

Integrating Multiple Technologies to Understand the Foraging Behavior and Habitat

Use of Monk Seals in the Main Hawaiian Islands

by

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Dissertation submitted in partial fulfillment of  
the requirements for the degree of Doctor  
of Philosophy, in the Department of  
Marine Science and Conservation in the Graduate School  
of Duke University

2014

ABSTRACT

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## **Abstract**

Hawaiian monk seal abundance is currently declining by about 4% per year with current population estimates around 1,100 individuals. Although the overall population continues to decline, a small sub-population in the main Hawaiian Islands (MHI) appears to be increasing by roughly 6% per year. Monk seal conservation and recovery efforts in the MHI have been hindered by the perception that seals do not belong there, and that they compete with fisheries and damage coral reefs. Education and outreach efforts describing the actual impact of monk seals in the MHI are currently underway, but we actually know very little about their at-sea behavior, especially in the MHI, even though Hawaiian monk seals have been studied extensively since the 1980s. The central objective of my dissertation was to describe monk seal behavior and develop a baseline for monk seal foraging ecology and habitat use in the MHI. To accomplish this I combined three-axis accelerometers, National Geographic Crittercams, and GPS tags to study monk seal foraging behavior. I instrumented 16 seals between 2010 and 2014 on the islands of Molokai, Kauai, and Oahu and deployed an additional 24 GPS tags without the accelerometer and Crittercam. I recovered each Crittercam/accelerometer package 3-6 days after deployment, resulting in an average of 6.14 hours of video footage per seal. The GPS tags continued to record data for 3-6 months providing long-term summaries of dive and haul-out behavior. Using a Bayesian framework I modeled

monk seal behavior and habitat use, and developed a method to identify feeding events from accelerometer data. There was a high level of individual variation in the movements of monk seals, but general descriptions of their behavior were accurate at the population level. On average, foraging trips lasted  $0.81 \pm 1.38$  days and seals traveled  $28.45 \pm 82.03$  km per trip. Most seals began benthic dives shortly after entering the water, with most dives occurring between 20-40 m. I used kernel density estimation to define the 50% (core area) and 95% (home range) utilization distribution for each seal. The median home range and core area size for seals in the MHI was 265.62 km<sup>2</sup> and 1,564.56 km<sup>2</sup>, respectively. The pitch axis of the accelerometer was a reliable metric, with over 70% accuracy, for identifying foraging events for monk seals. Body motion over the course of a dive, and how close the seal was to the seafloor during a dive (dive ratio) were the best predictors of these foraging events. Consequently, dive ratio was used to infer foraging in long-term telemetry records that lacked concurrent accelerometer data. Analysis of these data relative to habitat preferences revealed two distinct movement modes for monk seals in the MHI: near shore and offshore/inter-island. My research developed the first thorough understanding of monk seal movements and habitat use in the MHI and provided insight into the mechanisms contributing to the behavioral variability observed for this species. I hope that a detailed understanding of the foraging behavior of monk seals will provide insight into their true role in the ecosystem and help foster the recovery of this critically endangered species.

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## General Introduction

### *Historical Background*

There are three species of monk seal: the Hawaiian monk seal (*Neomonachus schauinslandi*), Mediterranean monk seal (*Monachus monachus*), and Caribbean monk seal (*Neomonachus tropicalis*). The Hawaiian and Mediterranean monk seals are the two most endangered pinniped species in the world, and the Caribbean monk seal was officially listed as extinct in 2005 (IUCN 2011). Monk seals are unique among phocids in that it is the only group to reside entirely in tropical and sub-tropical waters. Fossil records, DNA studies, morphological studies, and geological events all suggest that monk seals originated in the Mediterranean or Tethys Sea region (*Monachus monachus*) and began a westerly dispersion to the Caribbean (*Neomonachus tropicalis*) and into the central North Pacific (*Neomonachus schauinslandi*) in the middle of the Miocene era (Fyler et al. 2005). This dispersal suggests that initial colonization of the Pacific occurred during the mid-Pliocene era (~3.5 mya) when the Central American Seaway was still open (Fyler et al. 2005).

Little is known about the Hawaiian monk seal in antiquity. Written reports began with the Russian explorer Lisianski, who observed seals in the Northwestern Hawaiian Islands (NWHI) in 1805. Records from voyages in 1824 (the *Aiona*) and 1859 (the *Gambia*) suggest that the abundance of monk seals had declined since Lisianski's initial description due to unregulated hunting. Monk seal remains have been recovered

from an archaeological site on the Big Island of Hawaii and radiocarbon dated to 1400-1750 AD (Schultz et al. 2009), but their abundance in the MHI appears to have been limited following the arrival of Polynesian settlers 1500-1600 years ago (Schultz et al. 2009). It is likely that seals initially inhabited the MHI but were quickly extirpated there and pushed to the periphery of their range by the presence of Polynesians. This initial decrease in abundance may have reduced the seals to a tiny relict population (Schultz et al. 2009) that survived almost entirely in the NWHI where there was little or no contact with humans until the arrival of Europeans later in the 1800s. When humans finally arrived in the NWHI seals were killed for pelts and oil, and also for food by shipwrecked sailors and feather and guano hunters stationed in the NWHI. The number of seals killed was not documented, but the effects of this exploitation were likely severe and decreased both the abundance and genetic diversity of the population (Schultz et al. 2009).

The Hawaiian monk seal is endemic to the Hawaiian archipelago and is the only marine mammal found entirely within U.S. waters. Currently, most of the population resides in the uninhabited and protected Papahānaumokuākea Marine National Monument at six main breeding sub-populations in the NWHI: Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals (Figure 1). Necker and Nihoa Islands, at the south-east end of the NWHI chain also support smaller breeding sub-populations. Until recently, monk seals were rarely

observed in the MHI but since the 1990s an increasing number of births and sightings (Baker and Johanos 2004) suggest that the species is beginning to reestablish itself in this region.

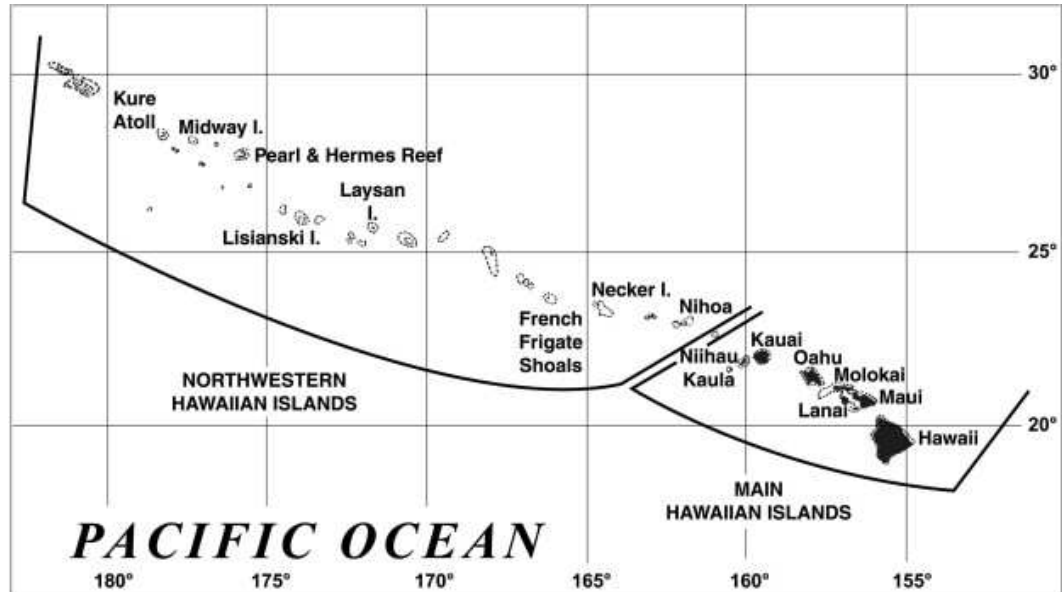


Figure 1: The Hawaiian Archipelago, indicating the main Hawaiian Islands and the primary Northwestern Hawaiian Islands subpopulations of monk seals at French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll (Baker et al. 2011).

### ***Ecology & Life History***

Adult Hawaiian monk seals measure between 2.13 - 2.44 m in length and weigh between 136 - 272 kg, with limited size differences between sexes. At birth, pups are approximately 91 cm long, weigh about 14 kg, and grow to 68 - 90 kg at weaning. They are born with a long, woolly, black coat, which is shed at around 6 weeks and replaced with a silver-gray coat near weaning (Kenyon and Rice 1959). All monk seals experience a catastrophic molt each year, in which the outer layer of skin and hair is shed and

replaced by a new silvery gray pelage. Females typically molt after weaning their pups and adult males and juveniles molt in late summer and fall (Kenyon and Rice 1959).

Hawaiian monk seals spend most of their lives at sea and come to shore only to breed, molt, and rest. As adults, they are typically found alone or in small groups, a behavior that differs from most other phocids who breed and molt in large aggregations at rookeries and communal haul-out sites. The species exhibits a scramble competition form of polygamy. Males do not hold harems or defend resources, but do fight for access to females in estrous; successful males will probably mate with multiple females in a single season. Females generally reach reproductive maturity between 4 - 10 years of age; and females in the MHI typically reach first parturition much earlier than their counterparts in the NWHI (Johanos et al. 1994, Baker and Johanos 2004). Gestation is 10-11 months and pups are born, most often, between March and August, although births have been documented during every month of the year. In the MHI, adult females tend to give birth every year. Females nurse their pups continuously for 4-6 weeks and then, like all phocids, abruptly wean and abandon the pup. Female seals typically mate 3 - 4 weeks after weaning and will molt 5 - 6 weeks after mating (NMFS 2007).

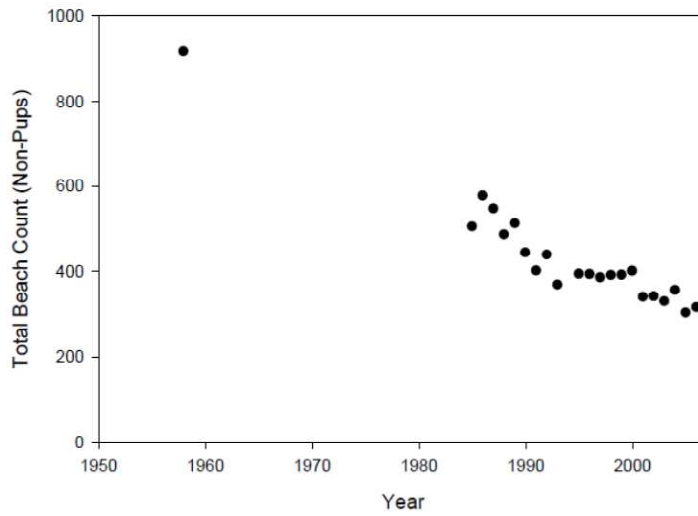
Monk seals are benthic foragers, and eat a variety of prey in areas ranging from shallow reefs to deep waters greater than 500 m. Their diet is diverse and includes fish, squid, octopus, eels, and crustaceans (crab, shrimp, and lobster) (Parrish et al. 2005, Piche et al. 2010, Cahoon 2011, Iverson et al. 2011). Monk seals forage primarily in

depths from 18 - 90 m, typically in waters surrounding atolls, islands, and areas farther offshore near reefs, submerged banks, and sea mounts (Parrish et al. 2000, Stewart et al. 2006, Cahoon 2011). Monk seals have also been found foraging in deep water coral beds (Parrish et al. 2002).

