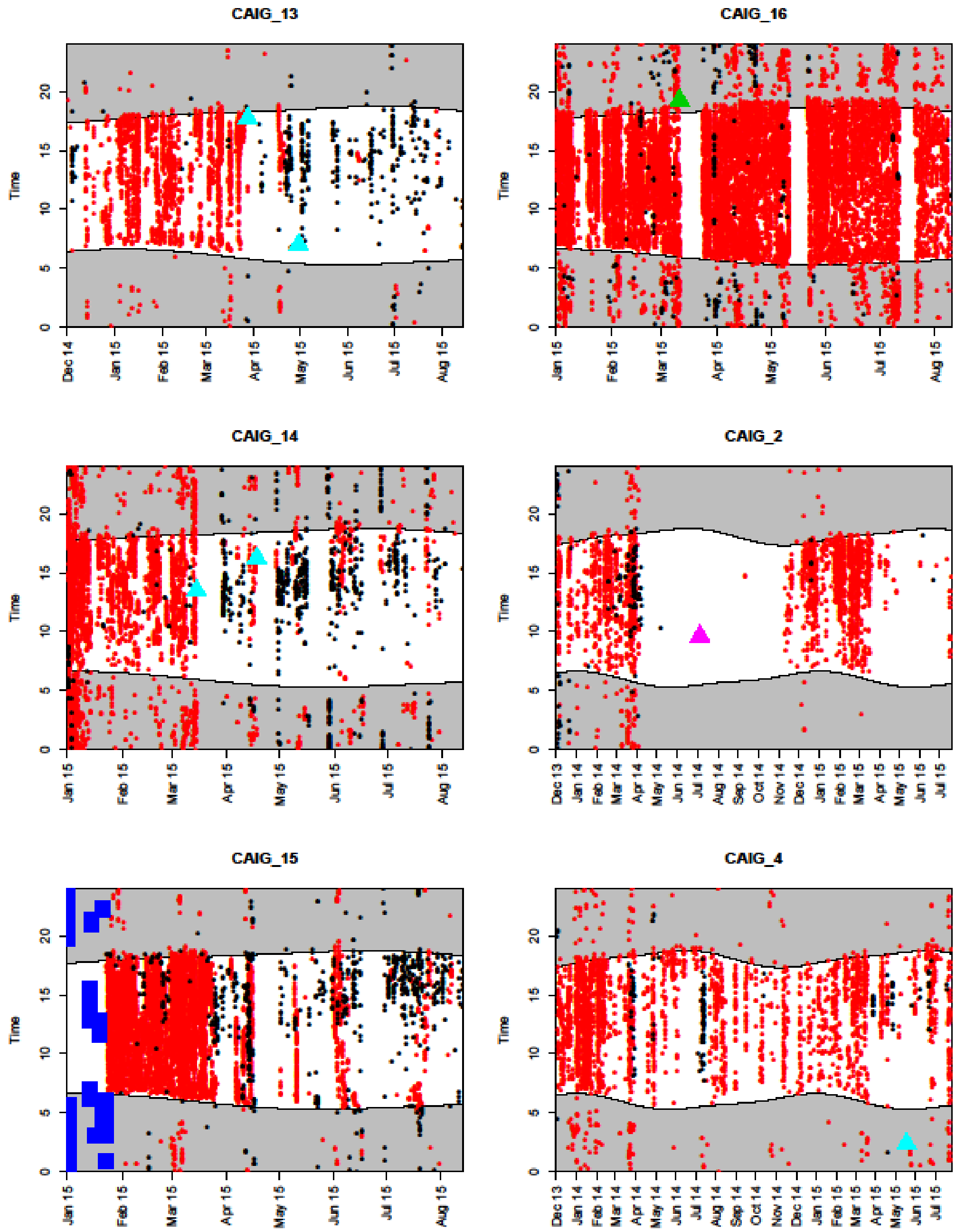

Figure 1.3b: Examples of diel scatter plots for giant trevally. Black dots indicate detections in subzone A of the Molokini MLCD, red dots indicate detections in subzone B, squares indicate detections at Kaho'olawe, and triangles indicate detections on Maui, with colors corresponding to individual VR2W's. Day and night shading is overlaid on the scatter plots based on the timing of sunrise and sunset over the duration of the monitoring period (note differing scales on the x-axis).

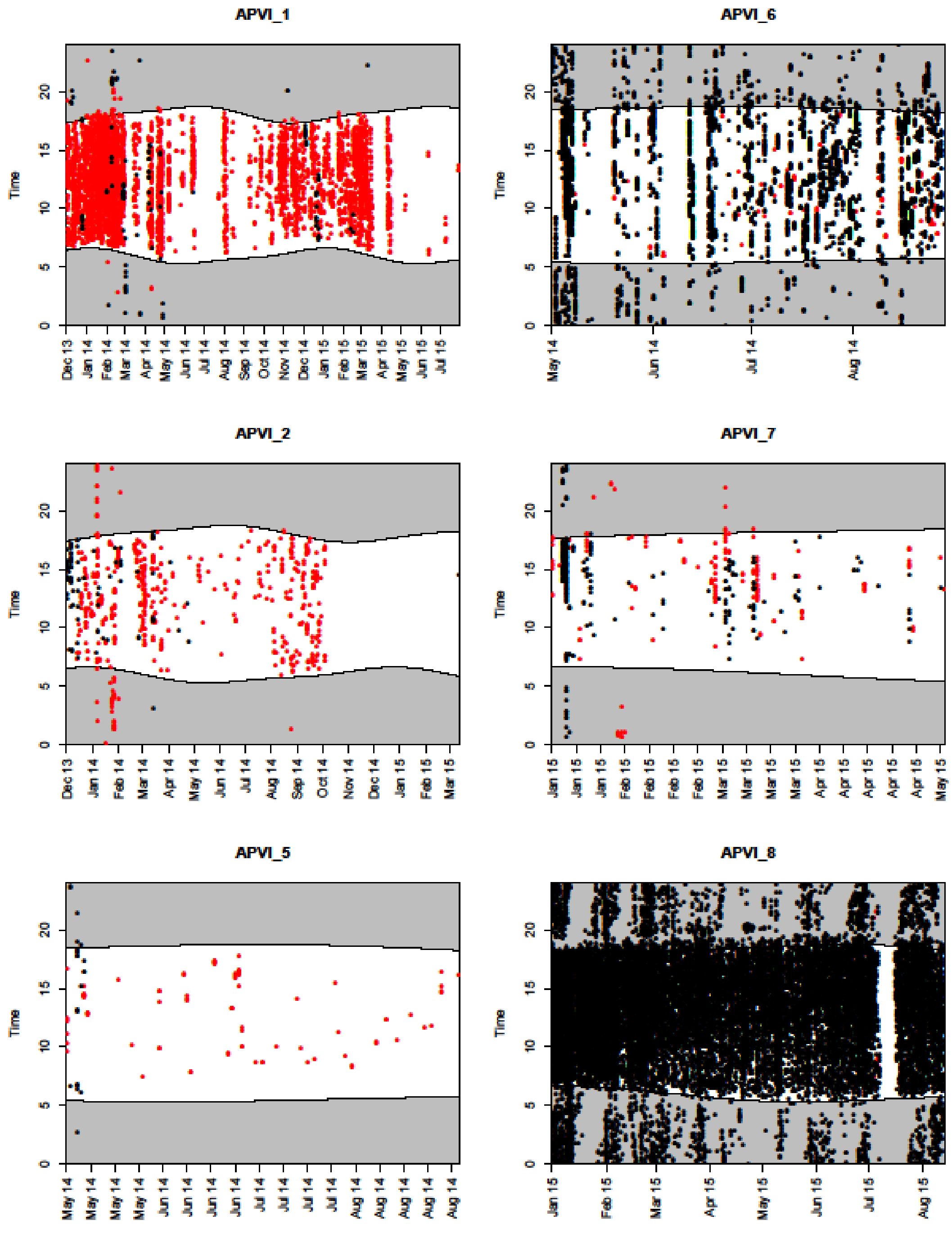

Figure 1.3c: Examples of diel scatter plots for green jobfish. Black dots indicate detections in subzone A of the Molokini MLCD, red dots indicate detections in subzone B, squares indicate detections at Kaho‘olawe, and triangles indicate detections on Maui, with colors corresponding to individual VR2W’s. Day and night shading is overlaid on the scatter plots based on the timing of sunrise and sunset over the duration of the monitoring period (note differing scales on the x-axis).

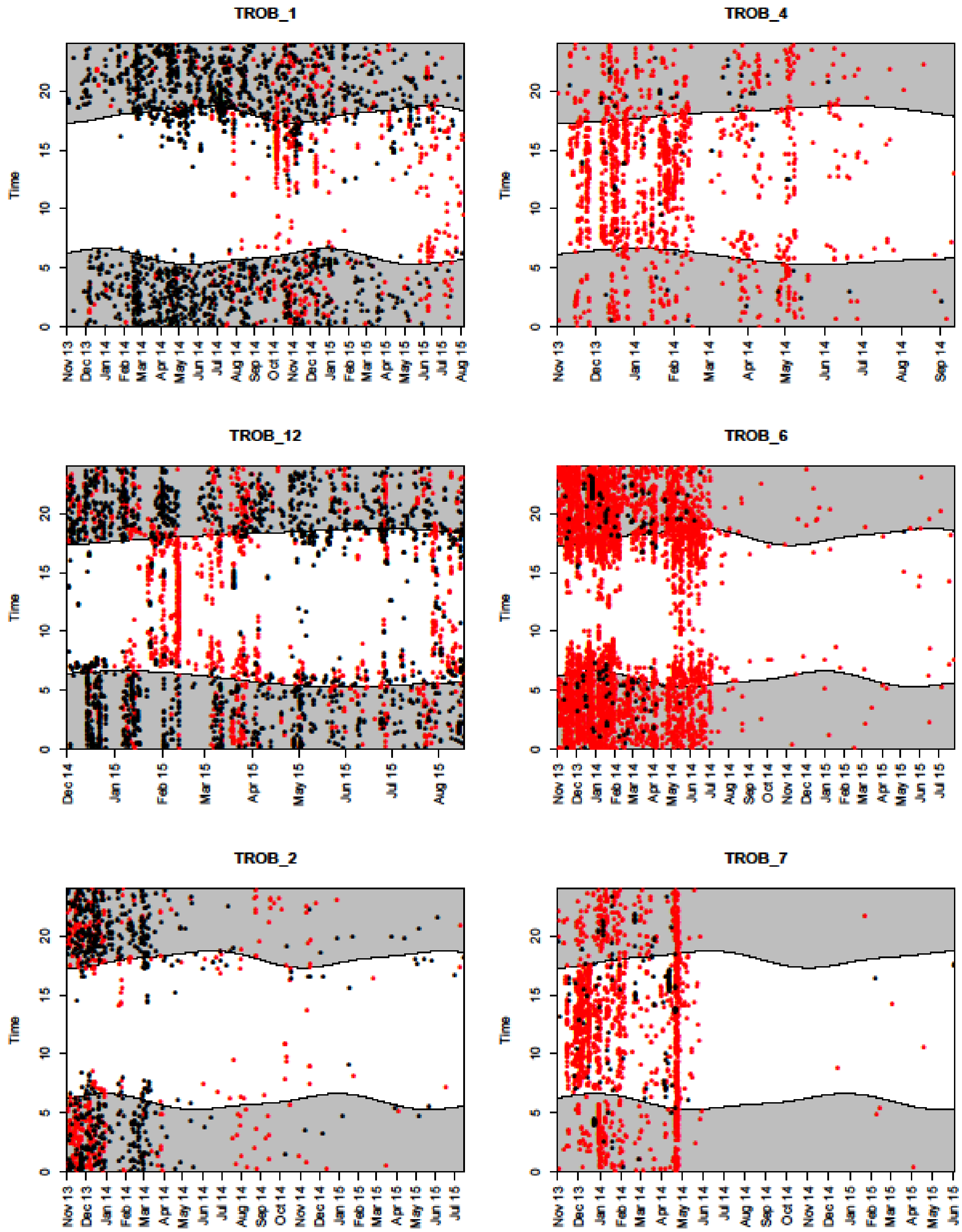

Figure 1.3d: Examples of diel scatter plots for whitetip reef sharks. Black dots indicate detections in subzone A of the Molokini MLCD, red dots indicate detections in subzone B, squares indicate detections at Kaho‘olawe, and triangles indicate detections on Maui, with colors corresponding to individual VR2W’s. Day and night shading is overlaid on the scatter plots based on the timing of sunrise and sunset over the duration of the monitoring period (note differing scales on the x-axis).