### ***Current Status***

Hawaiian monk seals were first listed as an endangered species under the U.S. Endangered Species Act in 1976, are listed as critically endangered in the International Union for the Conservation of Nature and Natural Resources (ICUN) Red List of Threatened species, and are included in Appendix I of the Convention on International Trade in Endangered Species (CITES). Several island-based sub-populations exist, but they are all managed as a single stock by the U.S. National Marine Fisheries Service. Genomic studies support management as a single stock (Schultz et al. 2009). Sampling of microsatellite loci revealed extremely low levels of allelic diversity and heterozygosity, suggesting low genetic diversity and no indication of population structure ( $K = 1$  population) (Schultz et al. 2009).

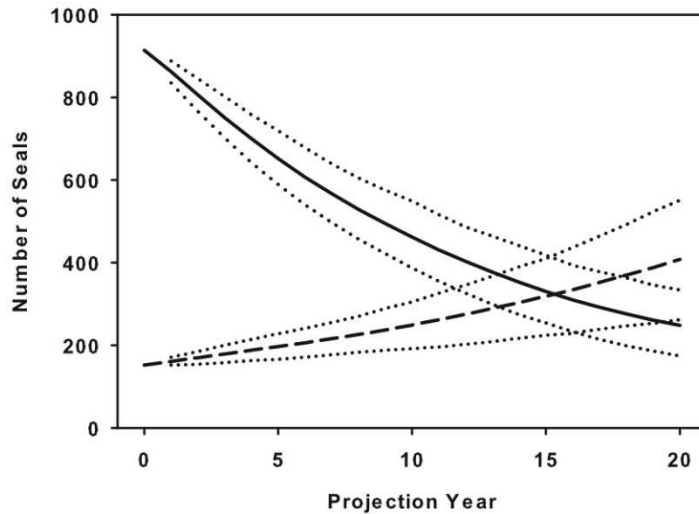
Between 1958 and 2006 mean beach counts of non-pups (juveniles, sub-adults and adults) in the main reproductive subpopulations decreased by 66% (Figure 2). The current population is estimated to be ~ 1,100 individuals and the population is declining by about 4% per year (Baker et al. 2011).



**Figure 2: Mean non-pup beach counts in the NWHI from 1985 – 2006 (NMFS 2007).**

The overall population continues to decline, but a small sub-population (~150 individuals) in the MHI is increasing by ~ 6% per year. This increase is occurring as the NWHI population continues to decline by ~ 4.5% per year (Baker et al. 2011). Current population trajectories indicate that the MHI population will equal the NWHI population in size in approximately 10 years (Baker et al. 2011) (Figure 3). The underlying ecological drivers behind these divergent demographic trends are unknown, but the proximate cause is different rates of juvenile survival. In the NWHI only 42 - 50% of pups survive their first year of life and only one in five seals will reach sexual maturity (4-6 years of age) (Baker and Thompson 2007). Low juvenile survival in the NWHI has generated an extremely skewed age structure across the NWHI sub-populations (Antonelis et al. 2006) and is contributing to the ongoing population decline.

In contrast, survival from weaning to one year of age in the MHI is roughly 77% (Baker et al. 2011) and most seals that survive their first year will reach sexual maturity.



**Figure 3: Twenty year population projection from 2010 - 2030.**

Resource limitation is thought to be the ultimate driving force behind the variation in juvenile survival rates between the regions, and the continued population decline in the NWHI. Resource limitation is, therefore, the factor unifying several hypotheses regarding the ecological causes of these demographic trends:

- 1) Increased foraging effort in the NWHI due to lower prey densities; seals have to forage for longer periods of time or dive to deeper depths to acquire the same resources as those in the MHI.
- 2) Distance to foraging grounds; NWHI seals must travel further than MHI seals to reach ideal foraging habitat
- 3) Increased competition for prey in the NWHI; NWHI seals may have to dive to greater depths to avoid competitors, such as large jacks and sharks

Recently weaned seals in the MHI are in significantly better condition (greater axillary girth and body length) than their counterparts in the NWHI. These

measurements are related to the foraging efficiency of the mother, and reflect better overall health of the pup at weaning, and the subsequent likelihood of survival to adulthood (Baker 2008). On average, weaned pups in the MHI are 14.3 cm longer and 17 cm larger in girth than pups weaned in the NWHI (Baker et al. 2011). Thus, females in the MHI are able to invest more energy in their pups, which likely reflects better environmental conditions and greater food resources in the MHI. Insufficient resources typically result in decreased survival, lower fecundity, and an older age of sexual maturity, all of which are observed the NWHI (Harting et al. 2007). Additional threats to survival are entanglement in marine debris (Henderson 2001), shark predation (Johanos and Baker 2001), and adult male aggression (Johanos et al. 2010), but these are not the driving factors of the continued decline.

### ***Recovery Efforts***

In the early 1980s, the National Marine Fisheries Service (NMFS) initiated efforts to monitor and foster the recovery of the Hawaiian monk seal population. Throughout NMFS's history, the Hawaiian Monk Seal Research Program (HMSRP) has focused on population assessment to determine abundance, age-sex structures of the subpopulations, survival and reproductive rates, and causes of injury and mortality. Beyond monitoring the population, efforts to actively improve survival have included: disentangling seals caught in marine debris; removing fishing hooks from seals; large-scale removal of marine debris from beaches and reefs; mitigating depredation by

Galapagos sharks (*Carcharhinus galapagensis*); and intra-specific male aggression. A recent analysis of survival of individual seals showed that at least 30% of the current population is alive today because of some type of intervention by NMFS personnel in the last 30 years (Harting et al. 2014). These efforts have had some success, but have not been sufficient to reverse the decline of the population.

### ***Approach***

The central objective of my dissertation is to identify potential factors contributing to the increased survivorship of monk seals in the MHI. Resource limitation is one of the primary hypotheses for the decline in the NWHI, so my goal was to develop a thorough understanding of monk seal foraging behavior and habitat use in the MHI and to develop a baseline for future comparisons with the NWHI. Chapter One begins with a general overview of behavior using traditional telemetry methodology. Chapter Two then builds on these results, adding multiple data streams from other, more sophisticated instruments; focusing on foraging behavior and identifying metrics I can use to identify foraging events. In Chapter Three I combine results from the previous two chapters to predict where monk seals forage in the MHI.

# **Chapter 1: Hawaiian Monk Seals in the Main Hawaiian Islands: an Overview of Movements and Behavior**

## ***Introduction***

The Hawaiian monk seal is one of the most endangered mammals in the world with current abundance estimated at 1,100 (Baker et al. 2011). Most of the population is found in the uninhabited and protected Northwestern Hawaiian Islands (NWHI), where abundance is declining by approximately 4% per year (Baker et al. 2011). A small sub-population inhabits the Main Hawaiian Islands (MHI) where, somewhat paradoxically, abundance is increasing by 6% annually (Baker et al. 2011). The underlying ecological drivers behind these counter-intuitive and divergent trends are unknown, but the proximate cause is different rates of juvenile survival. Juvenile survival is relatively high in the MHI, but very low in the NWHI, where many weaned pups and juveniles die of starvation (Baker et al. 2011). Understanding the movements and behavior of seals in both areas is key to understanding the potential drivers of these divergent demographic trends. In particular, a thorough understanding of foraging behavior in the MHI will enable me to begin addressing what behaviors, including foraging trip characteristics and space use, differ between the two regions and how such differences may affect survival.

## Using Telemetry to Understand Foraging Behavior

Satellite telemetry has been used to document animal movements and habitat use in a variety of marine mammals (McConnell et al. 1999, Tougaard et al. 2003, Lesage et al. 2004, Small et al. 2005, Austin et al. 2006b). The technology uses polar orbiting satellites operated by the Argos system (Argos 2007) to transmit data about an animal's location, behavior, physiological state, or environmental surroundings (Tremblay et al. 2006). Some of the drawbacks to this approach include the autocorrelation between consecutive locations and, particularly, the error associated with each location, which can be difficult to estimate (Hays et al. 2001, Vincent et al. 2002, Hardee 2008). Recent advances in tracking and telemetry technology (Fastloc™ GPS) have provided an alternative to the Argos system and allowed scientists to collect data from animals with improved location estimates (Kie et al. 2010, Tomkiewicz et al. 2010). The ability to obtain accurate estimates of location, even during a rapid surfacing event, represents a major step forward in our ability to track marine animals. When coupled with dive analysis, satellite/GPS telemetry allows for the estimation of dive locations by estimating a continuous movement path, which in turn leads to a better understanding of overall movement patterns, habitat use, and habitat preferences (Tremblay et al. 2006).

It has become routine to equip diving vertebrates with telemetry instruments that record pressure along with location data, allowing the reconstruction of two-dimensional dive records. However, it is often difficult to recover archival telemetry

instruments that store full dive records and the transmission of such large data sets requires considerable on-board processing power and battery life. As a result, it has become commonplace to bin dive data that are transmitted via the satellite network. However, many studies have documented the limitations of using binned dive data to infer at-sea behavior (Merrick and Loughlin 1997, Burns and Castellini 1998, Frost et al. 2001). GPS/GSM phone tags (Sea Mammal Research Unit, St Andrews, Scotland) include Fastloc™ GPS (Wildtrack Telemetry Systems Ltd), wet-dry, pressure, and temperature sensors. The on-board computer is able to store data for up to six months and transmit large amounts of high resolution data using the GSM mobile phone network, which allows for much greater transmission bandwidth than the Argos system. This increased bandwidth allows for the collection of the full dive record without having to recover the tag itself. These data are of much higher resolution and are more detailed than binned data, but are still summarized from the full dive record and therefore lack some important characteristics including ascent and descent rates that are available in the full record.

### **Telemetry Studies with Hawaiian Monk Seals**

The demography of Hawaiian monk seals has been monitored intensively since the early 1980s, but we still have a very limited understanding of their at-sea behavior. Most research effort to date has focused on the main breeding subpopulations in the NWHI. Between 1996 and 2002, for example, 147 satellite linked depth recorders

(SLDRs) were deployed on monk seals at all six NWHI major sub-populations (Stewart et al. 2006). These tags were programmed to transmit the number of dives occurring within a specific depth interval in 6-hr time periods (binned dives) through the Argos network (Argos 2007). This work revealed that seals preferred shallow (< 40 m) demersal habitats with most dives occurring within atoll lagoons, and on submerged banks and seamounts (areas of high bathymetric relief) outside the atoll lagoons (Stewart et al. 2006). However, dives to depths of 500 m were also recorded, suggesting that seals may use a wide range of habitats, perhaps to avoid competition while foraging (Parrish et al. 2000, Stewart et al. 2006) or to access different types of prey (Stewart et al. 2006). These relatively coarse summaries provided a first glimpse into the diving behavior of monk seals, but precluded any fine scale interpretation of their foraging patterns.

The first comprehensive study of monk seal foraging ecology in the MHI was completed by Cahoon (2011). In this study, 18 seals were tagged using Satellite-Linked Depth Recorders (SLDRs). These seals exhibited dive depths similar to those studied in the NWHI. MHI seals foraged primarily in waters shallower than 80 m and within the 200 m bathymetric contour surrounding the islands, on the shelf or near the shelf break (Cahoon 2011). Foraging trips in the MHI were shorter, both in distance traveled and duration of time spent at sea, than those in the NWHI. Cahoon (2011) used technology similar to that used in the NWHI, which facilitated comparison with the work of Stewart

et al. (2006), but still left much to be understood in regards to fine-scale resolution and a detailed understanding of foraging behavior in the MHI.

As noted above, the abundance of monk seals in the MHI is currently increasing. This trend is promising for the species, but brings a host of potential management concerns including interactions with humans and fisheries. To fully understand the role of monk seals in the MHI ecosystem, I must first understand their foraging behavior. The primary goal of the present study was, therefore, to develop a baseline of monk seal foraging behavior in the MHI. As mentioned in the introduction, it has been suggested that monk seals in the NWHI must travel further and spend more time at sea to acquire equivalent resources to seals in the MHI. Therefore, I hypothesized that seals in the MHI would spend less time at sea (shorter foraging trip distances and durations), and would have more compact home ranges than their counterparts in the NWHI. To investigate these hypotheses I deployed GPS phone tags on seals throughout the MHI.

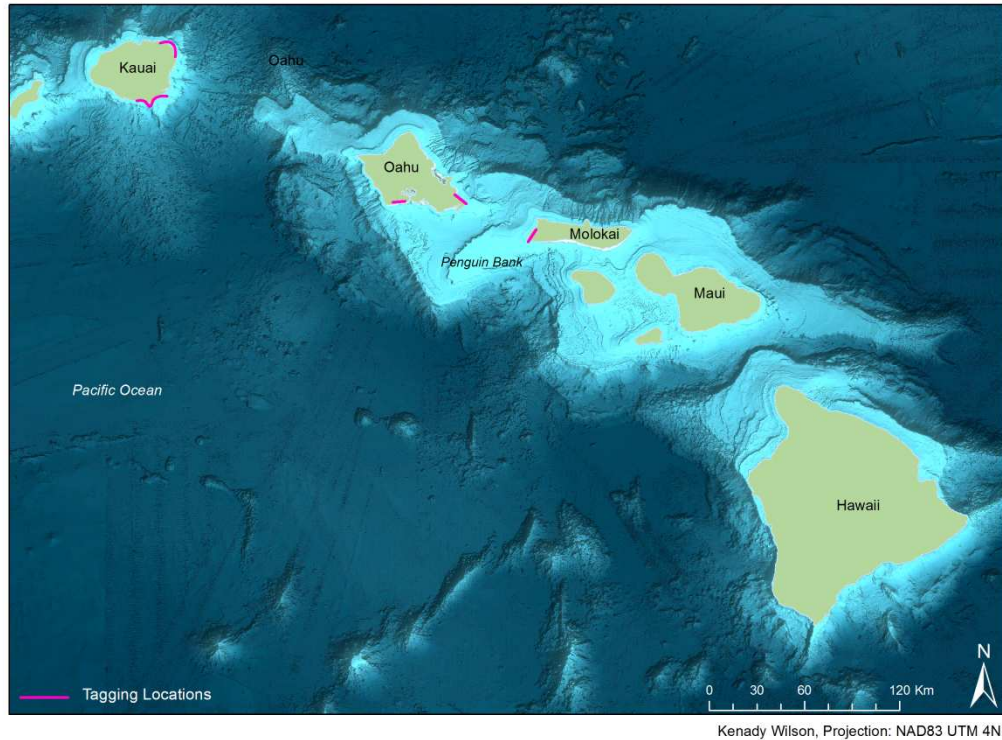
## ***Methods***

### **Study Site**

I captured seals on the islands of Oahu, Kauai, and Molokai. On Molokai, all seals were captured on the west end of the island between the Dixi Maru and Laau Point beaches (Figure 4). On Kauai and Oahu I used extensive volunteer networks to find seals throughout the islands, although I captured most seals on the south and west shores of Oahu and the south and east shores of Kauai.

## **Instrument Deployment**

Sub-adult and adult seals of both sexes were captured following the methods of Baker and Johanos (2002). I employed strict guidelines when selecting candidate seals to minimize any potential impacts on this critically endangered species. Mother-pup pairs, molting or potentially pregnant seals, were avoided; wounded, emaciated, and recently (< 2 weeks) molted seals, were never captured, and I did not attempt captures during hot windless weather (Baker and Johanos 2002). Seals that met my criteria were captured with a hoop net and then sedated with Diazepam (5mg/ml at 0.1-0.25 mg/kg IV). Weights were visually estimated prior to sedation and biomedical samples, including blood and blubber biopsies, were taken along with swabs of all orifices prior to instrument attachment. GPS phone tags were then glued to the pelage of the animal, along the dorsal midline between the shoulder blades using 10 min epoxy (Devcon, Danvers MA). Unless seals were underwater or hauled-out, the tags were programmed to record a GPS position every 20 min. Tags were programmed to record every day and were expected to jettison during the annual molt. These data were transmitted to the Scottish Oceans Institute via the GSM phone network (McConnell et al. 2004, Cronin and McConnell 2008).



**Figure 4: Capture locations of Hawaiian Monk Seals in the Main Hawaiian Islands.**

## **Data Processing**

I downloaded data from the Scottish Oceans Institute’s website. In previous calibration studies of GPS phone tags 95% of locations were accurate to  $\pm 55$  m and, even when information from fewer than four GPS satellites is received, mean error was less than 150 m (Vincent et al. 2010, Sharples et al. 2012). Therefore, I treated these GPS positions as error-free, known locations (Sharples et al. 2012). I used both the ‘haulout\_orig’ and ‘dive’ files to examine foraging behavior. Due to variable molt times, tag malfunction, and/or different durations of tag retention, the duration of data

collected for each individual varied. Therefore, I visually inspected data to designate a date where dive or haul-out behavior was observed to begin and end (i.e. if the tag fell off while the seal was hauled-out or if the tag was transmitting before deployment). After erroneous values were removed, the two files were merged and sorted by seal and the start date/time of each dive or haul-out.

I defined a 'trip' as the time spent at sea between two haul-out periods. Trip duration was calculated as the time between the end of a haul-out period and the end of the last dive before the next haul-out. Every dive for each tag deployment was assigned a unique trip number. The distance between every consecutive dive for each trip was calculated using the `trackDistance` function in R (Sumner 2013). Total trip distance was then calculated by summing the distances in each trip. Trip duration was determined by calculating the time difference between the end of the haul-out period that started the trip and the end of the last dive in the trip. Monk seals are known to rest in shallow tidal areas, sleep in underwater ledges near shore, and move between different sections of a beach, coming out of the water multiple times before hauling-out for any extended period of time. Therefore, any 'trips' lasting less than 2 h were not considered foraging trips. I calculated haul-out durations as the time elapsed between the start and end of each haul-out period. GSM phone tags designated haul-out, surface, and dive activity using the following criteria: the animal was considered hauled-out if the tag was dry for 10 min, it was at the surface if the tag was continuously wet for 40 s and shallower than

1.5 m, and it was diving if the tag was deeper than 1.5 m for at least 8 s. I calculated activity budgets using the amount of time spent diving, at the surface, and hauled-out during a 24 h period, and used these metrics as general descriptors of daily behavior.

Home ranges are good descriptors of space use and are most commonly defined as 'the area traversed by the individual in its normal activities of food gathering, mating and caring for young' (Burt 1943). Today, a number of different methods are used to describe and predict home ranges and habitat use using satellite or GPS data. The earliest and most basic models defined an area of use via minimum convex polygons (Odum and Kuenzler 1955), but a variety of statistical models, including harmonic mean (Dixon and Chapman 1980), and kernel density analysis (Worton 1989), have been used to summarize space use. Of the numerous models available, density estimation techniques, such as kernel smoothing, have become the most common empirical methods for quantifying animal home ranges (Laver and Kelly 2008, Kie et al. 2010). Monk seal home ranges were summarized using fixed kernel density estimation with an ad hoc smoothing parameter, following Curtice et al. (2011). I used the GPS locations from dives within foraging trips to calculate home ranges. I created 50% and 95% utilization distributions (UD) for all individual seals and used the 95% UD to define the home range (Worton 1989) and the 50% UD to delineate the core area of use. Home range calculations were completed using the `adehabitatHR` package in R (Chalenge 2006).

## Data Analysis

I investigated whether two indices of foraging effort, time spent at sea (trip duration) and distance covered (trip distance), could be predicted by a range of explanatory variables, including: time of year (month); inter-trip duration (time between the start of the current trip and the end of the previous trip); the island where the seal was initially captured; sex; and mean dive characteristics during a trip (Sharples et al. 2012). Note that inter-trip duration is not the same as haul-out duration because I defined a foraging trip as being different from any excursion into the water that may end a haul-out period. Additionally, 'percent area' was included as a metric of dive shape. To determine which predictors to include in the final model, trip distance and duration were modeled separately using Generalized Additive Mixed Models (GAMMs) in the `gamm4` package in R (Wood and Scheipl 2013). The fixed effects in the global model were sex, month, island, inter-trip duration, mean dive depth, mean dive duration, and mean percent area, individual seals were included as a random effect. Initial variable selection was performed by comparing adjusted  $R^2$  and AIC values for a suite of models. I chose the model with the lowest AIC value and highest adjusted  $R^2$  as the best fit and used those predictors in a final Bayesian model.

I also investigated how sex, the island where the seal was captured, median trip distance and duration influenced home range size. To determine which combination of predictors to include in the final model, I modeled core area and home range separately

using multiple linear regressions, with the above variables as fixed effects. I selected models by comparing adjusted  $R^2$  and AIC values for each candidate model. The most parsimonious model, with the fewest predictors and a  $\Delta AIC$  less than two, was chosen as the best fit. The predictors in the chosen model were then included in the final model, run using the `MCMCregress()` function in R (Martin et al. 2011). This function generates a sample from the posterior distribution of a linear regression model with Gaussian errors using Gibbs sampling with a multivariate Gaussian prior on the beta vector, and an inverse Gamma prior on the conditional error variance. In the final model, I used a Gaussian likelihood with an uninformative normal prior distribution. The model structure was:

$$y_i = x_i' \beta + \varepsilon_i \quad (1)$$

where  $y_i$  is the response variable representing home range size,  $x$  is a design matrix of predictor variables (chosen from previous model selection method), and  $\beta$  refers to the coefficients associated with each predictor (the effect of each predictor in determining home range size). The priors on  $\beta$  and  $\varepsilon_i$  were normal distributions with starting values specified as follows:

$$\varepsilon_i \sim \text{Normal}(0, \sigma^2) \quad (2)$$

$$\beta \sim \text{Normal}(b_0, B_0^{-1}) \quad (3)$$

$$\sigma^{-2} \sim \text{Gamma}(c_0/2, d_0/2) \quad (4)$$

The beta vector was initialized using the coefficient estimates from the model selection and the hyper-parameters used to initiate the priors were:  $b_0 = 94$  (mean of the starting beta values),  $B_0 = 0.001$ ,  $c_0 = d_0 = 0.001$ . Vague priors were used to allow the data to dominate the analysis and dictate the shape of the posterior distribution, while still accounting for the high levels of variability in home range size. The model was run for 100,000 iterations with a burnin of 2,000. All analyses were performed in R version 3.0.2.

## **Results**

Thirty nine instruments were deployed from 2010 – 2014 (3 females and 25 males), with one additional animal tagged in 2007. Seven animals were instrumented twice and one animal was instrumented three times over the study duration. Due to instrument and/or epoxy malfunction, I recovered data from 27 of the 40 instruments deployed, representing a 68% recovery rate, 19 individual seals (4 females and 15 males), and 1,505 days of data (Table 1). The average tracking duration was  $151.89 \pm 78.99$  days, with GPS locations received roughly every 20 min. The data coverage was not equal for all months (Figure 5), but nearly every month of the year was sampled.