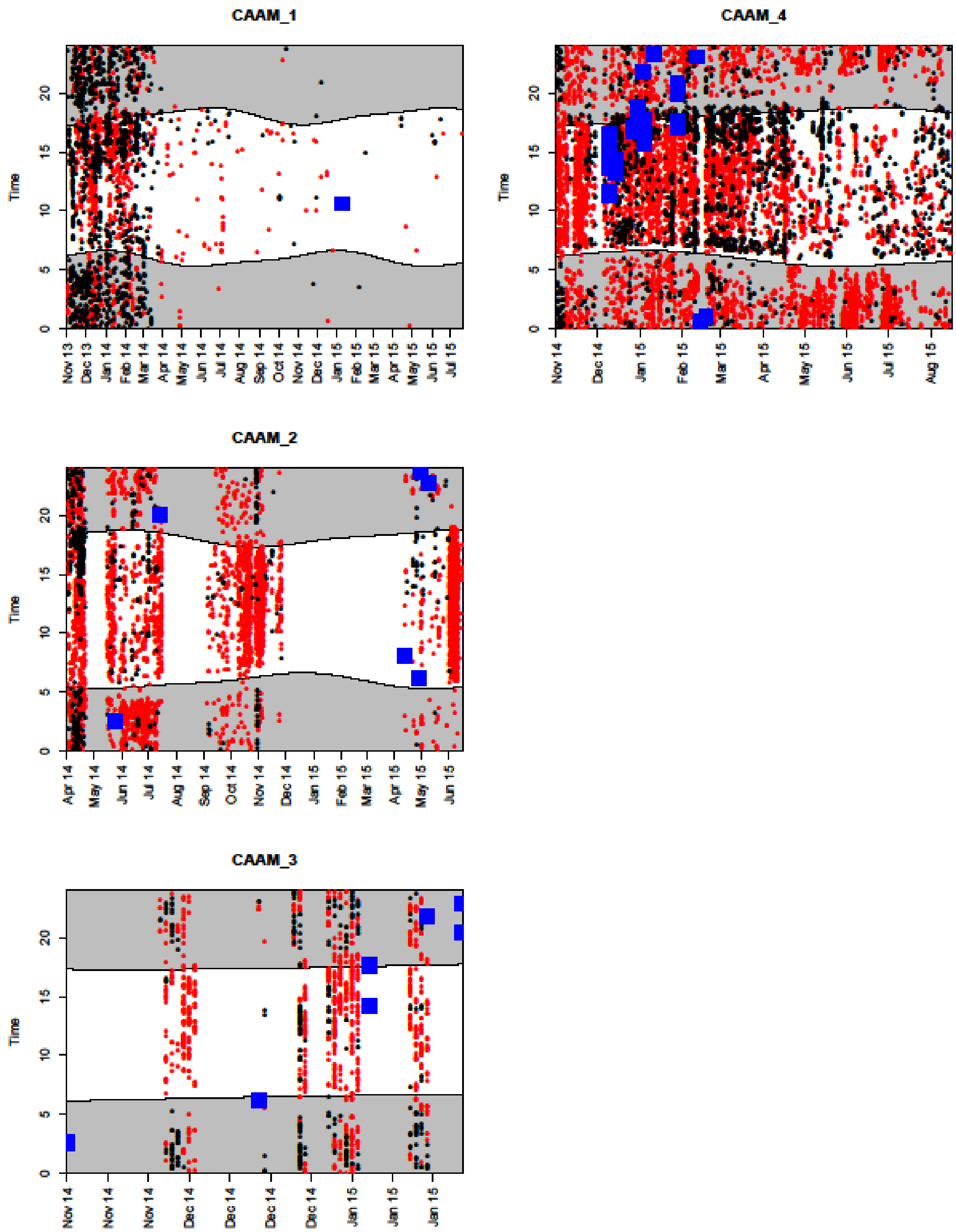

Figure 1.3e: Examples of diel scatter plots for grey reef sharks. Black dots indicate detections in subzone A of the Molokini MLCD, red dots indicate detections in subzone B, squares indicate detections at Kahoʻolawe, and triangles indicate detections on Maui, with colors corresponding to individual VR2W's. Day and night shading is overlaid on the scatter plots based on the timing of sunrise and sunset over the duration of the monitoring period (note differing scales on the x-axis).

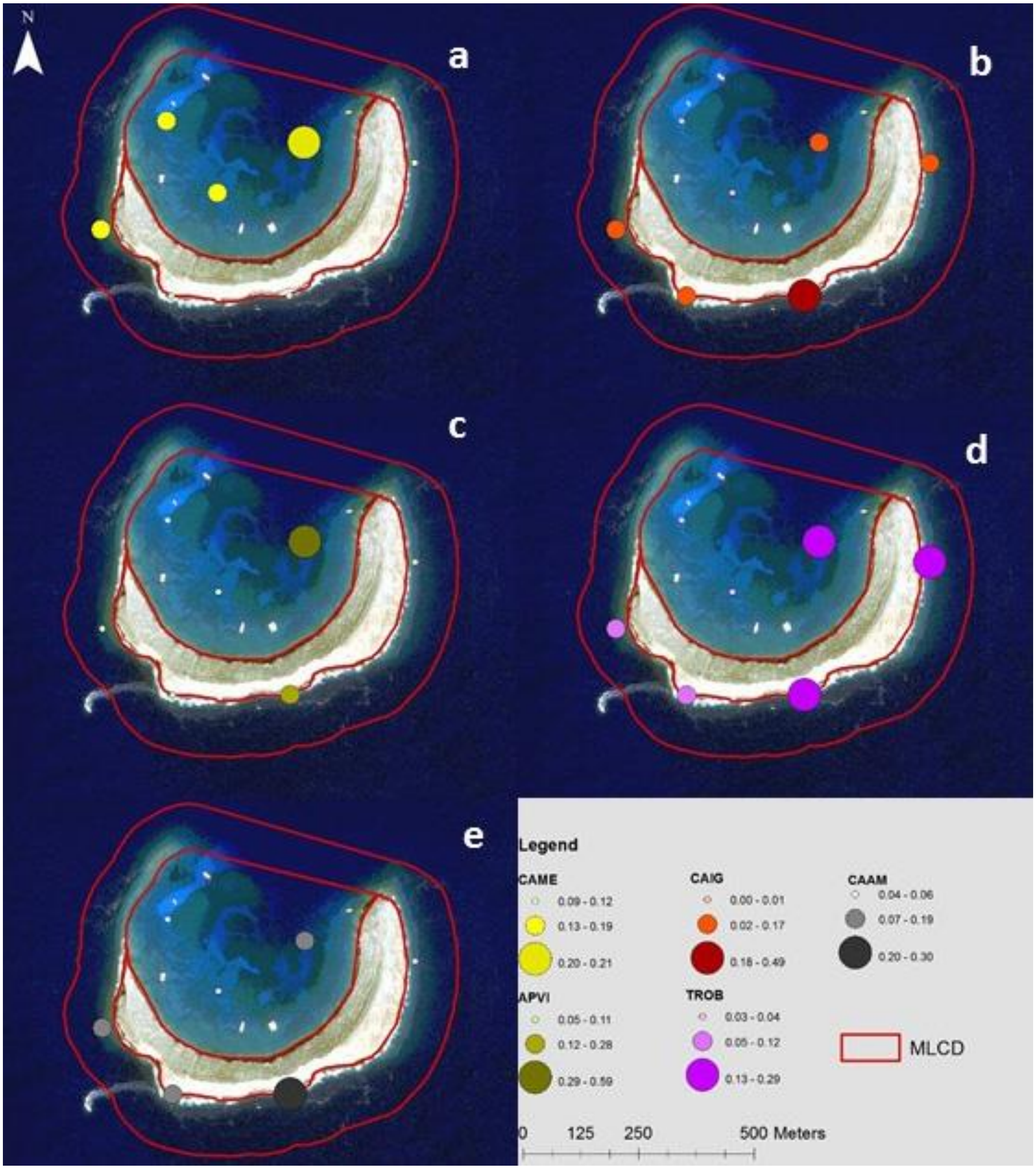

Figure 1.4: Scaled bubbles representing the mean receiver use index of predators at the seven receivers located in the Molokini MLCD. (CAME = bluefin trevally (yellow), GAIG = giant trevally (red), APVI = green jobfish (green), TROB = whitetip reef shark (purple), CAAM = grey reef shark (grey)).

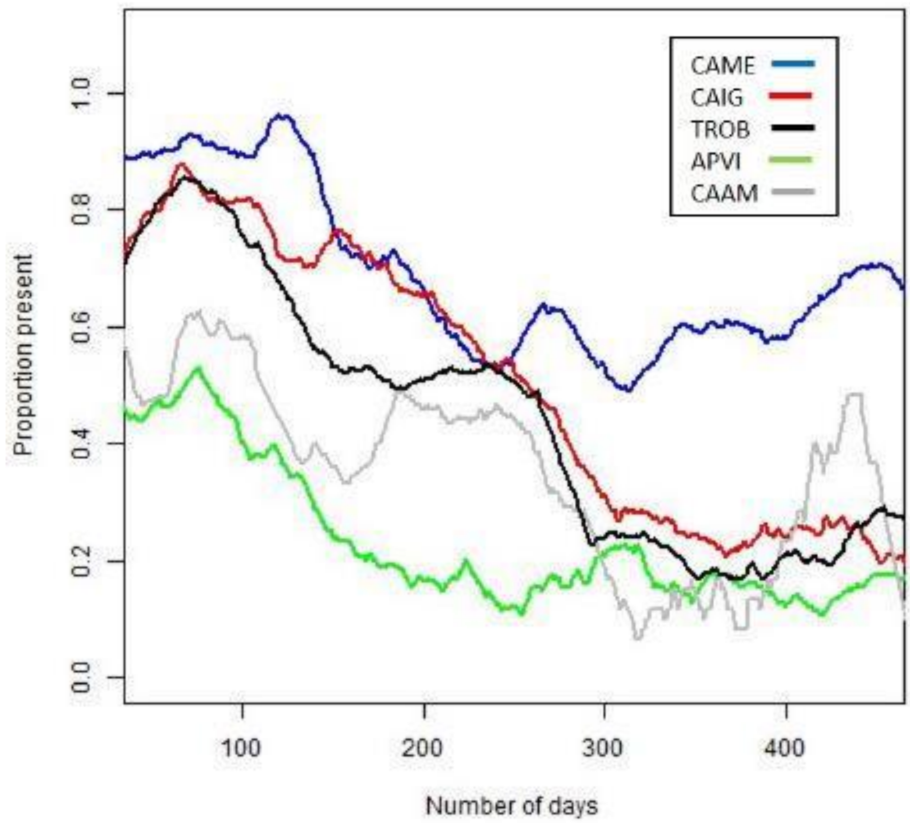

Figure 1.5: A 30 day moving average of the proportion of tagged individuals from each species present at the MLCD, plotted against days elapsed since initial tagging. Colored lines correspond to individual species (CAME = bluefin trevally, GAIG = giant trevally, TROB = whitetip reef shark, APVI = green jobfish, CAAM = grey reef shark).

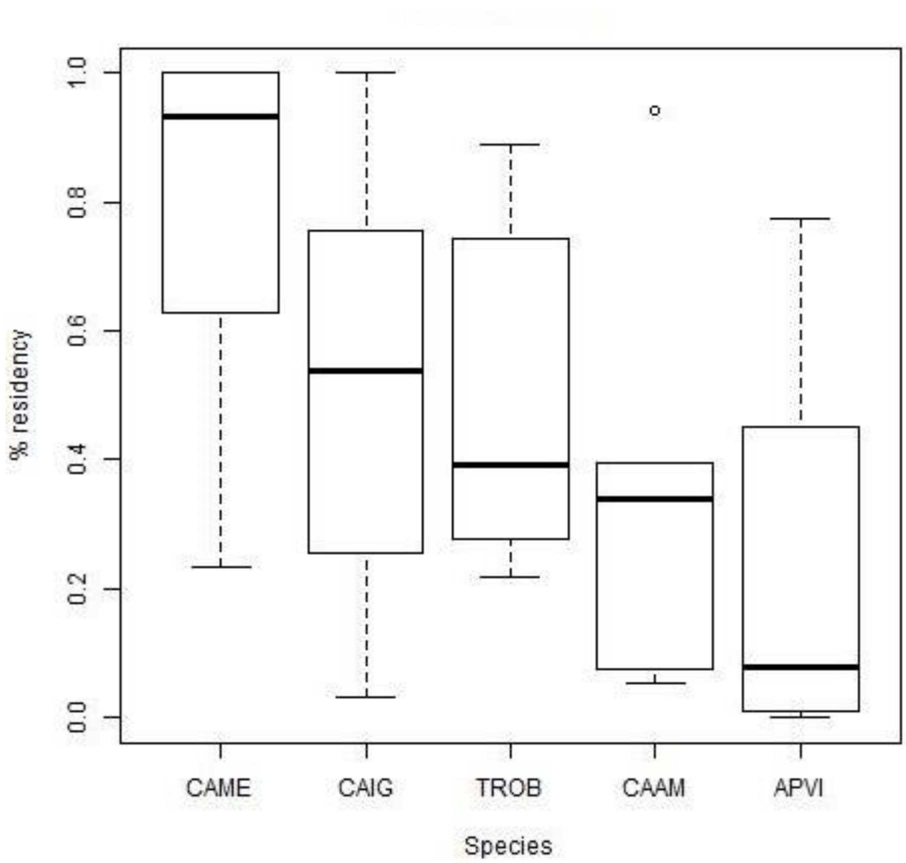

Figure 1.6: Boxplots of the inter quartile range of the percent residency index across the five species (CAME = bluefin trevally, GAIG = giant trevally, TROB = whitetip reef shark, APVI = green jobfish, CAAM = grey reef shark).

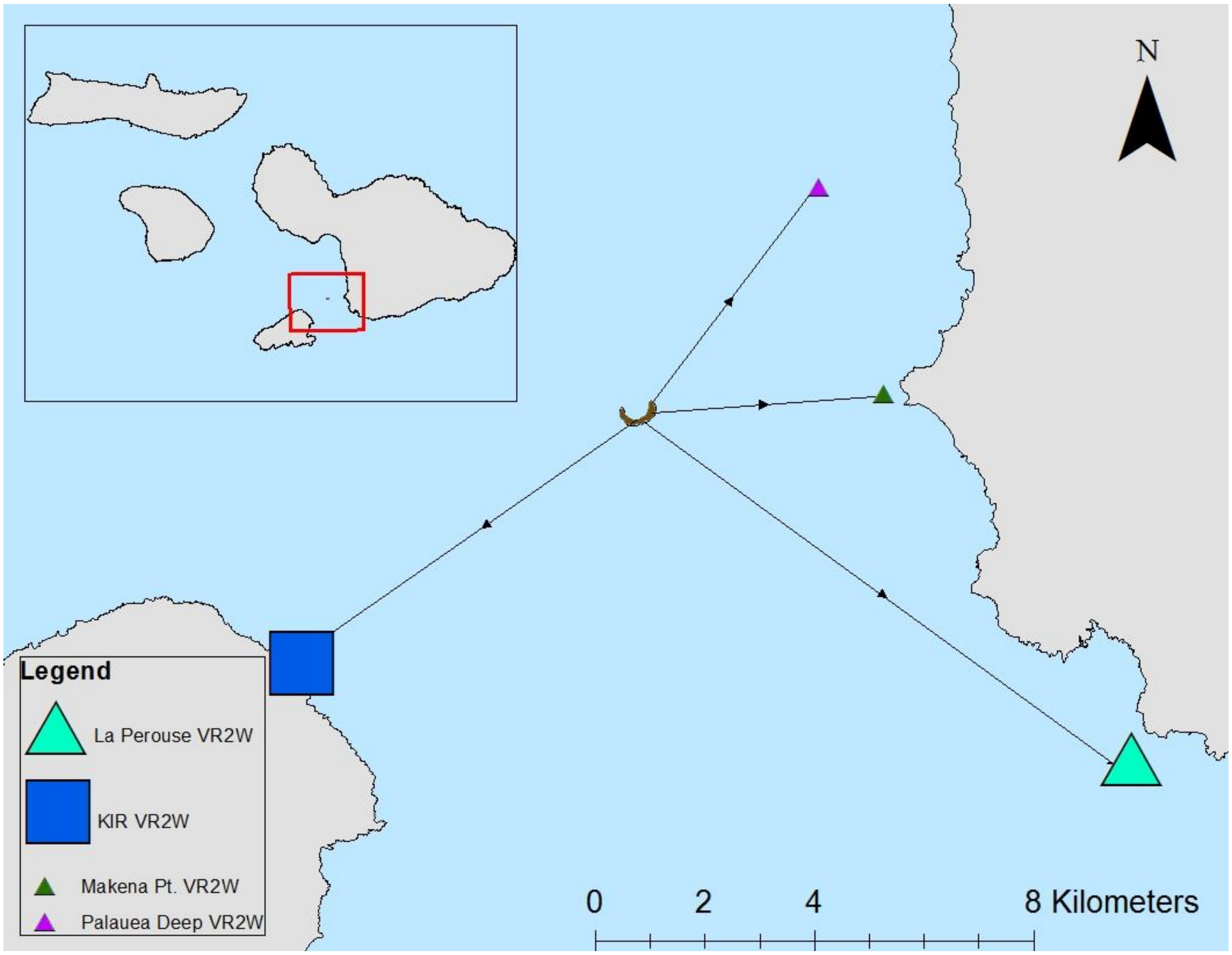

Figure 1.7: Large scale movements of giant trevally from the Molokini MLCD to receivers located in the Maui Nui Complex, with symbols corresponding to receiver locations presented in the diel scatter plots and scaled to the number of detections at each receiver.

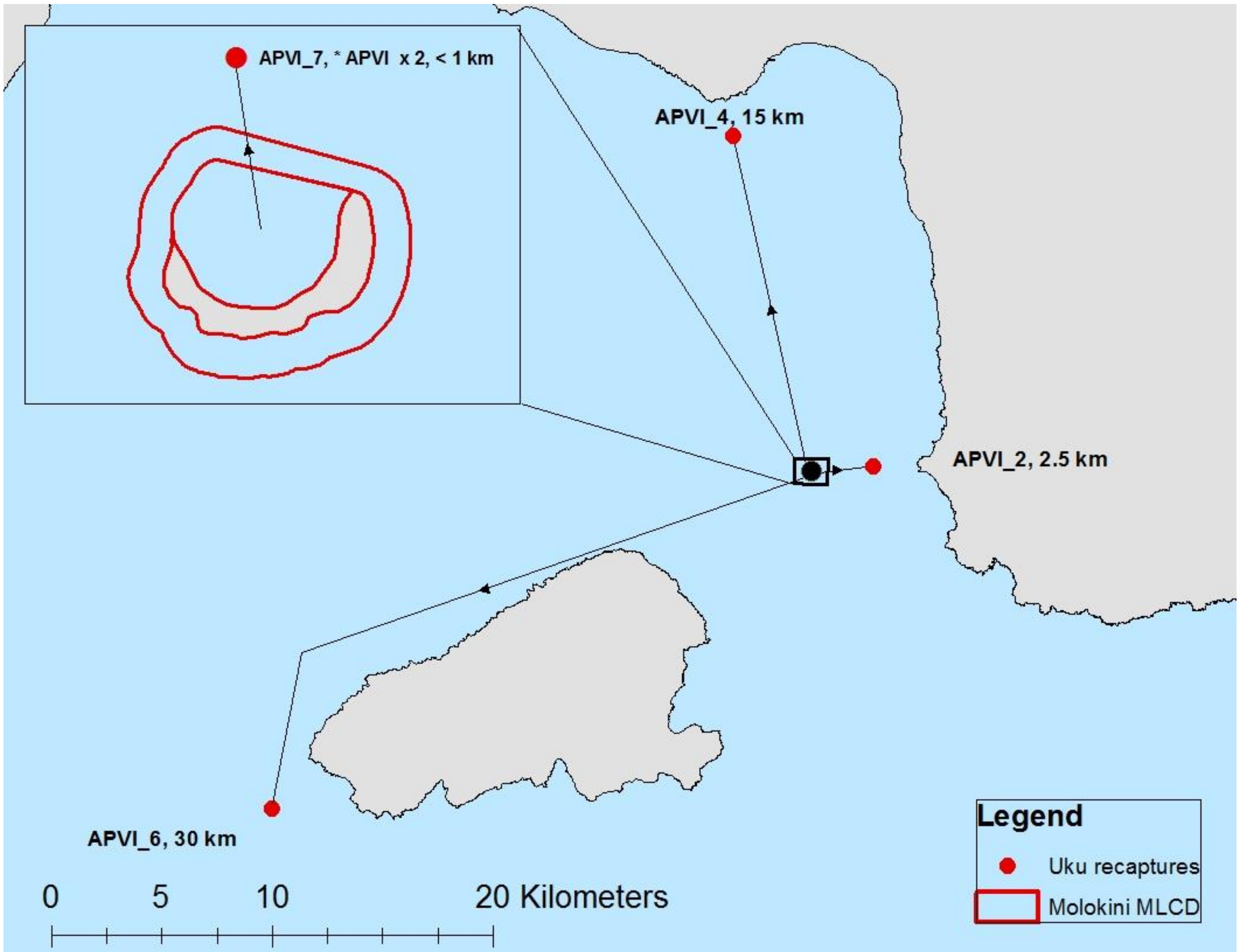

Figure 1.8: Large scale movements of green jobfish from the Molokini MLCD, with red dots indicating the recapture locations of green jobfish harvested in fisheries interactions.

VII. References

Barnett A, AbrantesKá KG, Seymour J, Fitzpatrick R (2012) Residency and spatial use by reef sharks of an isolated seamount and its implications for conservation. PLoS One 7:1–12. doi: 10.1371/journal.pone.0036574

Batista MI, Henriques S, Pais MP, Cabral HN (2015) A framework for the assessment of MPA effectiveness based on life history of fishes. Ocean Coast Manag 118:75–87.

Baum JK, Worm B (2009) Cascading top-down effects of changing oceanic predator abundances. J Anim Ecol 78:699–714.

CAP M (2014) Molokini Shoal Marine Life Conservation District.

Chapman MR, Kramer DL (2000) Movements of fishes within and among fringing coral reefs in Barbados. Environ Biol Fishes 57:11–24.

Chateau O, Wantiez L (2009) Movement patterns of four coral reef fish species in a fragmented habitat in New Caledonia: implications for the design of marine protected area networks. ICES J Mar Sci 66:50–55. doi: 10.1093/icesjms/fsn165

Everson a. R, Williams H a., Ito BM (1989) Maturation and reproduction in two Hawaiian eteline snappers, uku, Aprion virescens, and onaga, Etelis coruscans. Fish Bull 87:877–888.

Field IC, Meekan MG, Speed CW, et al (2010) Quantifying movement patterns for shark conservation at remote coral atolls in the Indian Ocean. Coral Reefs 30:61–71. doi: 10.1007/s00338-010-0699-x

Fitzpatrick R, Abrantes KG, Seymour J, Barnett A (2011) Variation in depth of whitetip reef sharks: Does provisioning ecotourism change their behaviour? Coral Reefs 30:569–577. doi: 10.1007/s00338-011-0769-8

Friedlander a. M, Brown EK, Jokiel PL, et al (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291–305. doi: 10.1007/s00338-003-0317-2

Friedlander A, Stamoulis K, Kittinger J, et al (2014) Understanding the Scale of Marine Protection in Hawai ' i : From Community-Based Management to the Remote Northwestern Hawaiian Islands. In: Advances in marine biology. Oxford:Academic Press, pp 153–203.

Friedlander AM, Brown E, Monaco ME (2007a) Defining reef fish habitat utilization patterns in Hawaii: Comparisons between marine protected areas and areas open to fishing. Mar Ecol Prog Ser 351:221–233. doi: 10.3354/meps07112

Friedlander AM, Brown EK, Monaco ME (2007b) Coupling Ecology and GIS to Evaluate Efficacy of Marine Protected Areas in Hawaii. Ecol Appl 17:715–730.

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264. doi: 10.3354/meps230253

Gaines SD, White C, Carr MH, Palumbi SR (2010) Designing marine reserve networks for both conservation and fisheries management. Proc Natl Acad Sci U S A

107:18286–18293. doi: 10.1073/pnas.0906473107

Gotelli NJ, Ellison AM (2013) EcoSimR 1.00.

Grüss A, Kaplan DM, Guénette S, et al (2011) Consequences of adult and juvenile movement for marine protected areas. Biol Conserv 144:692–702. doi: 10.1016/j.biocon.2010.12.015

Harrison HB, Williamson DH, Evans RD, et al (2012) Larval export from marine reserves and the recruitment benefit for fish and fisheries. Curr Biol 22:1023–1028. doi: 10.1016/j.cub.2012.04.008

Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. Trends Ecol Evol 23:202–2010. doi: 10.1016/j.tree.2008.01.003

Henningsen A (1994) Tonic immobility in 12 elasmobranchs : Use as an aid in captive husbandry. Biol Z O O 13:325–332. doi: 10.1002/zoo.1430130406

Heupel MR, Semmens JM, Hobday a. J (2006) Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13. doi: 10.1071/MF05091

Holland KN, Lowe CG, Wetherbee BM (1996) Movements and dispersal patterns of blue trevally (Caranx melampygus) in a fisheries conservation zone. Fish Res 25:279–292. doi: 10.1016/0165-7836(95)00442-4

Holland KN, Wetherbee BM, Lowe CG, Meyer CG (1999) Movements of tiger sharks (Galeocerdo cuvier) in coastal Hawaiian waters. Mar Biol 134:665–673. doi: 10.1007/s002270050582

Hooker SK, Cañadas A, Hyrenbach KD, et al (2011) Making protected area networks effective for marine top predators. Endangerd Species Res 13:203–218. doi: 10.3354/esr00322

Jackson JB, Kirby MX, Berger WH, et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science (80-) 293:629–637. doi: 10.1126/science.1059199

Kessel S, Simpfendorfer CA (2013) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish. doi: 10.1007/s11160-013-9328-4

Kramer DL, Chapman MR (1999) Implications of fish home range size and relocation for marine reserve function. Environ Biol Fishes 55:65–79.

Le Quesne WJ, Codling EA (2009) Managing mobile species with MPAs: the effects of mobility, larval dispersal, and fishing mortality on closure size. ICES J Mar Sci J du Cons 66:122–131.

Lester SE, Halpern BS (2008) Biological Responses in Marine No-Take Reserves versus Partially Protected Areas Biological responses in marine no-take reserves versus partially protected areas. Mar Ecol Prog Ser 367:49–56. doi: 10.3354/meps07599

Lowe CG, Topping DT, Cartamil DP, Papastamatiou YP (2003) Movement patterns, home range, and habitat utilization of adult kelp bass Paralabrax clathratus in a temperate no-take marine reserve. Mar Ecol Prog Ser 256:205–216.

McCoy K (2015) Estimating nearshore fisheries catch for the main Hawaiian Islands. Unpublished master's thesis, The University of Hawaii at Manoa, Honolulu, Hawaii.

Mesnildrey L, Gascuel D, Le Papee O (2013) Integrating Marine Protected Areas in fisheries management systems : Some criteria for ecological efficiency Integrating Marine Protected Areas in fisheries management systems : some criteria for ecological efficiency. Aquat Living Resour 26:159–170. doi: 10.1051/alr/2013056

Meyer CG, Holland KN, Papastamatiou YP (2007a) Seasonal and diel movements of giant trevally Caranx ignobilis at remote Hawaiian atolls: Implications for the design of marine protected areas. Mar Ecol Prog Ser 333:13–25. doi: 10.3354/meps333013

Meyer CG, Honebrink RR (2005) Transintestinal Expulsion of Surgically Implanted Dummy Transmitters by Bluefin Trevally—Implications for Long-Term Movement Studies. Trans Am Fish Soc 134:602–606. doi: 10.1577/T04-082.1

Meyer CG, Papastamatiou YP, Clark TB (2010) Differential movement patterns and site fidelity among trophic groups of reef fishes in a Hawaiian marine protected area. Mar Biol 157:1499–1511. doi: 10.1007/s00227-010-1424-6

Meyer CG, Papastamatiou YP, Holland KN (2007b) Seasonal, diel, and tidal movements of green jobfish (Aprion virescens, Lutjanidae) at remote Hawaiian atolls: Implications for marine protected area design. Mar Biol 151:2133–2143. doi: 10.1007/s00227-007-0647-7

Myers RA, Worm B (2005) Extinction , survival or recovery of large predatory fishes. Phil Trans R Soc B 360:13–20. doi: 10.1098/rstb.2004.1573

Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: The need for controls. Mar Ecol Prog Ser 419:295–301. doi: 10.3354/meps08864

Price JP, Elliott-fisk D (2004) Topographic History of the Maui Nui Complex, Hawai'i, and Its Implications for Biogeography 1. Pacific Sci 58:27–45.

Randall JE (1977) Contribution to the biology of the whitetip reef Shark (*Triaenodon obesus*). Pacific Sci 31:143–163.