**Table 1: Instrumentation data for Hawaiian monk seals tagged from 2007-2014**

Seal ID	Age	Sex	Year(s) Tagged	Island	Days of Data	# Dives	# Trips
RK35	A	F	2007,2011,2012	Kauai	143	19,803	126
RK36	A	M	2010	Kauai	297	41,404	296
R012	A	M	2012, 2014	Oahu	256	27,436	166
RI11	A	M	2010	Molokai	184	25,148	159
RE70	A	M	2010, 2014	Molokai	132	15,148	68
R018	A	M	2010, 2011	Kauai, Oahu	298	36,969	293
RR70	A	M	2010, 2014	Oahu	64	12,175	32
R4DF	A	F	2010	Oahu	140	23,765	120
RB24	SA	F	2011	Kauai	169	30,920	186
RB02	A	M	2011, 2012	Molokai	160	21,980	139
RW02	SA	M	2011, 2013	Kauai	239	35,491	212
T21M	A	M	2011	Oahu	151	16,562	124
RA12	A	M	2012	Oahu	128	26,119	92
RM38	A	M	2010	Molokai	55	7,124	42
RS00	A	F	2012	Oahu	153	29,114	93
RV18	A	M	2012, 2013	Kauai	164	23,630	209
R306	A	M	2013	Molokai	27	4,267	20
RK05	A	M	2014	Kauai	52	8,878	44
R1KK	A	M	2014	Molokai	74	7,642	18

## Seal Movements

Most seals were faithful to the island where they were tagged (only hauling-out on that island), but some individuals visited neighboring islands and/or travelled to multiple islands in the MHI chain (Figure 6). One animal, a sub-adult female, travelled from Oahu to the Big Island of Hawaii and back. Others circumnavigated the island where they were tagged, and some never left the side of the island on which they were

tagged. Most of the seals tagged on Molokai moved around the west end of the island and went on foraging trips out to Penguin Bank, but rarely left the island. Seals tagged on Kauai tended to stay near Kauai or traveled back and forth between Niihau and Kauai. Oahu seals were both the most faithful and the widest-roaming of all the seals tagged in this study. The mean distance traveled on a foraging trip was  $28.45 \pm 82.03$  km and the mean duration was  $0.81 \pm 1.38$  days. One adult male (R012) traveled 3,710.41 km on a trip that lasted roughly 36 days, but all other individuals remained closer to the islands with foraging trips typically lasting less than 1 day. There was considerable variation in the behavior of individual seals, but the mean trip distances and durations were similar for all seals (Figure 7, Figure 8). In fact, trip distances and durations were so similar that the comparison of a range of GAMMs used to predict foraging trip distance or duration proved futile. I was able to extract coefficients for the effect of my predictors (sex, inter-trip duration, island, and month), but model fit was very poor (adjusted  $R^2$  values  $< 0.10$ ). Unfortunately, none of the predictors I was able to measure with these instruments were good predictors of foraging trip distance or duration.

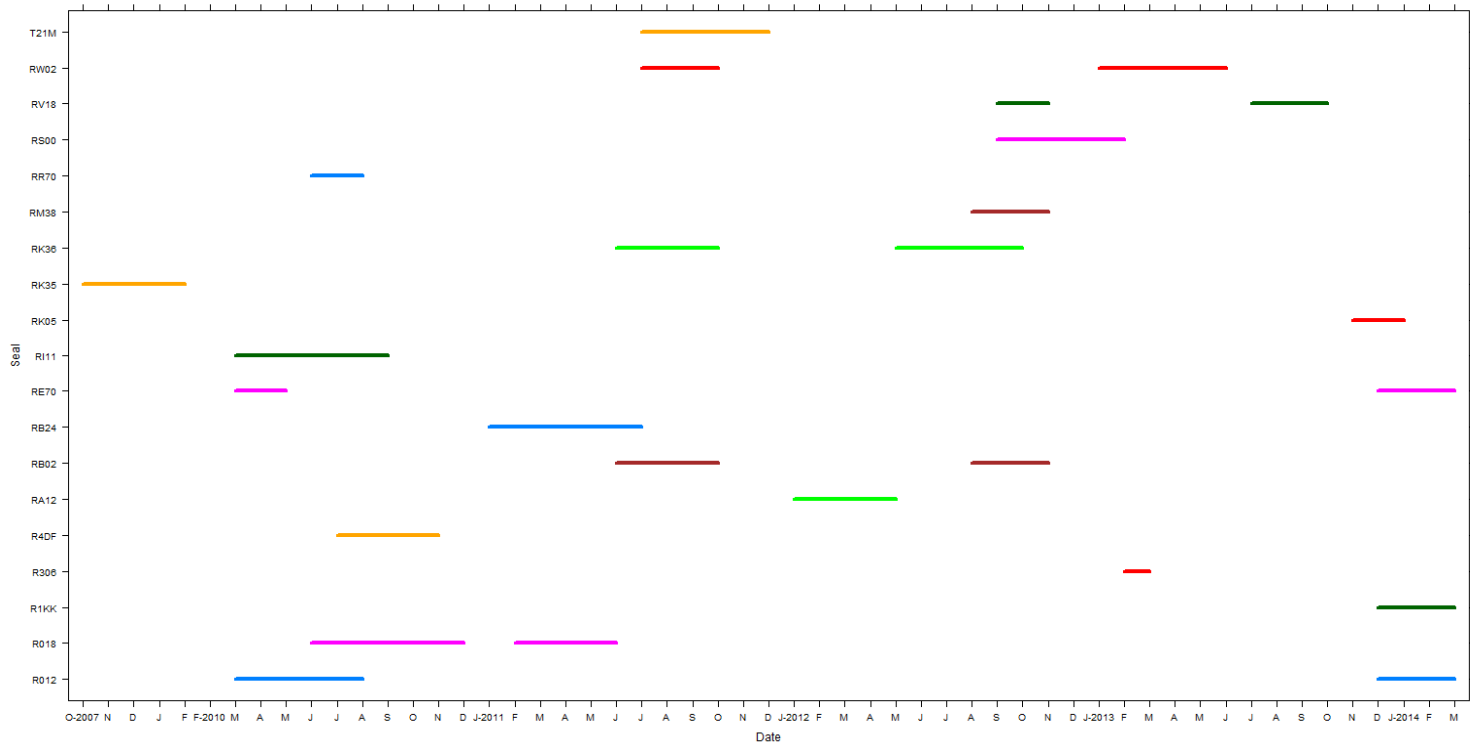
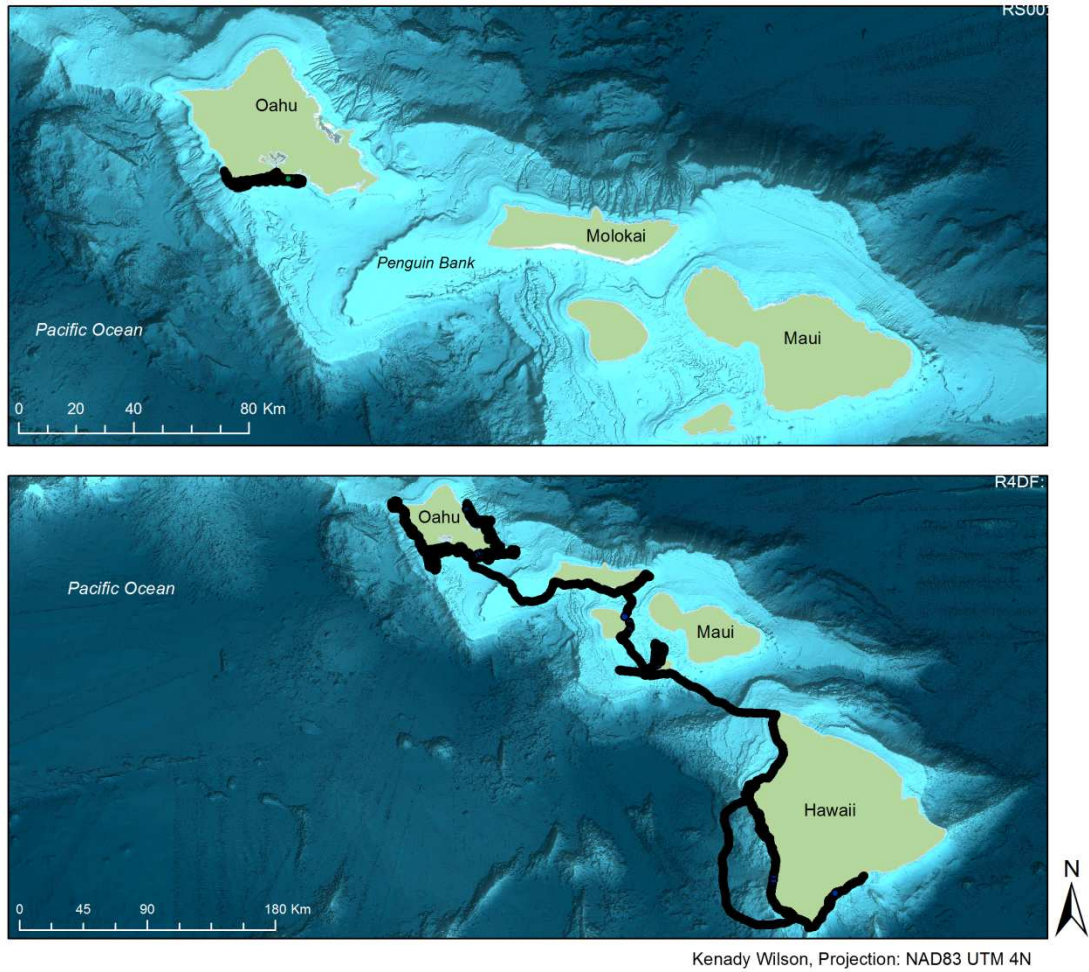
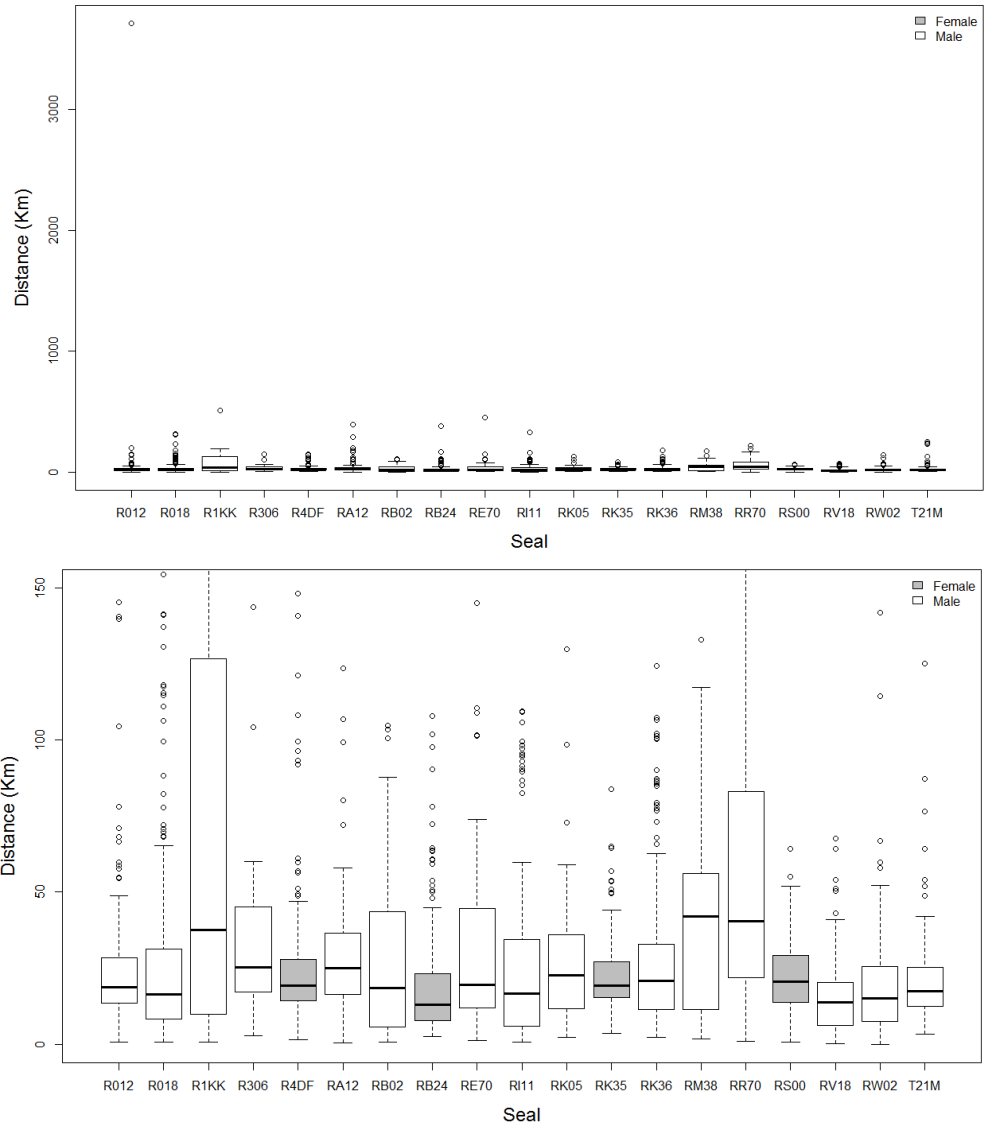