Rice J, Moksness E, Attwood C, et al (2012) The role of MPAs in reconciling fisheries management with conservation of biological diversity. Ocean Coast Manag 69:217–230. doi: 10.1016/j.ocecoaman.2012.08.001

Russ GR, Miller KI, Rizzari JR, Alcala AC (2015) Long-term no-take marine reserve and benthic habitat effects on coral reef fishes Long-term no-take marine reserve and benthic habitat effects on coral reef fishes. Mar Ecol Prog Ser 529:233–248. doi: 10.3354/meps11246

Sakihara TS, Nishiura LK, Shimoda TE, et al (2014) Brassy chubs Kyphosus vaigiensis display unexpected trans-island movement along inshore habitats. Environ Biol Fishes 1–9. doi: 10.1007/s10641-014-0245-8

Sale PF, Cowen RK, Danilowicz BS, et al (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol Evol 20:74–80. doi: 10.1016/j.tree.2004.11.007

Sandin SA, Smith JE, Demartini EE, et al (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. PLoS One. doi: 10.1371/journal.pone.0001548

Shomura R (2004) A historical perspective of Hawai’i's marine resources, fisheries, and management issues over the past 100 years. In: Status of Hawaii’s Coastal Fisheries in the New Millennium, revised 2004 edition. Proceedings of the 2001 fisheries symposium sponsored by the American Fisheries Society, Hawai'i Chapter. pp 6–11

Speed CW, Field IC, Meekan MG, Bradshaw CJ a (2010) Complexities of coastal shark movements and their implications for management. Mar Ecol Prog Ser 408:275–293. doi: 10.3354/meps08581

Sudekum A, Parrish JD, Ralston S (1991) Life History and Ecology of Large Jacks in Undisturbed, Shallow, Oceanic Communities. Fish Bull 89:493–513.

Tinhan T, Erisman B, Aburto-Oropeza O, et al (2014) Residency and seasonal movements in Lutjanus argentiventris and Mycteroperca rosacea at Los Islotes Reserve, Gulf of California. Mar Ecol Prog Ser 501:191–206. doi: 10.3354/meps10711

Toonen RJ, Wilhelm TA, Maxwell SM, et al (2013) One size does not fit all: The emerging frontier in large-scale marine conservation. Mar Pollut Bull 77:7–10. doi: 10.1016/j.marpolbul.2013.10.039

Vandeperre F, Higgins RM, Sanchez-Meca J, et al (2011) Effects of no-take area size and age of marine protected areas on fisheries yields : A meta- analytical approach. Fish Fish 12:412–426. doi: 10.1111/j.1467-2979.2010.00401.x

Wetherbee BM, Crow GL, Lowe CG (1997) Distribution, reproduction and diet of the gray reef shark Carcharhinus amblyrhynchos in Hawaii. Oceanogr Lit Rev 10:1144–1145.

Wetherbee BM, Holland KN, Meyer CG, Lowe CG (2004) Use of a marine reserve in Kaneohe Bay, Hawaii by the giant trevally, Caranx ignobilis. Fish Res 67:253–263. doi: 10.1016/j.fishres.2003.11.004

Whitney NM, Papastamatiou YP, Holland KN, Lowe CG (2007) Use of an acceleration data logger to measure diel activity patterns in captive whitetip reef sharks , Triaenodon obesus. Aquat Living Resour 20:299–305. doi: 10.1051/alr

Whitney NM, Pyle RL, Holland KN, Barcz JT (2012) Movements, reproductive seasonality, and fisheries interactions in the whitetip reef shark (Triaenodon obesus) from community-contributed photographs. Environ Biol Fishes 93:121–136. doi: 10.1007/s10641-011-9897-9

Wilhelm T, Sheppard C, Sheppard A, et al (2014) Large marine protected areas– advantages and challenges of going big. Aquat Conserv Mar Freshw Ecosyst 24:24–30.

Williams ID, Baum JK, Heenan A, et al (2015) Human , Oceanographic and Habitat

Drivers of Central and Western Pacific Coral Reef Fish Assemblages. PLoS One. doi: 10.1371/journal.pone.0120516

Williams ID, Ma H (2013) Estimating Catch Weight of Reef Fish Species Using Estimation and Intercept Data from the Hawaii Marine Recreational Fishing Survey. Pacific Islands Fish Sci Cent Admin Rep H-13-04: 53.

Wolfe BW, Lowe CG (2015) Movement patterns, habitat use and site fidelity of the white croaker (Genyonemus lineatus) in the Palos Verdes Superfund Site, Los Angeles, California. Mar Environ Res 109:69–80. doi: 10.1016/j.marenvres.2015.06.002

Chapter 2: Interaction between predatory reef fish and human use at the Molokini Marine Life Conservation District:

Abstract

The impact of marine ecotourism on reef predators is poorly understood and there is growing concern that overcrowding and anthropogenic noise in Marine Protected Areas (MPAs) may have a negative effect on the species that these areas were established to protect. To improve our understanding of the impact of anthropogenic activities on predators, we used acoustic telemetry to examine the relationship between the intensity of human use at the Molokini Marine Life Conservation District (MLCD; Hawaii's second most used MPA) and the residency patterns of five species of reef predators (*Caranx melampygus, Triaenodon obesus*, *Carcharhinus amblyrhynchos*, *Caranx ignobilis*, and *Aprion virscens*). During peak hours in human use, there was a significant negative relationship (R^2 = 0.77, P <0.001 between the presence of commercial vessels and the presence of bluefin trevally *(Caranx melampygus)* in subzone A. As the abundance of bluefin trevally declined in subzone A with increasing human use, there was a corresponding increase in the presence of bluefin trevally in subzone B where human activity is negligible (X^2 = 60.587, df = 2, P <0.001). No other significant relationships were observed in the other four species we studied. Nevertheless, bluefin trevally were displaced from subzone A of the Molokini MLCD during peak human activity and if the maintenance of a "natural" ecosystem is a desired management outcome, the issue of overcrowding should be considered when designing management strategies for MPAs.

I. Introduction

In recent decades, predators have experienced dramatic declines across the world's coral reef ecosystems (Jackson et al. 2001; Dulvy et al. 2004; Myers and Worm 2005; Sandin et al. 2008). In response to these declines Marine Protected Areas (MPAs) have been promoted as an effective management tool to improve the conservation of fish populations (Russ et al. 2004; Rice et al. 2012; Russ et al. 2015). Numerous studies have documented the increase in both abundance and size of fishes, particularly large predators inside MPAs (Friedlander and DeMartini 2002; McClanahan et al. 2007; Garcı-Rubies et al. 2013). The increase in biomass and diversity of fishes inside MPAs provides a major source of attraction to the marine tourism industry and the popularity of marine ecotourism (e.g., snorkeling, SCUBA, and boating) within MPAs has increased tremendously in recent years (Garrod and Wilson 2003; Needham et al. 2011). Marine ecotourism promotes non-consumptive resource use and stimulates local economic enterprises. However, this industry can have negative effects on the socio-ecological ecosystem, including damage to the marine environment and displacement of fisheries (Milazzo et al. 2002; Jentoft et al. 2007; Meyer and Holland 2008; Charles and Wilson 2009). Furthermore, the social perception of overcrowding in MPAs is common in the marine ecotourism industry (Bell et al. 2011), and little information exists on the potential effects of overcrowding on the behavior of marine fishes. Correspondingly, management strategies for non-consumptive recreational activities in MPAs are deficient (Davis and Tisdell 1995; Harriott et al. 1997; Needham and Szuster 2011; Thurstan et al. 2012).

In Hawaii, the Marine Life Conservation District (MLCD) program was established in 1967 to conserve and replenish Hawaii's marine resources for the purpose of education and human enjoyment (CAP 2014). The program has been successful in maintaining high biomass and diversity of fish assemblages within their management boundaries (Friedlander et al. 2003; Friedlander et al. 2007a; Friedlander et al. 2007b). Today, there are 11 MLCDs in the main Hawaiian Islands (MHI) and these locations have some of the most intact populations of reef predators in the region. Friedlander et al. (2007) found that there was a greater abundance (62%) and biomass (52%) of predators inside Hawaii's MLCDs when compared to adjacent outside areas. These predators and the abundant fish life within the States MLCDs are a significant attraction for Hawaii's marine tourism industry which is valued at $ 700 million USD per year (Cesar and Beukering 2004). The Molokini Shoals MLCD was established in 1977 and is the second most visited MPA in the state. Currently, there are 41 commercial vessels permitted to operate snorkel and dive tours to the Molokini MLCD and the annual economic benefit of these recreational activities is estimated at 20 million USD (Needham and Szuster 2011). Over the past decade, the number of visitors to the MLCD has been steadily increasing and in 2014, a total of 322,133 people visited the MLCD. The increasing popularity of recreational activities in Hawaii's MLCDs and other MPAs poses the question, is there a relationship between the intensity of anthropogenic use in an ecosystem and the presence of reef predators?

Several studies have documented negative behavioral effects on marine fishes in response to anthropogenic noise (Sarà et al. 2007; Popper and Hastings 2009; Holles et al. 2013; Voellmy et al. 2014), however; these studies have primarily been conducted on less mobile juvenile fishes or in caged environments, while field experiments in natural settings are deficient. Furthermore, published field research on this subject suffers from the inability to precisely measure human activities in the study sites and often relies on environmental variables that correlate with human activities to measure the intensity of anthropogenic use in an ecosystem (Chateau and Wantiez 2008). Direct measures of human activities such as vessel noise can provide a more accurate reflection of human disturbance on animals. In this study, we examined vessel noise and commercial logbooks (two measurements of human activities) to relate human activities to the behavior and movement of predatory fishes inside the Molokini MLCD based on observations from an acoustic telemetry array. Our objectives were to: (1) determine the species of predators that overlap with human use in the MLCD, (2) examine commercial tour operator logbook data to determine if vessel activity patterns correlate with anthropogenic noise in the MLCD, and (3) determine whether predators are displaced from important habitats in the MLCD at varying intensities of anthropogenic use.

II. Methods

Study site

Molokini is a small (31 ha) crescent shaped volcanic islet that is located in the Alalakeiki Channel between Maui and Kaho‘olawe. The inside of Molokini's crater is characterized by a shallow coral reef (<30 m) protected from major ocean swells, while the backside of the islet forms a steep vertical wall that descends to approximately 100 m. The Molokini MLCD is comprised of two management zones, subzone A and subzone B (Figure 2.1). Subzone A of the MLCD includes the inside of Molokini crater bounded by a line extending from the end of the submerged coral ridge on the west side of the crater to the east side of the crater. The harvest of marine life is prohibited in subzone A and the majority of boating and recreational activities occur in this region. To accommodate visitation of the MLCD, the State of Hawaii maintains 22 day use mooring buoys inside subzone A which are used by commercial tour vessels on a daily basis. Subzone B extends ~ 91 m (100 yards) seaward of subzone A and encompasses the entire perimeter of the islet, and only fishing using trolling gear is allowed in subzone B (CAP 2014).

Acoustic array design

A VR2W passive acoustic monitoring array was used to track the movements of tagged predators at the Molokini MLCD from November 14th 2013 to August 28th 2015. Seven VR2W acoustic receivers (308 mm long x 73 mm diameter, Vemco, Halifax, Nova Scotia) were deployed in strategic locations that enabled the observation of fish movements within the MLCD. In locations with sandy substrate, the VR2W receivers were secured to the bottom with sand screws (2 m long x 10 cm diameter) and attached to a 2 m section of 2 cm diameter polypropylene rope suspended by a small crab float (35 cm long x 15 cm diameter). At receiver sites where the substrate consisted of hard rock, the moorings were secured to the bottom by passing a section of 6 mm stainless steel wire rope covered by hydraulic hose, through a natural benthic feature and fastened with two stainless steel wire crimps. Three receivers were stationed inside subzone A and four receivers were stationed along the back side of Molokini crater in subzone B. The arrays design, management subzones, location of the Ecological Acoustic Recorder (EAR, see description below), and estimates of VR2W detection ranges are depicted in Figure 2.1.

Fish capture and transmiter deployment

Five species of reef predators including, whitetip reef shark (*Triaenodon obesus,* n=13), grey reef shark (*Carcharhinus amblyrhynchos,* n=5), giant trevally (*Caranx ignobilis,* n=16), bluefin trevally (*Caranx melampygus,* n=15) and green jobfish (*Aprion virscens,* n=10) were captured with hook and line inside the MLCD. The captured sharks were tail roped and restrained alongside the research vessel where they were induced into tonic immobility (Henningsen 1994). Teleost fishes were brought onboard the research vessel, inverted, and placed into a padded V board with a hose circulating sea water over the gills. Once catalepsy was achieved, the specimens were measured, sexed (sharks only), and tagged with Vemco V-13 coded transmitters (13 mm diameter, 45 mm long, Vemco, Halifax, Nova Scotia) programmed to transmit an individual identification number via a 69 kHz pulse, every 80 to 160 sec for up to 1019 days. The transmitters were surgically implanted into the body cavity of each animal through a 2 cm incision in the abdominal wall and closed with an interrupted nylon suture (Holland et al. 1999; Meyer and Honebrink 2005). After surgery, all specimens were externally tagged with a conventional ID tag (either an M-type tag (sharks and large teleost fish), or 10 cm plastic dart tag (Hallprint, South Australia)) before being released. These methods were reviewed and approved by the University of Hawaii's Institutional Animal Care and Use Committee, IACUC protocol number 13-1712.

Analysis of commercial vessel use of subzone A of the Molokini Shoals MLCD

The Maui Division of Aquatic Resources requires that all permitted commercial tour operators in the Molokini MLCD submit vessel log book data on a monthly basis. These data include the time of day (i.e., start and stop time), mooring buoy, and number of users (i.e., SCUBA divers and snorkelers) from every tour operator in the Molokini MLCD. Vessel log book data were obtained from November 14th 2013 to August 28th 2015 and analyzed to determine the total number of commercial vessels present inside subzone A of the MLCD for every hour of the study. In this forthcoming analysis, all values are means and sd of the mean unless otherwise stated. Peak hours in vessel activity were determined by taking the mean of the total number of vessels present in each hour of the diel cycle over the course of the monitoring period. To classify vessel intensity, we analyzed the distribution of the number of vessels in subzone A during peak hours (n=1,959, 11.96 ± 5.19) and categorized the intensity of human use based on the quartiles of the distribution (min= 0, Q1= 9, median = 12, Q3= 16, max=25), where peak hours with 0 to 8 vessels were classified as low intensity (<Q1 , n = 460), peak hours with 9 to 16 vessels are moderate intensity (Q1 to Q3, n = 1130) and peak hours with 17 to 25 vessels are high intensity (>Q3, n = 369).

To determine if the number of commercial vessels was significantly related to anthropogenic noise in the crater, an Ecological Acoustic Recorder (EAR) was deployed inside subzone A of the MLCD. This device records ambient acoustic noise and was programmed to record on a duty cycle of 30 sec 'on' every 5 min at a sampling rate of 25 kHz, providing an effective recording bandwidth of 12.5 kHz. The root-mean-square (RMS) sound pressure level of each acoustic file was determined, and the RMS sound pressure level of the 0-0.78125 kHz bandwidth corresponds with noise generated from vessels and anthropogenic activity (Lammers and Howe 2014). With these data, we calculated the mean RMS sound pressure level for the 0-0.78125 kHz bandwidth for every hr of the study. We then performed a least-squares linear regression between the number of boats present per hr and the mean sound pressure level of the corresponding hr, during the peak hrs in human use of subzone A.

Range testing of the acoustic array

Range testing of the acoustic array was conducted throughout the MLCD by towing a V13 range test tag with 10 sec fixed delay from a vessel, and simultaneously tracking the GPS location with a VR-100 acoustic receiver. The timing of tag detections by VR2W acoustic receivers was linked to the timing of tag detections by the VR-100 and the corresponding GPS coordinates. The location of each tag detection was plotted in Arc Geographic Information Systems (GIS) to generate a map of tag detections in the array. The maximum possible detection ranges of each VR2W was determined by measuring the straight line distance from a given receiver to the farthest point of tag detection.

To evaluate potential biases in fish detection patterns in our VR2W array from both natural and human acoustic interference (Payne et al. 2010), we conducted 48 hr range tests across the diel cycle by placing four V13 range test tags 4 m from the bottom at staggered intervals from the VR2W's located in subzone A. This enabled us to test receiver performance at a range of distances from 0 to 280 m for receivers located in subzone A. This design allowed us to calculate the percentage of detections successfully decoded at different distances by dividing the total number of detections per hr received by VR2Ws at a given distance by the total number of signals transmitted by a test tag during that hr. Because we were interested in detection ranges of our VR2Ws during daylight hours, these data were filtered to only include detections between 7:00 to 19:00. A binomial general additive model was fitted to these data to determine the distances at which a minimum of 5% of detections transmitted by stationary test tags were decoded. This distance represented the maximum receiver detection range in our study. Finally, to investigate receiver performance over extended periods of time, a V13 sentinel tag with a 580-620 sec duty cycle was deployed at receiver R2. This VR2W was selected to investigate acoustic detection performance because it is the shallowest VR2W (10 m) in the array and is located at the center of Molokini crater, where the majority of boating and wave action occurs. The presence of this test tag allowed us to investigate the performance of receivers R2 and R1, at two distances 0 m and 176 m, in the presence and absence of boats. We tested for a correlation between the presence of the test tag and the number of boats in subzone A during the peak hrs (8, 9, and 10 am HST), with Spearman's rank correlation.

Analysis of vessel intensity in the MLCD and the movements of reef predators

To investigate the relationship between human use at the MLCD and movements of predators in subzone A, we generated individual diel scatter plots of detections for all the species tagged in the study, and examined patterns in habitat use in subzone A that coincided with peak hrs in human use at the MLCD (SOM 1). We then pooled fish detections from the three receivers located inside subzone A and examined the presence and absence of each fish during a given hr based on the criteria that it was detected at least once by any of the three receivers. To obtain the response variable of the proportion of the species present in subzone A for every hr of the study we calculated the total number of individuals from a given species present in subzone A within each 24 hr period and divided the number of a species present in subzone A at each hr by the total number present each day. To determine if a correlation existed between anthropogenic use of the MLCD and predator abundance, we filtered our data to include only daylight hrs (7:00-17:00) and performed a Spearman's rank correlation between the mean proportion of the species present and at a given number of vessels in subzone A for all five species. Finally the p-values from the Spearman's rank correlations were tested with a Bonferroni correction to reduce the possibility of type I error (Rice 1989).

Relationship between vessel intensity and of presence of bluefin trevally (Caranx melampygus) in the MLCD

In order to describe the relationship between the presence of bluefin trevally and the intensity of vessels in subzone A, we calculated the mean proportion of bluefin trevally present in subzone A at a given number of vessels (0-25) following the procedure described above and excluded non-peak hours to eliminate the potential for bias of crepuscular behavior. We then plotted the mean proportion of bluefin trevally present against the number of commercial vessels present in subzone A. To determine if these two variables were significantly related, we performed a least-squares linear regression between the square root transformed mean proportion of bluefin trevally present in subzone A and the number of vessels during the corresponding hour. Finally, we used the regression equation to predict the point at which the mean proportion of bluefin trevally present in subzone A declined to 50% of the maximum value we observed in our study.

Differences between presence of bluefin trevally in subzone A and subzone B at different intensities of human use

To examine the patterns in habitat use between subzone A and subzone B at different levels of human use, and determine whether bluefin trevally displaced from subzone A move to subzone B, we pooled fish detections from the three receivers located inside subzone A into one group and the four receivers located in subzone B into another. After which, we determined the presence and absence of each individual fish in these two management zones for every hr of the study based on the criteria described above. We then filtered our data to identify individual bluefin trevally that were present in subzone A within the 24 hr period and selected the detections of these individuals in both management zones that occurred during peak hrs in human use.

We binned the presence and absence of bluefin trevally in each management zone based on the three levels of vessel intensity (low, moderate, and high) and calculated the number of bluefin trevally present in each management zone during the three levels of vessel intensity. The counts of bluefin trevally in each management zone during low, moderate, and high levels of human use were then tested for significance with a Chi square test.

III. Results

Commercial vessel use of subzone A of the Molokini Shoals MLCD

Between November 14th 2013 and August 28th 2015, 599,440 people visited the Molokini MLCD, with a mean of 23 (± 8) vessels and 924 (± 411) people per day. During this time, the peak hrs in human use were 8, 9, and 10 am HST with the corresponding mean number of commercial vessels in subzone A, being 12, 15, and 10 respectively (Figure 2.2). During peak hrs in anthropogenic use of the MLCD, the mean RMS sound pressure level of the 0-0.7815 KHz band width recorded by the EAR was significantly related to the mean number of vessels in subzone A (R^2 =0.95, P <0.001, Figure 2.3).

Range testing

Maximum instantaneous detection ranges in the VR2W acoustic array ranged from 160 to 270 m, with a mean of 227 ± 39 m. The binomial general additive model of detection efficiency during day light hours, generated from the results of the 48 hr range test, was significant (R^2 = 0.93, P <0.0001, Figure 2.4). The predictions estimated from these models indicated that the maximum range (the distance at which 5% of the detection efficiency is reached) during the day was 203 m. The test for a correlation between the presence of the sentinel tag at receivers R1 and R2 indicates that at 0 m (R2) there is no influence in the number of boats and the chance of detecting the tag, with ρ = 0. At distances nearing the maximum detection range (~176m), there was a slightly significant correlation between the presence of boats and the probability of R1 detecting the sentinel tag (ρ = -0.50, P = 0.03). This suggests that the detection range of our receivers was only marginally reduced during high levels of vessel activity. However, owing to the detection range and degree of overlap among receivers, the array design is effective in distinguishing fish movements between the management zones of the MLCD.

Reef predator use of subzone A

Over the course of the study, the seven receivers detected 58 of the 59 predators with detection spans ranging from 2 to 542 days. Bluefin trevally were the most common species present in subzone A during daylight hours (Figure 2.5) and this species presence was negatively correlated with the number of vessels in subzone A (ρ = -0.77, P = <0.001). None of the other four species showed a significant correlation between vessel activity and habitat use of subzone A (Table 2.1). There was a decrease in the mean proportion of bluefin trevally present in the MLCD with increasing vessel intensity (Figure 2.6). This reduction in habitat use is described by a negative linear relationship between the square root transformed mean proportion of bluefin trevally present in subzone A and the number of vessels (R^2 =0.73, P <0.001). The estimate of the number of vessels, at which the mean proportion of bluefin trevally present in subzone A is reduced to 50% of the maximum observed abundance is 12, with 95% CI [0.19, 0.15] or 3% and 2% (Figure 2.7).

An analysis of the presence of bluefin trevally in the two subzones of the MLCD indicates that as the count of bluefin trevally present in subzone A decreased across three intensities of human use, (low = 130, moderate = 94, high = 18), there was a concomitant increase in their abundances in subzone B (low= 25, moderate = 64, high= 43) and these differences were statistically significant (X^2 = 60.59, df = 2, P <0.001, Figure 2.8).

IV. Discussion

As the demand for recreational activities in MPAs increases, the study of the interactions between predators and humans in the marine environment is becoming an important topic in the management of marine reserves. The results of this study are some of the first empirically measured documentation of the displacement of a predator in response to vessel activity in an MPA and can be used to inform the management of recreational activities in MPAs in Hawaii and other locations around the world. To date, the majority of research on the effects of humans on predators has focused on the impact of provisioning in shark feeding ecotourism (Hammerschlag et al. 2012). Several of these studies have shown that the natural behavior and movement patterns of wild animals can be influenced by human activities (Laroche et al. 2007; Bruce and Bradford 2013; Brunnschweiler and Barnett 2013). However, few field studies have addressed the impact of vessel activity on the natural behavior of marine fishes in MPAs.

Previous studies have suggested that with an increase in ambient noise generated by vessels, the detection range of acoustic receivers can be effected (Heupel et al. 2006). The acoustic receivers we used in this study to monitor fish movement's detect a sound frequency of 69 kHz. The acoustic noise that was significantly related to the presence of commercial vessels was between 0-0.78 KHz, which suggests that overlap between these two bandwidths is minimal. However, we noted a marginal decrease in the detection efficiency of our receivers at the maximum extent of their detection ranges (~176m), during extreme levels of vessel intensity. Fluctuations in detection range in response to environmental noise are real constraints in any acoustic monitoring study, and likely introduce a source of error in making conclusions about animal movements (Payne et al. 2010; Kessel et al. 2013).

Despite this limitation, we are confident that the results of this study represent the displacement of bluefin trevally from subzone A of the MLCD for several reasons. Firstly, the maximum detection ranges of our receivers are overlapping, and reductions in detection ranges at the scale we observed do not create gaps in our array. Nonetheless, should minor gaps in the array occur, in contrast to a fixed sentinel tag, bluefin trevally are highly mobile predators, and over the course of an hr, their position inside the crater changes, therefore, their chance of detection is not static. Furthermore, our response variable is conservative and the presence of an individual fish in subzone A during a given hour is based on a single detection, across three pooled receivers. Therefore, fish presence is weighted equally regardless of the total number of detections. Finally, we documented a reciprocal increase in the presence of bluefin trevally in subzone B, as the presence of bluefin trevally in subzone A declines across an increasing gradient of vessel use. These changes in the presence of bluefin trevally in each management zone indicate that during high levels of vessel use the species is being displaced from subzone A and moving to subzone B. The evidence presented above leads us to conclude that the trends we observed are not an artifact of minor reductions in the ranges of VR2W's in our acoustic array.

None of the other four species we tagged in this study showed strong evidence for a relationship between habitat use of subzone A and the intensity of human activities. The lack of this relationship could be attributed to natural differences in the spatial and temporal habitat use for each species that result in a limited overlap with humans. Detections from giant trevally and grey reef sharks primarily occurred at receivers located in close proximity to deep water along the back wall of the MLCD in subzone B and although whitetip reef sharks were active in subzone A, the majority of these detections occurred during nocturnal hrs (SOM1). Alternatively, the overall absence of these of predators from subzone A during daylight hours may be attributed to the anthropogenic displacement, but this remains beyond the scope of this research. Green jobfish were the only other species that exhibited spatial and temporal overlap in habitat use within the MLCD, but the majority (80%) of the individuals we tagged exhibited transient behavior at the MLCD (SOM1) and as a result, we were unable to obtain a sufficient sample of days with varying levels of human use to confidently determine if a relationship exists for this species.

The exact mechanism driving the displacement of bluefin trevally from subzone A of the MLCD during peak hours is uncertain, however, one possible driver is acoustic noise generated by motor vessels. Over 800 species of fishes are known to produce sound (Radford et al. 2014) and sound production and cognition is thought to play a critical role in predator prey interactions, schooling behavior, reproduction, and territoriality in coral reef associated fishes (Lobel et al. 2010). High levels of acoustic noise could negatively affect fishes by masking biologically important sounds and reducing sensory abilities, which in turn could affect their ability to forage, find mates, and avoid predators (Amoser et al. 2004; Popper and Hastings 2009; Radford et al. 2014). Bluefin trevally and other jacks are known to produce a croaking noise and although the social and biological function of this sound production is unknown, acoustic noise could interfere with this form of communication (Taylor and Mansueti 1960). With an increase in the number of commercial vessels present in the MLCD, the RMS sound pressure level increased significantly and during the peak in human activity at the MLCD the average sound pressure levels can be over 5 dB higher than when humans are absent. Although the auditory thresholds of fishes are likely species-specific, the majority of fishes are believed to be able to detect sound levels between 50 and 500-1500 Hz (Popper and Fay 1999; Radford et al. 2014) This suggests that the increasing 0 - 0.78 kHz sound levels generated by commercial vessels in subzone A overlaps with the hearing range of fishes and a potential for interference exists.