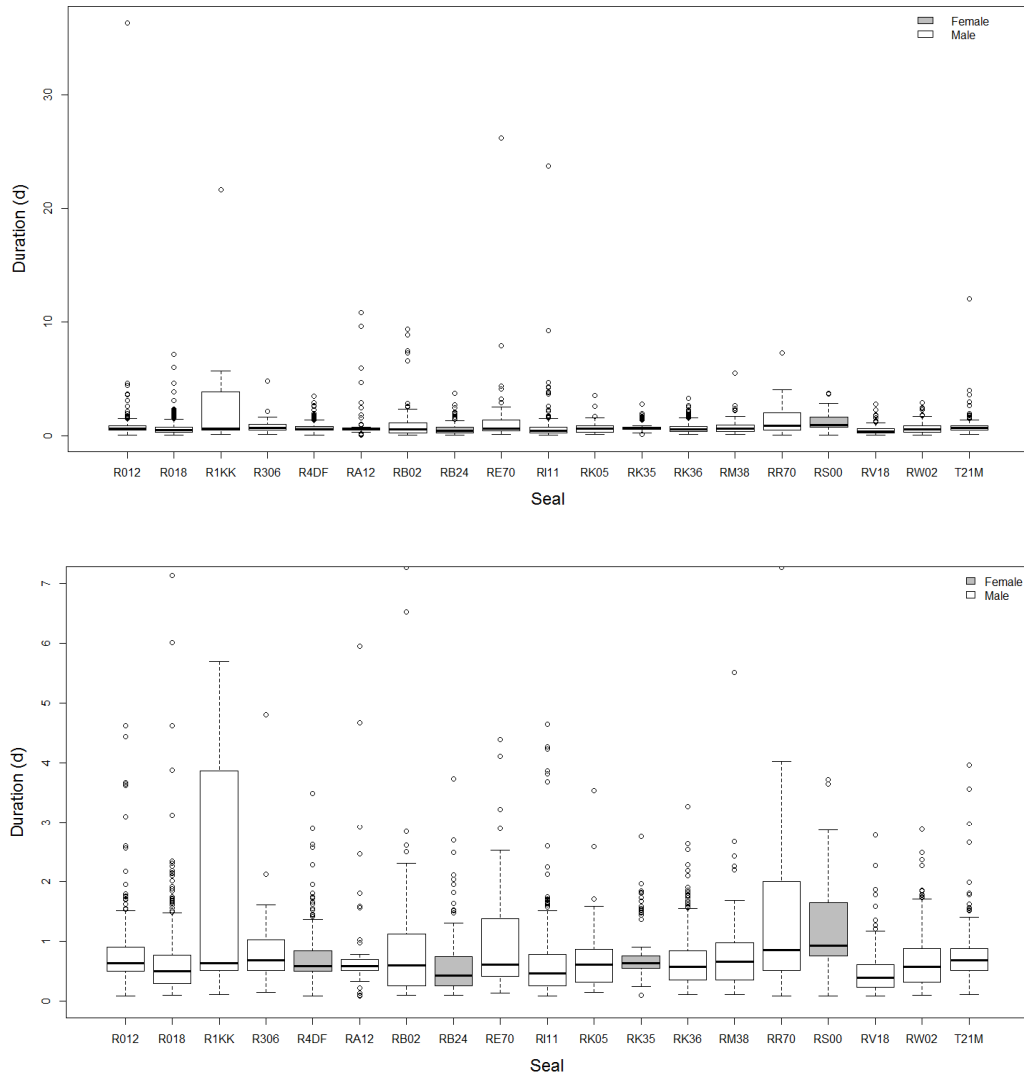
Figure 5: Operating duration of GSM-GPS phone tags deployed on monk seals in the Main Hawaiian Islands



**Figure 6: Variation in the movements of monk seals in the Main Hawaiian Islands. The top panel shows one seal that remained near shore on the island where it was instrumented, the bottom panel shows one seal that traveled throughout the archipelago.**



**Figure 7: Foraging trip distance for monk seals in the Main Hawaiian Islands. The top panel shows all the data, while the bottom panel excludes extreme outliers.**



**Figure 8: Foraging trip duration for monk seals in the Main Hawaiian Islands. The top panel shows all the data, while the bottom panel excludes extreme outliers.**

## Home Ranges

Estimates of home range size varied from 61 to over 35,000 km<sup>2</sup> with most being less than 2,000 km<sup>2</sup> (Table 2). The mean core area size for individual seals was  $956.43 \pm 1,532.80$  km<sup>2</sup>, with a home range size of  $6,132.35 \pm 9,838.08$  km<sup>2</sup>. The large variability in home range size is likely due to three seals that traveled extensively between multiple islands, which skewed the data. The median home range was 1,564.56 km<sup>2</sup> and core area was 265.62 km<sup>2</sup>, which are more representative summary statistics for these data due to the influence of outliers on the mean.

Median trip duration and island provided the most parsimonious fit for predicting both core area and home range sizes. The 36 day foraging trip of R012 likely skewed these data so that individual trip was removed prior to analysis. The Rafferty & Lewis diagnostic suggested that 3,800 iterations were needed to reach convergence for all of the model variables, so after 100,000 iterations I achieved good convergence for all variables. Additionally, the dependence factors (I) for all variables were close to one indicating low autocorrelation between variables and low 'stickiness' in the MCMC algorithm.

**Table 2: Home range and core area sizes for monk seals in the MHI.**

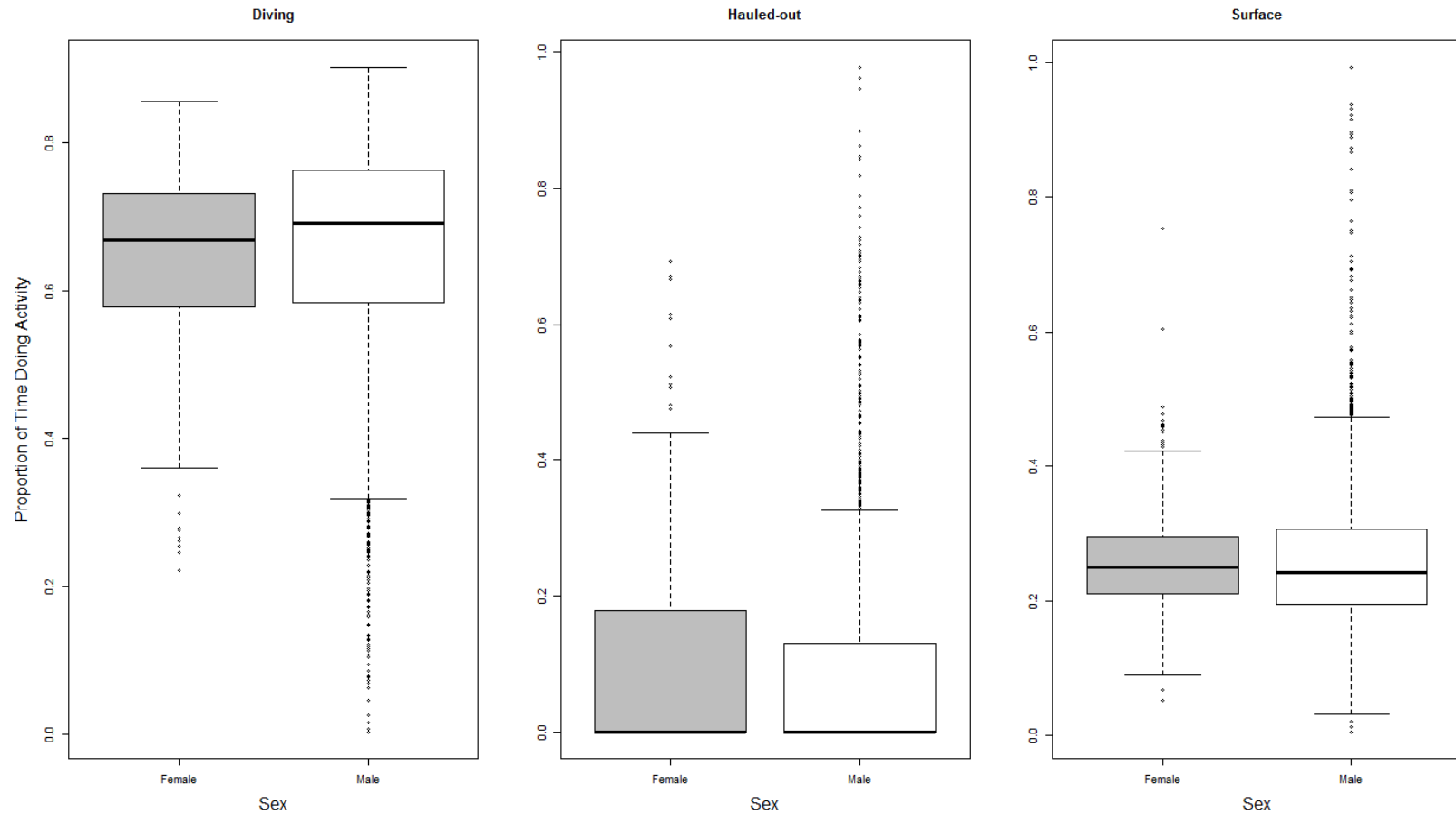
Seal ID	Num. Locations	Island	50% UD Area (km <sup>2</sup> )	95% UD Area (km <sup>2</sup> )
RK35	19803	Kauai	116.26	410.21
RB24	30920	Kauai	184.47	1113.92
RI11	25334	Molokai	138.89	1567.51
RK36	41404	Kauai	1344.91	6596.48
R4DF	23765	Oahu	4664.85	35946.75
R018	36969	Kauai, Oahu	4439.32	23183.14
RE70	15148	Molokai	127.72	1564.56
R012	27436	Oahu	653.99	9690.91
RR70	12175	Oahu	318.99	1906.15
RB02	21980	Molokai	265.62	1427.14
RV18	23630	Kauai	141.98	922.86
RW02	35491	Kauai	60.00	336.02
T21M	16562	Oahu	3810.54	20838.88
RA12	26119	Oahu	958.29	5967.54
RM38	7124	Molokai	162.50	885.60
RS00	29114	Oahu	10.10	61.79
R306	4267	Molokai	145.13	931.89
RK05	8878	Kauai	353.99	1860.60
R1KK	7642	Molokai	274.54	1302.62

Seals tagged on Molokai and Oahu had larger core areas than those tagged on Kauai. Mean core area size on Oahu was  $2,554.3 \pm 788.3$  km<sup>2</sup> larger and on Molokai it was  $222.6 \pm 742.8$  km<sup>2</sup> larger than the mean core area of seals tagged on Kauai. Both the mean and median trip durations significantly influenced the model, but in an effort to use the most parsimonious model, I chose to only include median duration because the AIC value for that model was slightly lower. For every additional day a seal spent at sea (median trip duration), core area size decreased by  $5,455.6 \pm 2,588.4$  km<sup>2</sup>. The same

predictors were used in the model of home range size. As median trip duration increased, home range size decreased by 35,533 km<sup>2</sup>. Similar to the analysis of core area, seals tagged on Molokai and Oahu had larger home ranges (1,787 ± 4,587 km<sup>2</sup> and 17,147 ± 4,868 km<sup>2</sup>, respectively) than those tagged on Kauai.

### **Activity Budgets**

On average, monk seals spent 65.4 % of their day diving, 26.1 % at the surface, and only 8.5 % of the day hauled-out on land. There was no significant difference in the proportion of time spent diving, at the surface, or hauled-out between sexes (Figure 9) or among the islands (Figure 10). There was, however a difference in the mean dive budget for at least two of the months I collected data ( $P = 0.005$ ) (Figure 11). There was also a significant difference in the mean dive budget amongst individuals ( $P < 0.001$ ) (Figure 12).



**Figure 9: General activity budget for Hawaiian monk seals in regards to sex. The budget refers to the proportion of a 24 h period that a seal spent either diving, hauled-out or at the surface.**

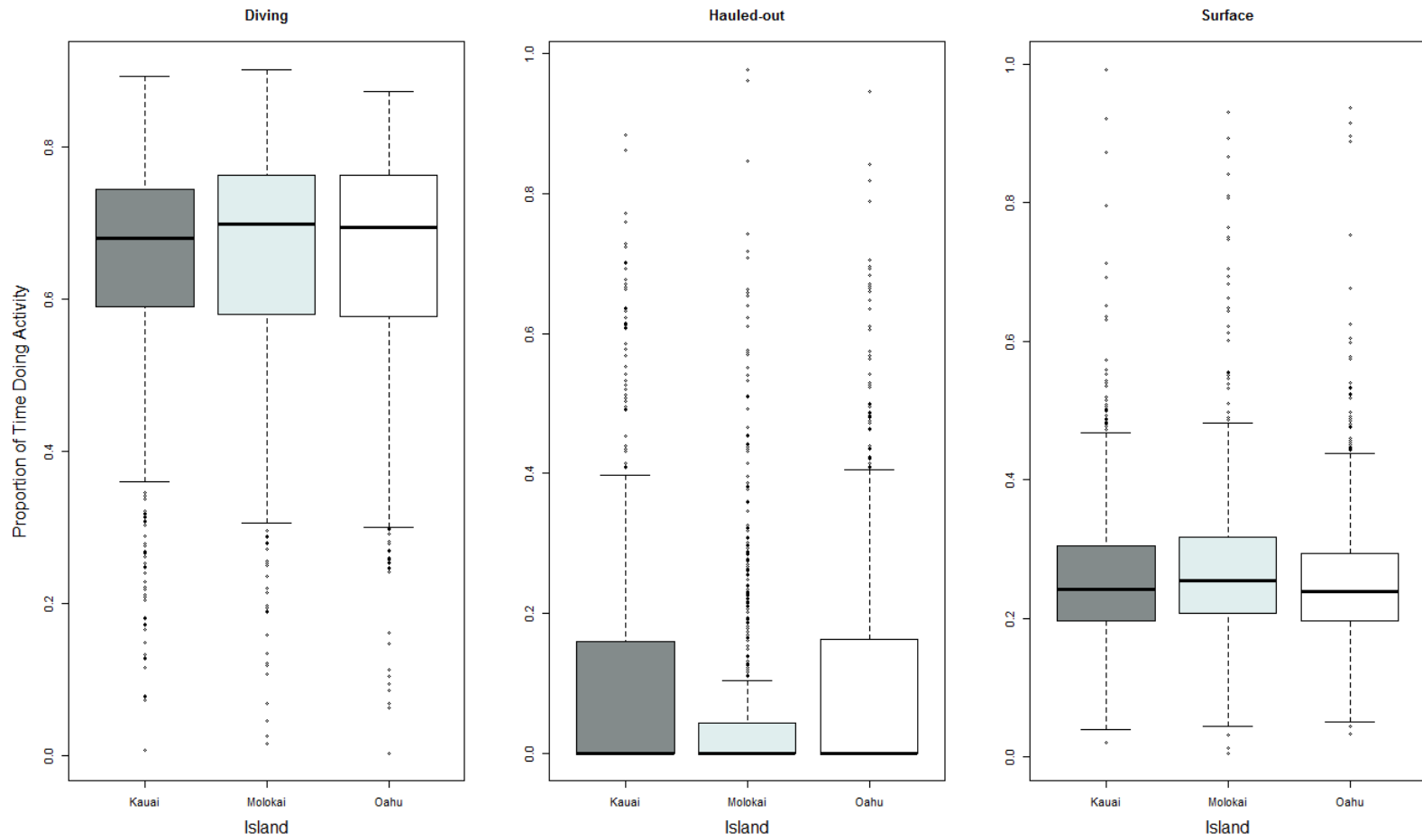


Figure 10: Activity budget for Hawaiian monk seals in regard to the island where the seals were tagged. The budget refers to the proportion of a 24 h period that a seal spent either diving, hauled-out or at the surface.

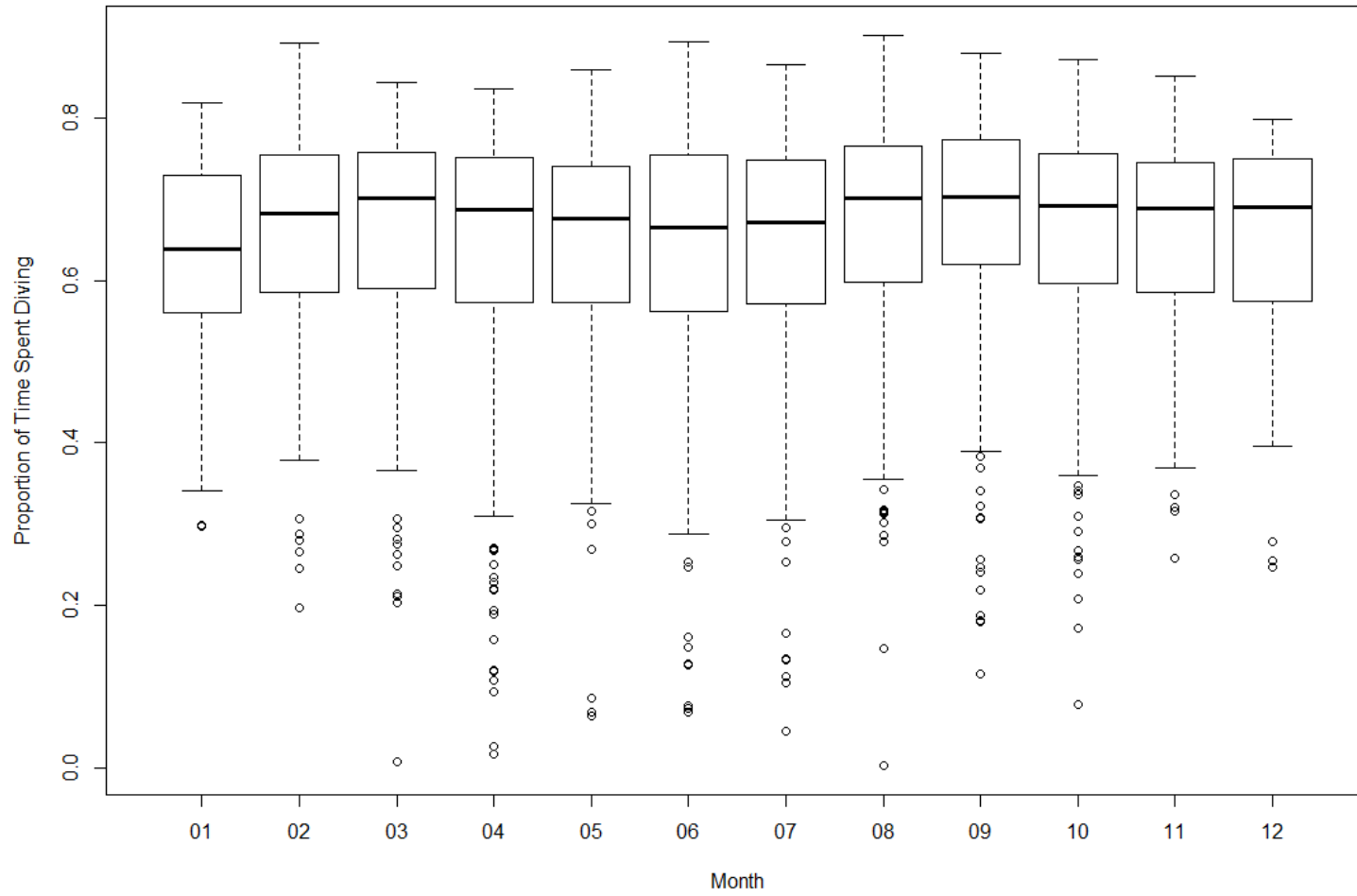


Figure 11: Proportion of time spent diving over a 24 h period for Hawaiian monk seals in regards to the month in which the data was collected.