The exact physiological effect of intense anthropogenic noise on fishes is poorly understood, but previous studies have shown that vessel noise can alter the behavior of fishes. Sarà et al. (2007) observed the schooling behavior of Atlantic bluefin tuna (*Thunnus thunnus*) in net pens exposed to the acoustic noise of transiting hydrofoils, ferries, and small motor vessels. In the presence of larger vessels, such as hydrofoils and ferries, the tuna school structure changed from coordinated and uniform swimming to uncoordinated diving movements that suggests avoidance as vessels approached the pen (Sarà et al. 2007). This pattern of vessel avoidance has also been documented in Atlantic herring (*Clupea harengus*), with dramatic reductions in the abundance of acoustically monitored herring observed at the closest point of vessel approach (Vabø et al. 2002). Voellmy et al. (2014) documented reduced foraging efficiency and increased startle response in two species of closely related fishes (three-spined stickleback - *Gasterosteus aculeatus*, and common minnow - *Phoxinus phoxinus)* when exposed to intense boat noise.

In addition to noise, the physical presence of human's may be another factor influencing the displacement of bluefin trevally from the study area. Many species of marine fishes exhibit a "flight response" in the presence of humans and the severity of flight response is most of often associated with the intensity of fishing pressure at a given location (Feary et al. 2010; Januchowski-Hartley et al. 2011; Usseglio 2015). Although the recreational activities in the Molokini MLCD are non-extractive, the number of users can be up to 1,702 people a day and the presence of humans at this magnitude may be contributing to the relationship we observed in this study.

The consequences of the displacement of bluefin trevally from the shallow waters of the Molokini crater to deep water in subzone B during peak hours in human use are unknown. On the individual level, physical displacement from optimal habitats may lead to reduced fitness as a result of several non-exclusive factors including: 1) lost foraging opportunities, 2) reduced reproductive success, and 3) increased competition for resources in refuge areas (Codarin et al. 2009; Popper and Hastings 2009; Jacobsen et al. 2014; Radford et al. 2014). Furthermore, on the ecosystem level, reef predators play a critical role in maintaining the balance of marine environment by regulating the abundance of mid-level predators and imposing a top down effect on lower trophic groups (Baum and Worm 2009, Ritchie and Johnson 2009). Therefore, the natural ecosystem function that a reserve is established to protect may be compromised by the absence of these predators during these times.

Conclusions and implications for management

Marine ecotourism is a growing industry and an important component of the economy and education (Cesar and Beukering 2004; Zeppel 2008; Needham et al. 2011). Overall, ecotourism in places like the Molokini MLCD provides a net benefit to society and ultimately the environment, through increasing support for MPAs and the conservation of marine resources. Nevertheless, this research does however, indicate that in extreme circumstances, the species that overlap with human use can be displaced from their preferred habitats and could be negatively impacted by non-consumptive human activities. The perception of overcrowding at the Molokini MLCD has been investigated from the human perspective (Bell et al. 2011; Needham et al. 2011; Needham and Szuster 2011). Surveys of marine park users indicated that 67% of individuals felt overcrowded during their experience at Molokini and this perception led 66 - 79% of users to support restrictions on use of the MLCD. The maximum number of vessels that was perceived to be acceptable from the human perspective was determined to be 15 -16 at any given time (Bell et al. 2011). Further research is needed to determine whether reducing the noise generated by commercial vessels would be an effective mitigation strategy or if reducing the total number of users is necessary to prevent the displacement of bluefin trevally and potentially other species from the MLCD. The combination of both ecological and social evidence suggests that the issue of overcrowding may warrant regulation in the management of Hawaii’s MLCDs.

V. Tables

Table 2.1: Summary of detections for 59 predators in subzone A of the Molokini Marine Life Conservation District (MLCD). With ρ and Bonferroni corrected significance of Spearman's rank correlation between the mean proportion of the species present and number of vessels in subzone A during daylight hours.

Species	N	x̄ FL	Median days detected	Median detections	ρ	P-value	Bonferroni sig.
CAME	15	54 ± 13	115	3150	-0.77	<0.001	Y
APVI	10	67 ± 11	18	75.5	-0.45	0.02	N
CAAM	5	116 ± 25	97	625	-0.43	0.03	N
TROB	13	87 ± 14	117	384	-0.33	0.11	N
CAIG	16	92 ± 18	76.5	574.5	-0.3	0.14	N

VI. Figures

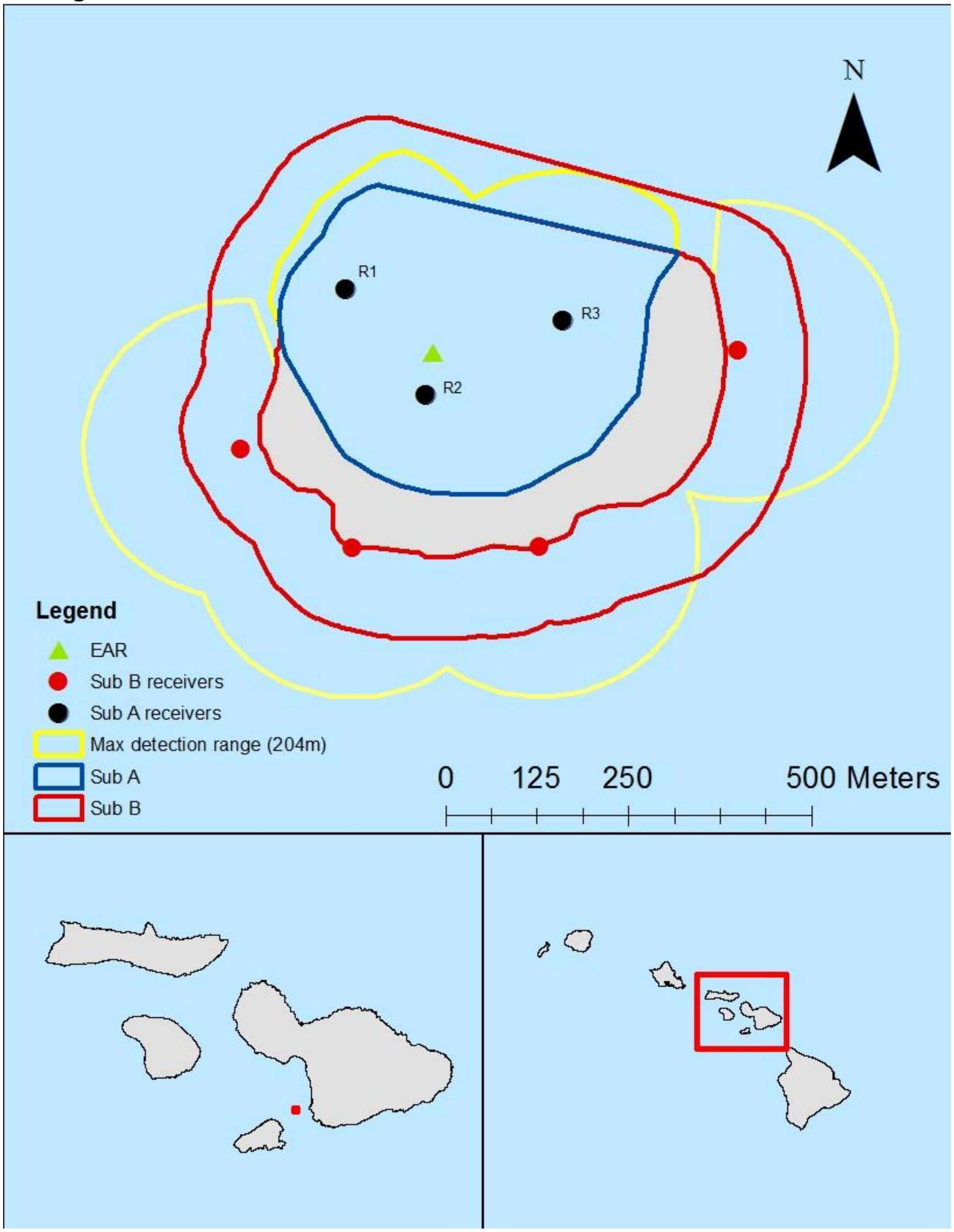

Figure 2.1: The location of the Molokini MLCD and acoustic array. Red lines indicate subzone demarcation. Black dots indicate locations of subzone A receivers, red dots represent subzone B receivers, yellow triangle indicates the location of the ecological acoustic recorder (EAR) and yellow bands represent the 204 m theoretical maximum detection range of the receivers in the acoustic array.

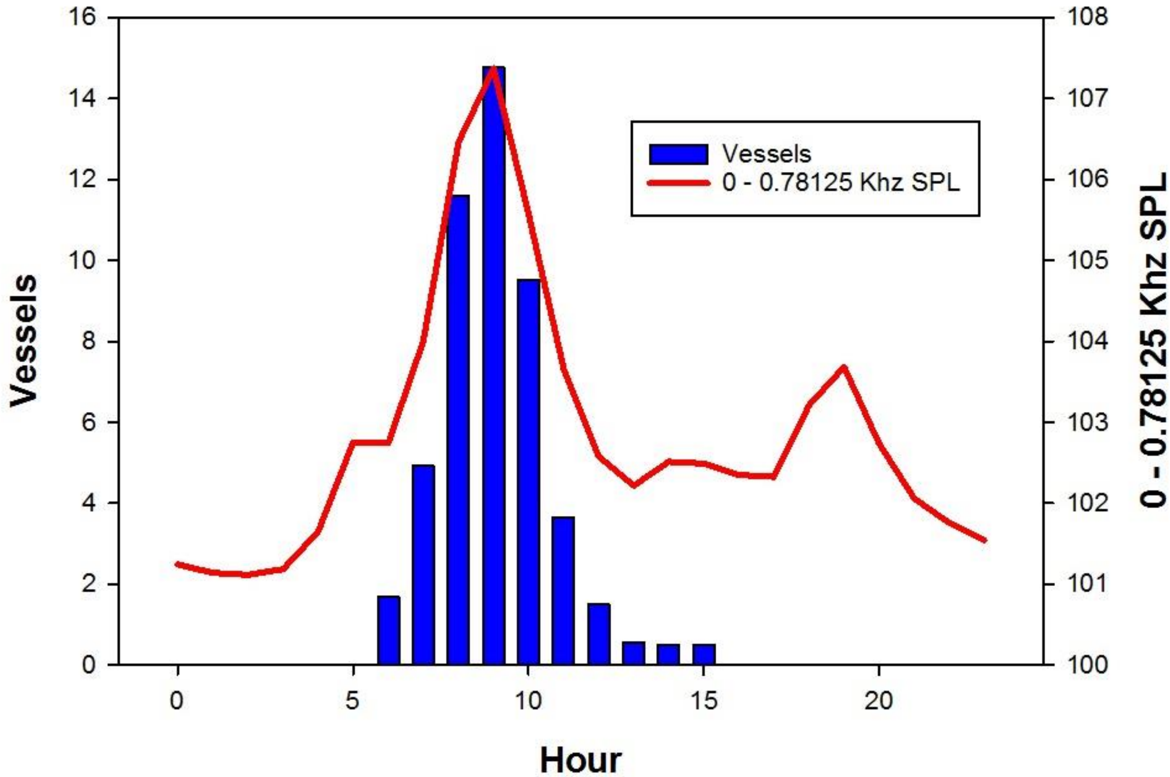

Figure 2.2: The average number of vessels per hour in subzone A (left y axis) plotted against the average sound pressure level (SPL) of the 0 – 0.78 KHz bandwidth (second y axis), during the corresponding hour.

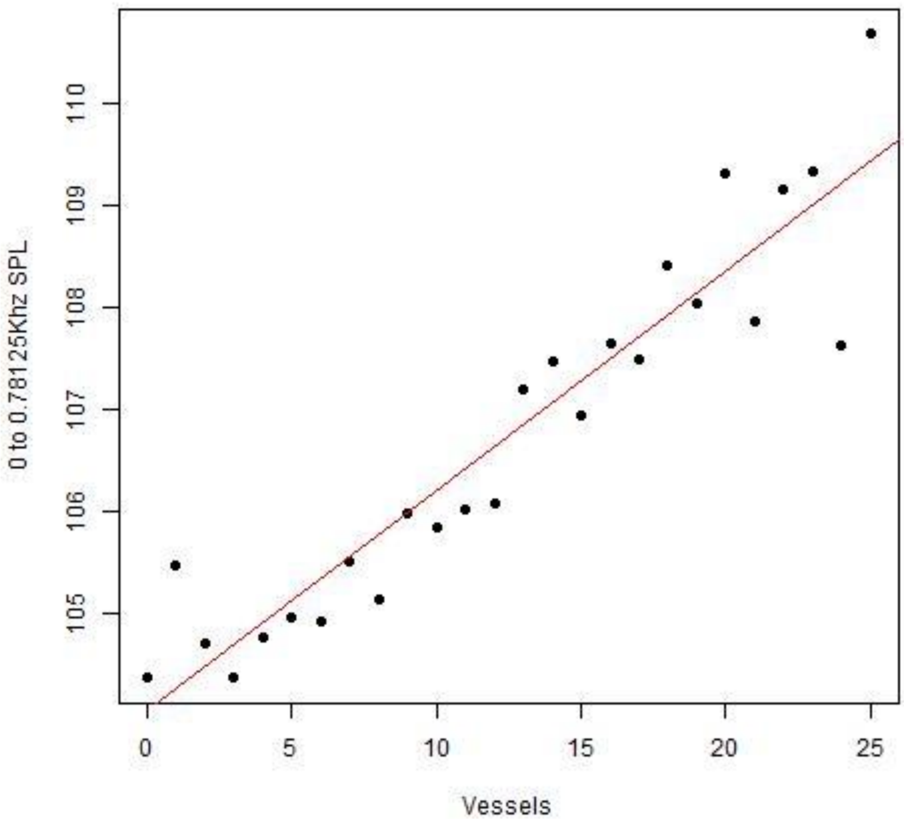

Figure 2.3: The liner regression between the mean sound pressure level (SPL) of the 0 - 0.78 KHz bandwidth and the number of boats in subzone A during the peak hours in human use of the MLCD (8, 9, and 10am HST), Y = -0.21x + 104.05, R^2 = 0.87, P = <0.001.