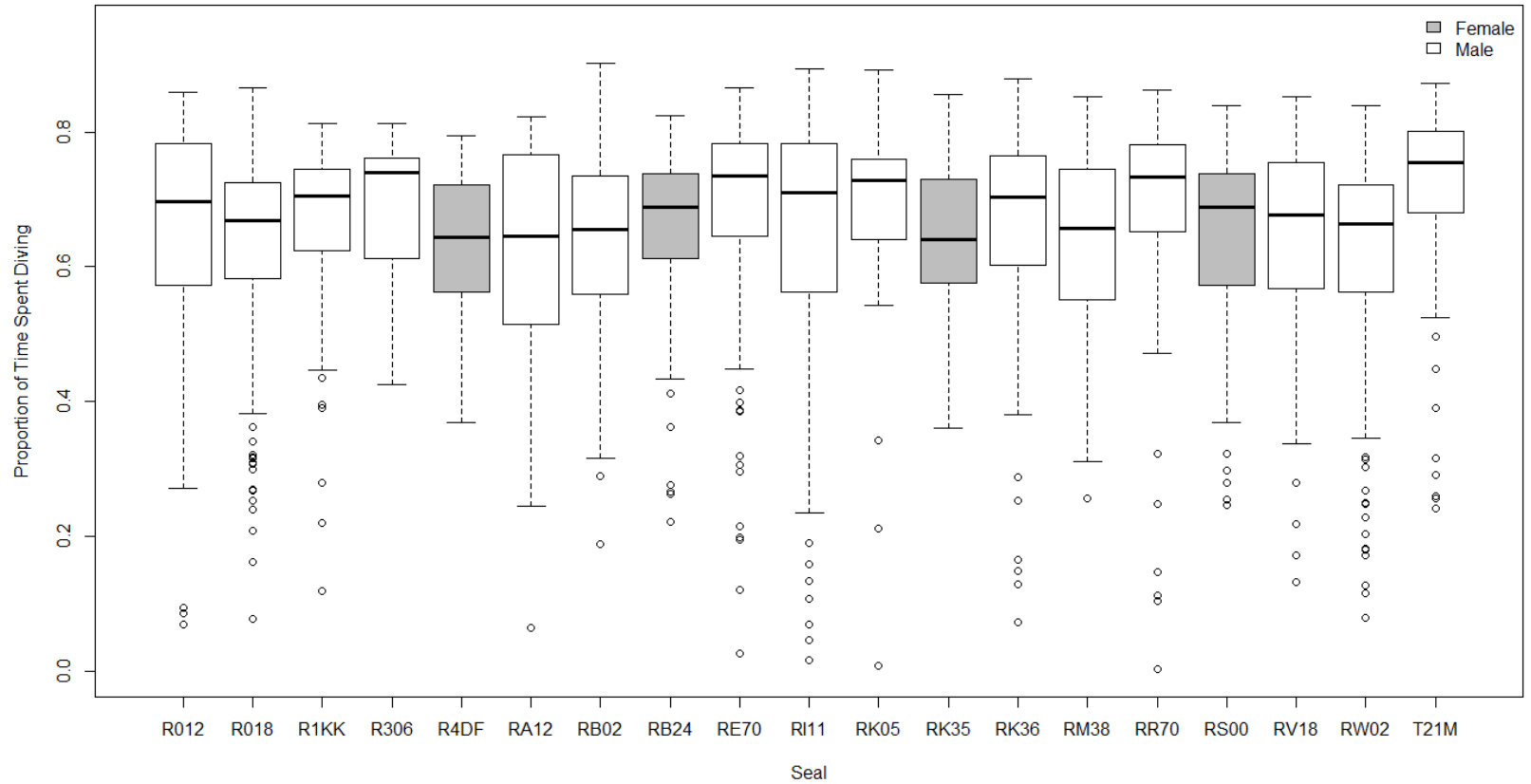


Figure 12: The proportion of time spent diving, over a 24 h period, for individual Hawaiian monk seals in the Main Hawaiian Island

## ***Discussion***

The behavior of Hawaiian monk seals was highly variable, but mean values of metrics describing their foraging behavior were similar across all individuals. The mean and inter-quartile ranges were similar for nearly all metrics of behavior (dive depth, dive duration, and foraging trip distance and duration) for all individuals, but data for nearly every individual contained outliers. This suggests that, while it may be difficult to predict what an individual seal may be doing on a particular day, I can draw broad generalizations of monk seal movements and foraging that describe their behavior over longer periods of time.

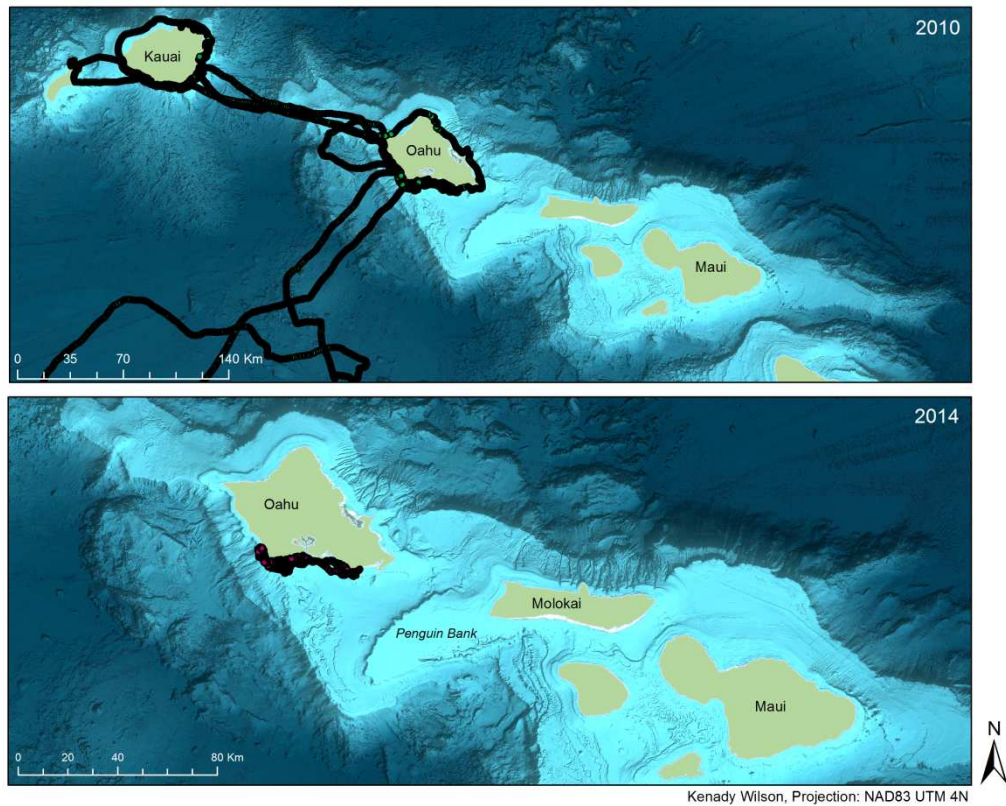
## **Seal Movements**

The only previous study of monk seal movements in the MHI (Cahoon 2011) showed that foraging trips were similar to those found in the NWHI and typically lasted more than 1 day. In contrast, my results show that, on average, seals in the MHI are spending much less time at sea with mean trip durations of  $0.81 \pm 1.28$  d. The difference between my results and those of the previous study could be due, at least in part, to different instruments and methods used for data collection. Cahoon (2011) used a combination of GPS and Argos satellite tags and did not interpolate a movement path, while I used an interpolated path of GPS locations to identify the complete track of a foraging trip. As these are the first two studies to examine foraging behavior for monk seals in the MHI, there has been no comparison of accuracy between the two methods,

but I feel that identifying as much of the animal's path as possible is a more accurate representation of the time spent at sea and the distance traveled. However, this difference should only affect the calculation of foraging trip distance; trip durations should be similar because both studies had similar methods for calculating trip duration (the time between two haul-out periods). I am confident in my methods, but am unable to reconcile the differences between these results and those from Cahoon's (2011) study. The differences are interesting, however, and may imply that the choice of instruments will affect how trip characteristics are calculated and thus complicate meta-analysis in which data were collected using multiple instrument types.

The difference in trip duration between the two studies could also be caused by the seals themselves and how quickly their behaviors may adapt. For example, R012 was instrumented twice, once in 2010 and again in 2014. His 36 day foraging trip out into the open ocean occurred during the first deployment period, which also included trips from Oahu to Kauai and Niihau. During the second deployment, R012 did not leave the southwest shore of Oahu (Figure 13). This dramatic shift in behavior occurred in just four years and while other life history traits, including age and/or dominance status, may have contributed to the change, I must also consider that seals in the MHI are specializing or developing preferred foraging areas over time. While I believe instrumentation plays a key role in the differences observed between Cahoon (2001) and this study, behavioral changes cannot be ignored. Continued monitoring in the MHI is

needed to further develop the baseline of behavior for these individuals and to monitor additional changes over time. Additionally, a re-analysis of Cahoon's (2011) data using interpolation might help to reconcile some of the differences observed between our studies.



**Figure 13: Movements for Hawaiian monk seal R012 from March - August in 2010 (top) and from February – May in 2014 (bottom).**

The large individual component of variation in foraging trip characteristics explains my limited ability to model or predict trip distance or duration. Mean and median values were similar for all individuals, across all islands and sexes, but there

were a large number of outliers for all seals. The data did not violate model assumptions, but the presence of these outliers likely reduced my predictive capability. The means and inter-quartile ranges were similar for all seals, but the existence of the outliers is interesting. Every seal tagged in this study performed foraging trips that were longer in duration or farther in distance than what I considered 'typical'. Could these long trips represent exploratory excursions to assess new potential foraging areas? As the population of seals increases in the MHI, are the less-efficient individuals forced to occasionally stay at sea longer or travel farther in order to find food due to intra-specific competition? Or, are the seals occasionally resting and/or sleeping at sea instead of coming ashore? R307, an adult male seal tagged on Molokai was not seen hauled-out on shore as often as some of the other Molokai residents. Data for this individual were excluded from this analysis because only one haul-out period was recorded, resulting in extremely long foraging trips. In plotting his GPS data in a GIS there appears to be a 'hot spot' of activity less than a kilometer offshore. It is highly likely that R307 returned from foraging trips, but instead of hauling-out on land, rested in the water just off shore. The limited resolution of the data make it difficult to know for certain if he was resting in the water, but he was not seen on land as regularly as the other individuals, and monk seals do sleep underwater (personal observation of Crittercam footage), so this was likely the case. The outliers for other individuals may also represent resting at sea, which could result in accidentally combining multiple 'trips' into one because the seal never hauls-

out on land to rest. As monk seal abundance in the MHI continues to increase, bringing more frequent interactions with humans on resting beaches, this type of behavior may become more common and it will be important to develop a way to distinguish these resting locations from extended foraging trips.

GSM-GPS tags are extremely useful tools for collecting high resolution spatial data with concurrent summary dive characteristics, but they are limited in their ability to collect detailed dive and behavior data. Combining these tags with 3-axis accelerometers or similar instruments would help reconstruct complete dive profiles and aid my understanding of monk seal behavior at sea. This would also increase the types of data I could include as potential predictors of foraging trip characteristics (feeding events, stroke rate etc.). With additional predictors I could develop a better model of monk seal foraging behavior and also gain insight into the effect each predictor has on the duration of time and distance traveled by monk seals in the MHI.

## **Home Ranges**

Kernel smoothing has become the most common empirical method for quantifying animal home ranges and is used for many marine species (Laver and Kelly 2008, Kie et al. 2010). My results revealed that the size of a seal's home range or core area varied depending on the island on which they were tagged. There was variation in foraging location and trip duration, but there were also distinct patterns observed on each island. Seals on Kauai had the smallest core areas and tended to stay near the

island, or travelled occasionally to Niihau and back, but rarely ventured far from shore. There were, of course, exceptions to this rule. One sub-adult female (RB24) tagged on Kauai made a few long foraging trips out to sea (lasting 2-4 days each) and one male instrumented on both Oahu and Kauai often traveled between the islands. Molokai seals also tended to be faithful to their island, but had larger core areas and home ranges than seals from Kauai. This increase in space use is likely due to the proximity of the island to Penguin Bank, a shelf area near the island. All of the seals tagged on Molokai travelled back and forth along the west end of the island and most went on foraging trips out to Penguin Bank. These excursions likely explain the increased space use for Molokai seals. Oahu seals had both the largest and the smallest core areas and home ranges. The smallest home range and core area was exhibited by an adult female (RS00) initially from Midway Atoll which travelled to the MHI in 2000, where she had her first pup in 2001. She is now one of the most successful breeding females in the MHI with a total of 8 pups born since 2001, and is a fixture on the west side of Oahu. For a seal that travelled so far to reach the MHI, I expected her to exhibit a large home range, but during the 5-6 months she was instrumented, she remained in the small area of the island where she was tagged. The largest core area and home range belong to a sub-adult female (R4DF) who traveled from Oahu to the Big Island and back during the deployment period. If R012s 36 day foraging trip had not been removed, he would have had the largest core area and home range.