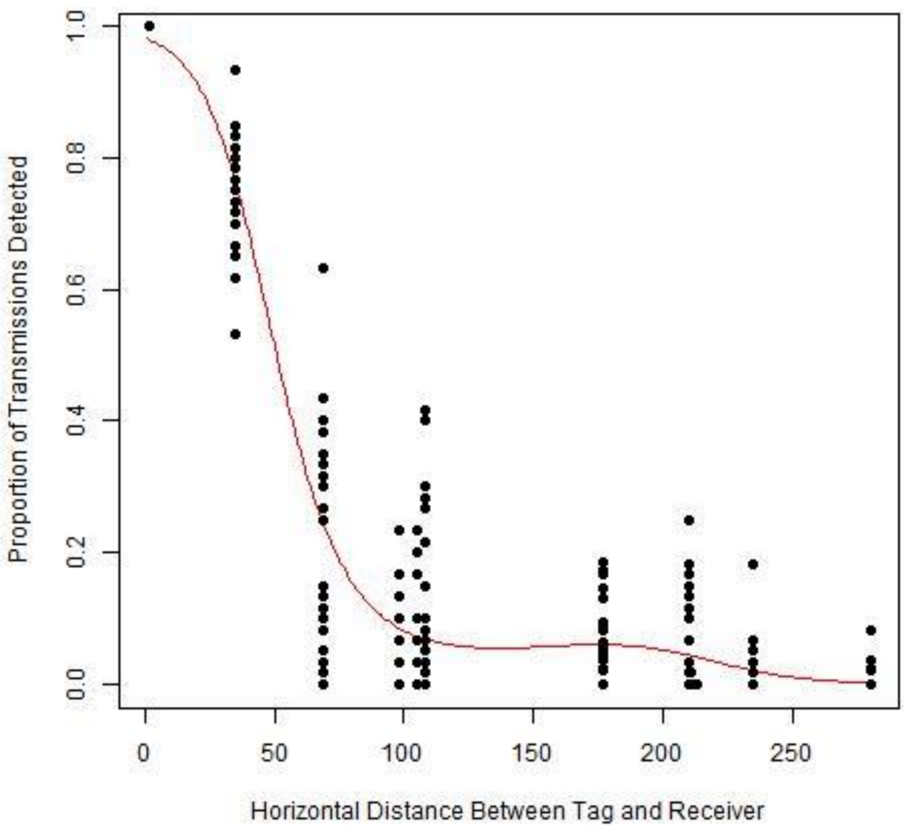

Figure 2.4: The proportion of transmissions successfully detected from range test tags placed at varying distances from acoustic receivers in subzone A during day light hours. Red line represents the predicted fit of the binomial general additive module (R^2 = 0.93, P = <0.001).

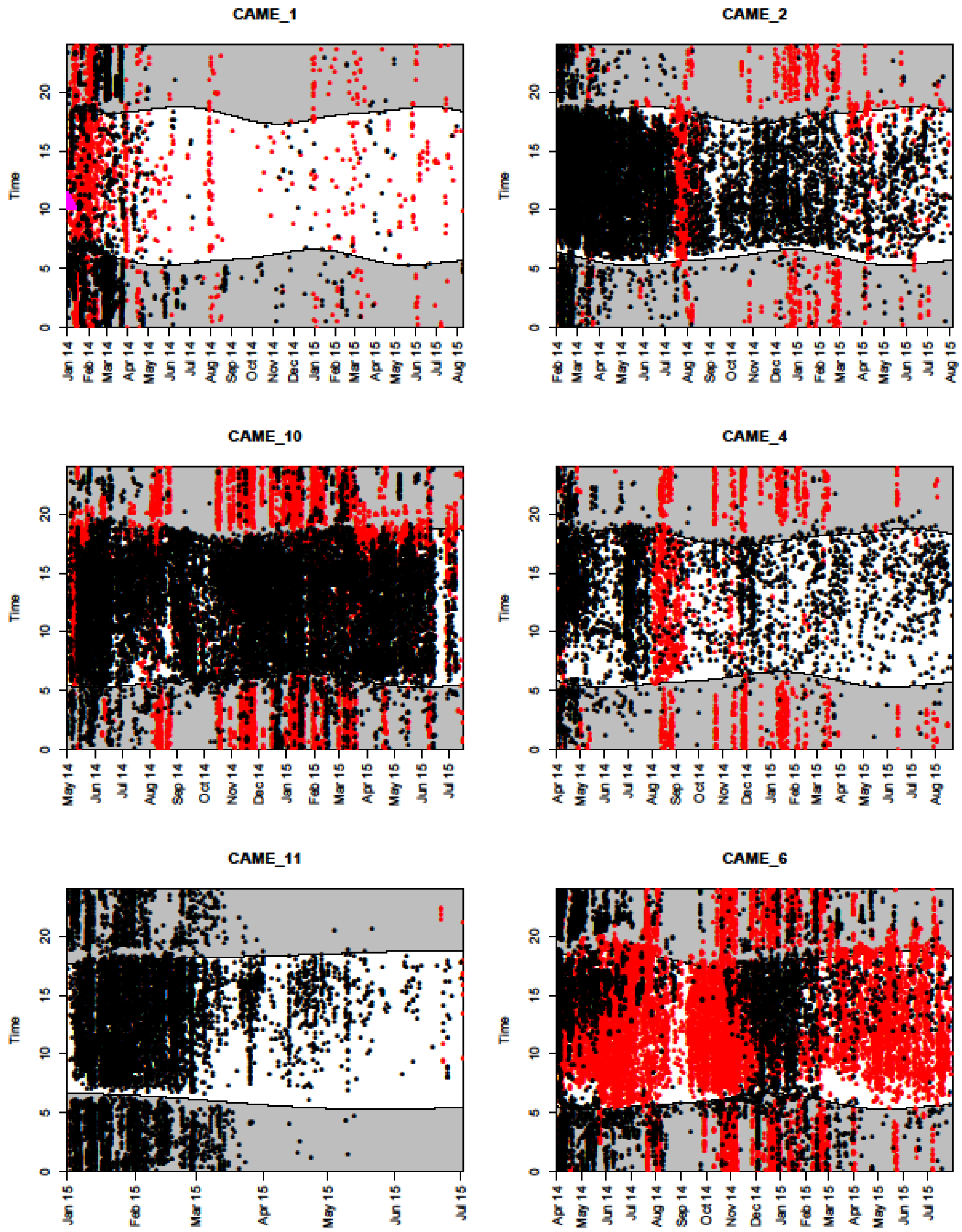

Figure 2.5: The diel scatter plots of 6 bluefin trevally at the Molokini MLCD with day (white) and night (grey) shading over the course of their monitoring periods. Black dots indicate detections in subzone A, red dots indicate detections in subzone B (note differing scales on the x-axis).

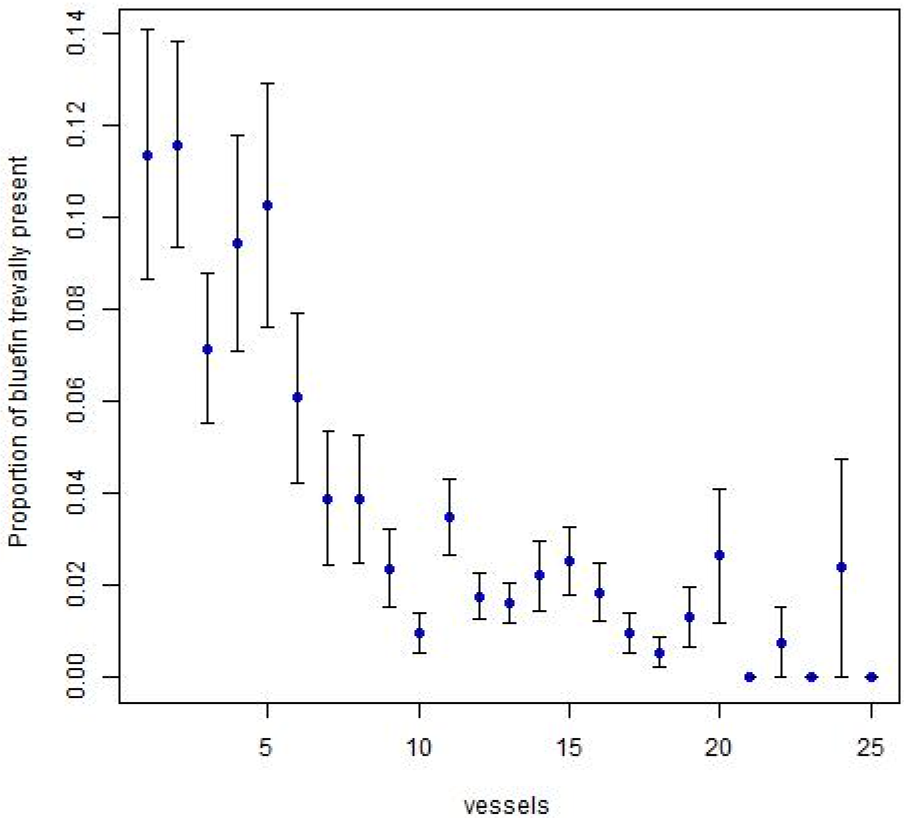

Figure 2.6: The proportion of bluefin trevally present in in subzone A, at a given number of vessels during the peak hours (8-10 am HST) in human use. Values are means with error bars equal to the standard error of the mean.

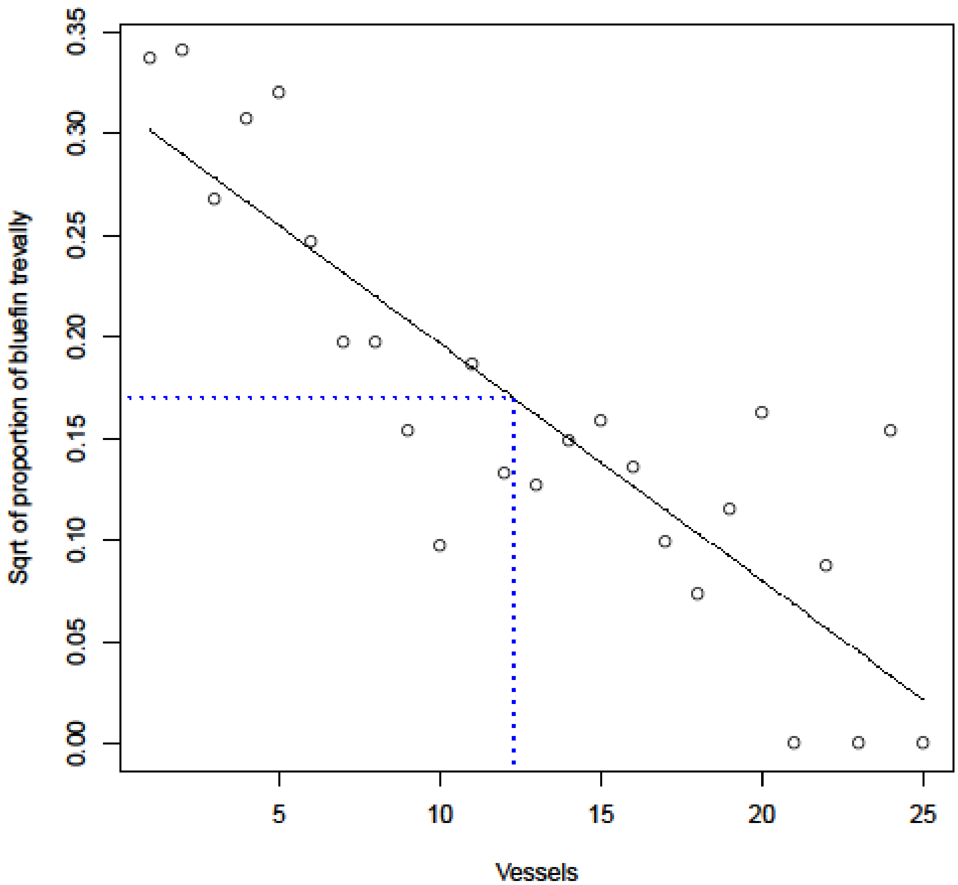

Figure 2.7: Relationship between mean proportion of bluefin trevally present (sqrt[proportion]) in subzone A and number of vessels in subzone A during peak hours in human use of the MLCD (8-10 AM). Blue lines indicate the point at which the number of vessels (12) is predicted to reduce the response variable by 50% of the maximum level observed (Y = -0.01x + 0.31, R^2 =0.73, P = <0.001).

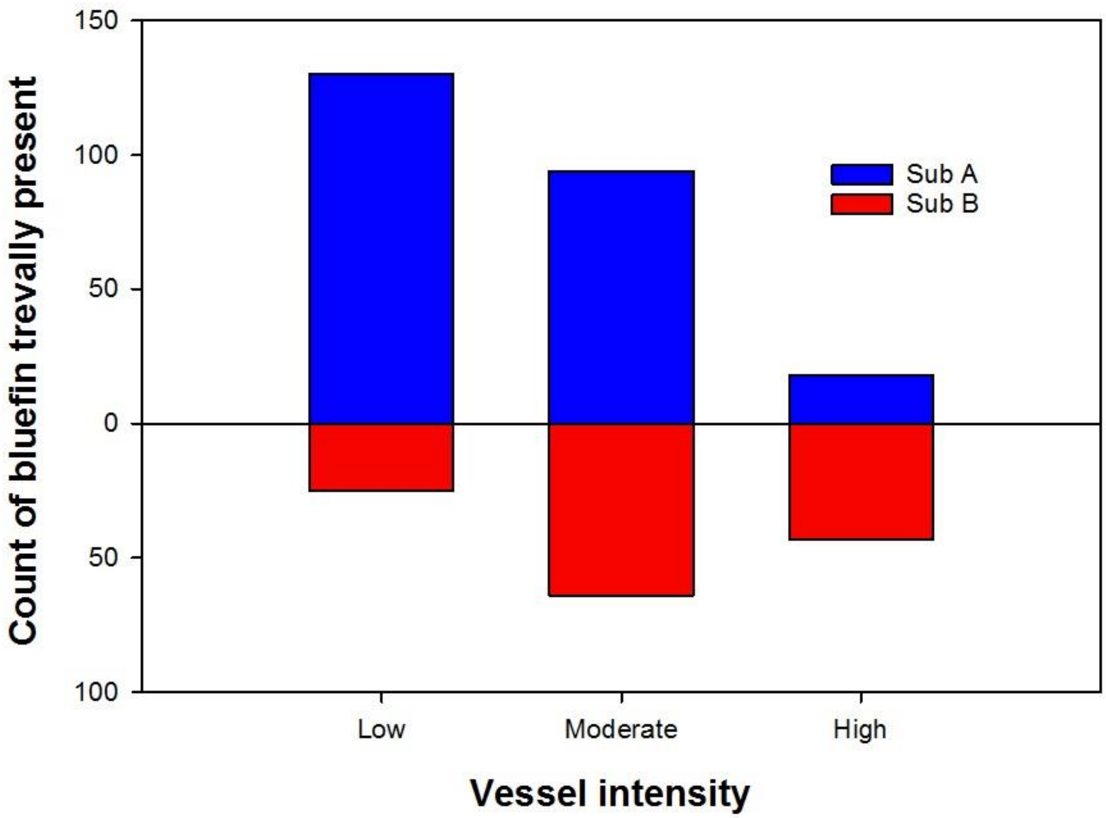

Figure 2.8: A comparison of the count of bluefin trevally presences in subzone A (blue) and subzone B (red) across a gradient of vessel intensity, during peak hours (8-10 AM) in human use at subzone A.

VII. References

Amoser S, Wysocki LE, Ladich F (2004) Noise emission during the first powerboat race in an Alpine lake and potential impact on fish communities. J Acoust Soc Am 116:3789–3797. doi: 10.1121/1.1808219

Bell CM, Needham MD, Szuster BW (2011) Congruence among encounters, norms, crowding, and management in a marine protected area. Environ Manage 48:499–513. doi: 10.1007/s00267-011-9709-1

Bruce BD, Bradford RW (2013) The effects of shark cage-diving operations on the behaviour and movements of white sharks, Carcharodon carcharias, at the Neptune Islands, South Australia. Mar Biol 160:889–907. doi: 10.1007/s00227-012-2142-z

Brunnschweiler JM, Barnett A (2013) Opportunistic Visitors: Long-Term Behavioural Response of Bull Sharks to Food Provisioning in Fiji. PLoS One. doi: 10.1371/journal.pone.0058522

CAP M (2014) Molokini Shoal Marine Life Conservation District.

Cesar HSJ (Herman SJ., Beukering P Van (2004) Economic valuation of the coral reefs of Hawaii. Pacific Sci 58:231–242. doi: 10.1353/psc.2004.0014

Charles A, Wilson L (2009) Human dimensions of marine protected areas. ICES J Mar Sci J du Cons 66:6–15.

Chateau O, Wantiez L (2008) Human impacts on residency behaviour of spangled emperor, Lethrinus nebulosus, in a marine protected area, as determined by acoustic telemetry. J Mar Biol Assoc UK 88:825–829. doi: 10.1017/S0025315408001434

Codarin A, Wysocki LE, Ladich F, Picciulin M (2009) Effects of ambient and boat noise on hearing and communication in three fish species living in a marine protected area (Miramare , Italy). Mar Pollut Bull. doi: 10.1016/j.marpolbul.2009.07.011

Davis D, Tisdell C (1995) Recreational scuba-diving and carrying capacity in marine protected areas Derrin Davis a & Clem Tisdell b. Ocean Coast Manag 26:19–40. doi: 10.1016/0964-5691(95)00004-L

Dulvy NK, Freckleton RP, Polunin NVC (2004) Coral reef cascades and the indirect effects of predator removal by exploitation. Ecol Lett 7:410–416. doi: 10.1111/j.1461-0248.2004.00593.x

Feary D a., Cinner JE, Graham N a J, Januchowski-Hartley F a. (2010) Effects of Customary Marine Closures on Fish Behavior, Spear-Fishing Success, and Underwater Visual Surveys. Conserv Biol 25:341–349. doi: 10.1111/j.1523-1739.2010.01613.x

Friedlander a. M, Brown EK, Jokiel PL, et al (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291–305. doi: 10.1007/s00338-003-0317-2

Friedlander AM, Brown E, Monaco ME (2007a) Defining reef fish habitat utilization patterns in Hawaii: Comparisons between marine protected areas and areas open to fishing. Mar Ecol Prog Ser 351:221–233. doi: 10.3354/meps07112

Friedlander AM, Brown EK, Monaco ME (2007b) Coupling Ecology and GIS to Evaluate Efficacy of Marine Protected Areas in Hawaii. Ecol Appl 17:715–730.

Friedlander AM, DeMartini EE (2002) Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian islands: The effects of fishing down apex predators. Mar Ecol Prog Ser 230:253–264. doi: 10.3354/meps230253

Garcı-Rubies A, Hereu B, Zabala M (2013) Long-Term Recovery Patterns and Limited Spillover of Large Predatory Fish in a Mediterranean MPA. PLoS One. doi: 10.1371/journal.pone.0073922

Garrod B, Wilson JC (2003) Marine ecotourism: issues and experiences. Channel View Publications.

Hammerschlag N, Gallagher AJ, Wester J, et al (2012) Don't bite the hand that feeds: assessing ecological impacts of provisioning ecotourism on an apex marine predator. Funct Ecol 26:567–576.

Harriott VJ, Davis D, Banks S a (1997) Recreational Diving in Marine Its Impact Australia in Eastern and Protected Areas. R Swedish Acad Sci 26:173–179.

Henningsen A (1994) Tonic immobility in 12 elasmobranchs : Use as an aid in captive husbandry. Biol Z O O 13:325–332. doi: 10.1002/zoo.1430130406

Heupel MR, Semmens JM, Hobday a. J (2006) Automated acoustic tracking of aquatic animals: Scales, design and deployment of listening station arrays. Mar Freshw Res 57:1–13. doi: 10.1071/MF05091

Holland KN, Wetherbee BM, Lowe CG, Meyer CG (1999) Movements of tiger sharks (Galeocerdo cuvier) in coastal Hawaiian waters. Mar Biol 134:665–673. doi: 10.1007/s002270050582

Holles SH, Simpson SD, Radford AN, et al (2013) Boat noise disrupts orientation behaviour in a coral reef fish. Mar Ecol Prog Ser 485:295–300. doi: 10.3354/meps10346

Jackson JB, Kirby MX, Berger WH, et al (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science (80-) 293:629–637. doi: 10.1126/science.1059199

Jacobsen L, Baktoft H, Jepsen N, et al (2014) Effect of boat noise and angling on lake fish behaviour. J Fish Biol 84:1768–1780. doi: 10.1111/jfb.12395

Januchowski-Hartley F a., Graham N a J, Feary D a., et al (2011) Fear of fishers: Human predation explains behavioral changes in coral reef fishes. PLoS One. doi: 10.1371/journal.pone.0022761

Jentoft S, van Son TC, Bjørkan M (2007) Marine protected areas: A governance system analysis. Hum Ecol 35:611–622.

Kessel ST, Cooke SJ, Heupel MR, et al (2013) A review of detection range testing in aquatic passive acoustic telemetry studies. Rev Fish Biol Fish. doi: 10.1007/s11160-013-9328-4

Lammers MO, Howe M (2014) Examination of the influence of vessel traffic on the movement patterns of apex predators in the Molokini Marine Life Conservation District: Preliminary Report.

Laroche RK, Kock A a., Dill LM, Oosthuizen WH (2007) Effects of provisioning ecotourism activity on the behaviour of white sharks Carcharodon carcharias. Mar Ecol Prog Ser 338:199–209. doi: 10.3354/meps338199

Lobel PS, Kaatz IM, Rice a. N (2010) Acoustical behavior of coral reef fishes. In: Reproduction and Sexuality in Marine Fishes: Evolutionary Patterns and Innovations. pp 307–386

McClanahan TR, Graham NA, Calnan JM, MacNeil MA (2007) TOWARD PRISTINE BIOMASS : REEF FISH RECOVERY IN CORAL REEF MARINE PROTECTED AREAS IN KENYA. Ecol Appl 17:1055–1067.

Meyer CG, Holland KN (2008) Spatial dynamics and substrate impacts of recreational snorkelers and scuba divers in hawaiian marine protected areas. J Coast Conserv 12:209–216. doi: 10.1007/s11852-009-0043-1

Meyer CG, Honebrink RR (2005) Transintestinal Expulsion of Surgically Implanted Dummy Transmitters by Bluefin Trevally—Implications for Long-Term Movement Studies. Trans Am Fish Soc 134:602–606. doi: 10.1577/T04-082.1

Milazzo M, Chemello R, Badalamenti F, et al (2002) The impact of human recreational activities in marine protected areas: What lessons should be learnt in the Mediterranean Sea? Mar Ecol 23:280–290.

Myers RA, Worm B (2005) Extinction , survival or recovery of large predatory fishes. Phil Trans R Soc B 360:13–20. doi: 10.1098/rstb.2004.1573

Needham MD, Szuster BW (2011) Situational influences on normative evaluations of coastal tourism and recreation management strategies in Hawai'i. Tour Manag 32:732–740. doi: 10.1016/j.tourman2010.06.005

Needham MD, Szuster BW, Bell CM (2011) Encounter norms, social carrying capacity indicators, and standards of quality at a marine protected area. Ocean Coast Manag 54:633–641. doi: 10.1016/j.ocecoaman.2011.06.004

Payne NL, Gillanders BM, Webber DM, Semmens JM (2010) Interpreting diel activity patterns from acoustic telemetry: The need for controls. Mar Ecol Prog Ser 419:295–301. doi: 10.3354/meps08864

Popper AN, Fay RR (1999) The auditory periphery in fishes. In: Comparative hearing: fish and amphibians. Springer New York, pp 43–100

Popper AN, Hastings MC (2009) The effects of human-generated sound on fish. Integr Zool 4:43–52. doi: 10.1111/j.1749-4877.2008.00134.x

Radford a. N, Kerridge E, Simpson SD (2014) Acoustic communication in a noisy world: can fish compete with anthropogenic noise? Behav Ecol 00:1–9. doi: 10.1093/beheco/aru029

Rice J, Moksness E, Attwood C, et al (2012) The role of MPAs in reconciling fisheries management with conservation of biological diversity. Ocean Coast Manag 69:217–

230. doi: 10.1016/j.ocecoaman.2012.08.001

Rice W (1989) Analyzing Tables of Statistical Tests. Evolution (N Y) 43:223–225.

Russ GR, Alcala AC, Maypa AP, et al (2004) Marine reserve benefits local fisheries. Ecol Appl 14:597–606. doi: 10.1890/03-5076

Russ GR, Miller KI, Rizzari JR, Alcala AC (2015) Long-term no-take marine reserve and benthic habitat effects on coral reef fishes Long-term no-take marine reserve and benthic habitat effects on coral reef fishes. Mar Ecol Prog Ser 529:233–248. doi: 10.3354/meps11246

Sandin SA, Smith JE, Demartini EE, et al (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. PLoS One. doi: 10.1371/journal.pone.0001548

Sarà G, Dean JM, D'Amato D, et al (2007) Effect of boat noise on the behaviour of bluefin tuna Thunnus thynnus in the Mediterranean Sea. Mar Ecol Prog Ser 331:243–253. doi: 10.3354/meps331243

Taylor M, Mansueti RJ (1960) Sounds Produced by Very Young Crevalle Jack , Caranx hippos , from the Maryland Seaside. Coast Estuar Res Fed 1:115–116.

Thurstan RH, Roberts CM, Hawkins JP, et al (2012) Are marine reserves and non-consumptive activities compatible ? A global analysis of marine reserve regulations analysis of marine reserve regulations. Mar Policy 36:1096–1104. doi: 10.1016/j.marpol.2012.03.006

Usseglio P (2015) 33 Quantifying reef fishes : bias in observational approaches. In: Mora C (ed) Ecology of Fishes on Coral Reefs. Cambridge University Press, pp 270–273

Vabø R, Olsen K, Huse I (2002) The effect of vessel avoidance of wintering Norwegian spring spawning herring. Fish Res 58:59–77. doi: 10.1016/S0165-7836(01)00360-5

Voellmy IK, Purser J, Flynn D, et al (2014) Acoustic noise reduces foraging success in two sympatric fish species via different mechanisms. Anim Behav 89:191–198. doi: 10.1016/j.anbehav.2013.12.029

Zeppel H (2008) Education and conservation benefits of marine wildlife tours: Developing free-choice learning experiences. J Environ Educ 39:3–18.

General Conclusions

This research contributes to our understanding of predator biology in a unique ecosystem with a predator assemblage that is becoming increasingly rare in the main Hawaiian Islands. The results of chapter one allowed us to describe the ethology of an entire guild of reef predators and identify species specific differences in the spatial and temporal use of the MLCD's two contrasting habitats. Furthermore, the comparison of residency and movement patterns between the fives species of predators at the MLCD, indicates that small isolated MPAs are effective in conserving site attached fish such as the bluefin trevally, but species with larger home ranges (i.e., green jobfish and grey reef sharks) or species that make frequent moments for spawning (i.e., giant trevally) are only provided temporary refuge from fishing activities. On a larger scale, the spatial detections of each fish at Maui and Kaho'olawe provide the first evidence of a biological connection between the populations of these species in Molokini MLCD and the greater Maui Nui Complex. Future marine management in Hawaii can benefit from the description of these movement patterns, as MPA's can be designed to protect these species with the knowledge that bluefin trevally are well protected in small MPAs but other species require larger areas to be completely protected from fishing. Further research is needed to identify critical habitats such as the location of spawning aggregations and extent of nightly movements for these additional species. Finally in chapter two, the documentation of the reduction in bluefin trevally habitat use of subzone A during intense levels of human use at the MLCD, provides the first documentation of the displacement of predators from an MPA from non-consumptive resources use in a natural setting. As the popularity of marine recreation increases in the state of Hawaii and around the world, an understanding of the relationship provided by this work will be invaluable to future marine management. Future research is needed to identify the exact mechanism driving the displacement of bluefin trevally (i.e., noise, the presence of humans) and what levels of anthropogenic intensity are acceptable to maintain natural ecosystem function.