Mean and median trip duration were the least correlated of the trip summary statistics (correlation = 0.53) and were therefore used in the home range analysis instead of trip distance measures. The fact that median duration provided a slightly better fit to the data suggests that the large number of outliers likely skews the means, making prediction more difficult. Increases in the median trip duration resulted in a decreased core area and home range size, suggesting that if a seal spends an additional day at sea its utilization density does not increase. This decrease in space use may be explained by a combination of monk seal behavior and an artifact of the method I used to calculate home ranges. Most of the seals tagged in this study foraged near the islands, but did not exhibit typical area-restricted search behavior; instead, they either traveled in a single path or 'loop' out to sea and then back to shore, or moved up and down one section of coastline. This loop behavior would not cluster a number of observations into a small region indicating distinct travel and foraging states (area restricted search), but would suggest an increase in core area or home range size with additional time spent at sea. Not all of the seals made these loop trips, but all of them did spend time near shore foraging along the coastline. This type of behavior would cluster observations into the near shore regions, and depending on how much time was spent in that area would increase the density of points near shore. Consequently, this increased density of dives would decrease the core area or home range size as more time was spent at sea. Additionally, as noted above, Hawaiian monk seals do sleep at sea. This behavior may

cluster locations into a small area with very little lateral movement of the seal over multiple hours, decreasing the home range size of the individual. Previous studies have shown the benefits of density estimation for describing and summarizing the space use of animals, but the drawback of this method is in its failure to analyze the underlying determinants of the observed patterns of space use (Moorcroft et al. 2006). I was able to describe monk seal home ranges and space use and explore the effects of some predictors on determining the size of home ranges, but I am still unable to identify the factors that influence development of the home range itself or the drivers of monk seal space-use.

### **Activity Budgets**

Like other pinnipeds, Hawaiian monk seals in the MHI spend most of the day diving, with less than 10% of each day hauled-out on land. Preliminary analysis of dive behavior suggests that monk seals begin performing square-shaped dives along the sea floor as soon as they enter the water. Square-shaped dives typically indicate benthic foraging (Coltman et al. 1997, Baechler et al. 2002) and monk seals are benthic foragers that prefer cryptic prey. The large portion of time spent diving, coupled with the square-shaped dives, may indicate continuous foraging (searching for and consuming prey) while at sea. Other species, including fur seals (*Callorhinus ursinus*) and sea lions (*Zalophus californianus*), also spend a considerable amount of time diving at sea, but typically show some sort of area restricted search. They travel to and from specific

foraging areas and their behavior changes between distinct traveling and foraging time periods. Monk seals, however, do not exhibit this type of foraging strategy. Instead, they continuously search for prey as they move along the sea floor. This may be an artifact of their preferred strategy to target cryptic prey in or under coral rubble or in high relief areas. These types of habitats are dispersed throughout the MHI and likely do not appear to cluster in specific 'hot spots'. If a seal prefers prey that hides in or under rocks, then it is plausible that more time must be spent swimming along the benthos in search of prey or habitats that may contain prey. This increased time spent searching would explain the high proportion of time spent diving and the apparent lack of area restricted search for this species.

The dive budget, the amount of time spent diving in a 24 h period can be interpreted as a metric of foraging effort. The mean dive budgets for all individuals in this study were similar, but there were significant differences between at least two individuals. All of the seals tagged in this study maintained a good body condition throughout the duration of tag deployment. The difference in dive budget suggests that, to maintain good body condition, some individuals may have to spend more time diving than others. With continued monitoring and instrumentation, it would be interesting to see how this effort changes over time and ontogeny for individual animals.

## **Conclusions**

Variability in the movements and foraging of Hawaiian monk seals can be attributed largely to the behavior of individual seals. It is difficult to predict what an individual monk seal will do on any particular day, but it is possible to draw broad generalizations of their behavior in the main Hawaiian Islands. I was unable to predict foraging trip distance or duration, but was able to identify the effects of both island and trip duration on home range size. Seals from Oahu had the largest home ranges, likely due to individuals that moved more often between the islands. Molokai seals had the next largest home ranges, likely due to their proximity to Penguin Bank. The decrease in home range size as trip duration increased suggests that most seals focused their time at sea in the near shore shelf regions resulting in an increased density of location estimates in this area. Excluding Penguin Bank, which is a shelf area that extends farther from shore, the near shore habitats were similar among all the islands suggesting that the variability among the islands may therefore be representative of different foraging strategies among individuals and not necessarily island-specific traits.

The current abundance estimate for monk seals in the MHI is 150 – 200 animals, meaning that I collected data from roughly 10% of the population. The ability to accurately generalize the behavior of this critically endangered population will be important in helping to designate critical habitat and developing management strategies as abundance continues to increase in this region. The MHI population continues to

grow rapidly and has shown a progression of colonization from Niihau eastward over the decades. This pattern is expected to continue with seals beginning to establish themselves in greater numbers on the islands of Maui, Lanai, Kahoolawe, and Hawaii, which currently have very sparse seal populations. Understanding how the topography and ecology of each island affects the behavior and space use of individuals will be key to developing a better understanding of monk seal behavior. My observations help to quantify these island-specific differences and provide an improved baseline of monk seal behavior in the region.

## Chapter 2. Fine-Scale Analysis of Foraging Behavior in Hawaiian Monk Seals

### ***Introduction***

Two-dimensional (2D) classification of dive shapes has been used to group diving behaviors in many marine vertebrates (Schreer and Testa 1995, Wilson et al. 1996, Hochscheid et al. 1999, Baechler et al. 2002). Dive profiles are generally characterized as one of four shapes: square, V, skewed right, and skewed left (Schreer et al. 2001), with behavior inferred from these shapes or some variation on these fundamental patterns. However, it is difficult to infer behaviors from single dives and, at least for some species, foraging behavior is characterized more accurately by examining bouts of diving (Boness et al. 1994, Boyd et al. 1994, Baechler et al. 2002, Lea et al. 2002, Beck et al. 2003, Austin et al. 2006b). Some researchers have used more direct evidence of feeding, such as stomach temperature telemetry (Lesage et al. 1999, Austin et al. 2006a), jaw movement (Liebsch et al. 2007, Ydesen et al. 2014), and video (Bjørge et al. 1995, Davis et al. 2003) to infer the functions of different dive shapes or bout types. These studies were able to demonstrate that certain dive shapes, such as square dives, are commonly associated with foraging activity. Nevertheless, there remains a high degree of uncertainty in the interpretation of 2D dive behavior; especially in species that exhibit considerable inter-individual variation in their diving and those in which dive behavior has not been studied extensively.

Marine mammals live in a three-dimensional (3D) environment so it would seem appropriate to examine their foraging behavior in all three dimensions. Dive classification based on 3D movements is a relatively new technique that can provide a more accurate understanding of the fine scale movements of animals while diving. For example, acoustic tracking techniques have been used to examine the 3D movements of Weddell seals (*Leptonychotes weddellii*), and demonstrated that classification of dive types based on time and depth profiles alone oversimplifies a complex suite of behavior (Harcourt et al. 2000). Acoustic tracking describes movements in greater detail than 2D dive classification, but does not allow classification of behavior or provide inference on the ecological functions of different dive types (Wartzok et al. 1992, Harcourt et al. 2000, Hindell et al. 2002). Three-axis accelerometers measure animal orientation and the dynamics of movement (Yoda et al. 2001, Shepard et al. 2008), enabling researchers to reconstruct three-dimensional diving behavior in free-ranging marine animals (Tsuda et al. 2006, Shepard et al. 2008, Wilson et al. 2008). Acceleration along three axes provides a measure of animal movement in all three spatial dimensions, which, in turn, provides more accurate estimates of acceleration and body motion. This approach has the added benefit of being able to differentiate different types of behavior based on signals in the accelerometer data (Shepard et al. 2008, Wilson et al. 2008). Three-dimensional dive profiles have also been constructed by recording the time, depth, speed, and compass bearing of the animal while diving (Davis et al. 2003, Watwood et al. 2006). A complete

suite of parameters, including compass bearing, time, depth, speed, accelerometry and video recording, allow for the computation of an animal's 3D dive path coupled with direct observations of the functions of each dive (pursuit or capturing prey, exploring, traveling etc.) (Davis et al. 1999, Davis et al. 2003). This combination is, thus far, the only approach that simultaneously records and validates the assigned function of the behavior of an animal while diving.

### **Monk Seal Foraging Ecology**

The first comprehensive study of Hawaiian monk seal foraging ecology in the main Hawaiian Islands (MHI) was completed by Cahoon (2011). In this study, 18 seals were tagged that demonstrated dive depths similar to those in the Northwestern Hawaiian Islands (NWHI). Seals in the MHI foraged primarily in waters shallower than 80 m and within the 200 m bathymetric contour surrounding the islands (on or near the shelf or shelf break). Cahoon (2011) used technology similar to that used in the NWHI, which made for ready comparison with historical data, but left much to be understood in regards to fine-scale resolution and a detailed understanding of foraging behavior in the MHI. In Chapter 1 I described a follow-up study conducted in the MHI using GPS-GSM cell phone tags (Sea Mammal Research Unit, St Andrews, Scotland) in which I demonstrated that foraging trips in the MHI were shorter in both distance traveled and the duration of time spent at sea than observed by either of the previous studies. These data suggested that most of the variability in the movements and foraging of Hawaiian

monk seals could be attributed to variation in the behavior of individual seals. I was able to show that it was possible to draw broad generalizations of monk seal behavior, but that it was difficult to predict the behavior of individual animals. Monk seals spend most of each day at sea and spend less than 10% of each day hauled-out on land. These summaries are helpful in developing a general understanding of monk seal movements and space-use, but do not allow for any fine-scale interpretation of at-sea behavior.

Additionally, in Chapter 1 I showed that monk seals traveled continuously along the sea floor while diving during foraging trips and that individual seals returned to the same general area to forage on multiple trips, but did not follow a typical area restricted search pattern with directed travel to and from a specific foraging area. My observations suggested that seals may be actively searching for food the entire time they are at sea, but without a way to identify dives that contained feeding or feeding attempts, I was unable to separate travel along the sea floor from active foraging.

Recent advances in recording technology and miniaturization of instruments have allowed scientists to attach multiple instruments to a single animal without affecting the long-term survival or behavior of the animal itself (Littnan et al. 2004). These animal-borne instruments are able to document the fine-scale behavior of diving animals through inertial motion sensors, the behavior of both predators and prey through video and, in some cases, aspects of the physical environment such as temperature and habitat (Davis et al. 1999, Bowen et al. 2002, Parrish et al. 2002, Davis et

al. 2003). In the present study I used a combination of GPS telemetry, animal-borne video, and 3D inertial motion sensors to record underwater behavior. I combined these data streams to gain a better understanding of the fine-scale foraging behavior of monk seals in the MHI and to develop a method to identify feeding events. The overall goals of my study were to identify a reliable metric of feeding for Hawaiian monk seals using telemetry instruments and to examine the environmental and behavioral variables that may influence feeding events.

## ***Methods***

### **Instrument Deployment**

Due to the size of the instrument package, only sub-adult and adult seals were captured on Oahu, Molokai, and Kauai (Figure 4) following the methods of Baker and Johanos (2002). I initially targeted both males and females, but due to strict capture guidelines (Baker and Johanos 2002), I was only able to instrument one female during the entire first year of deployments. For the remainder of the study, I targeted only sub-adult and adult males. Seals that met the capture guidelines were captured with a hoop net and then sedated with Diazepam (5mg/ml at 0.1-0.25 mg/kg IV). Weights were visually estimated prior to sedation and biomedical samples including blood and blubber biopsies were taken along with swabs of all orifices prior to instrument attachment. The instrument package included a National Geographic Crittercam, Loggerhead Instruments Open Tag (3-axis accelerometer, magnetometer, gyroscope, and

pressure sensor), a GPS-GSM phone tag, and a VHF transmitter (Table 3). The package was glued to the pelage of the animal, along the dorsal midline between the shoulder blades using 10 min epoxy (Devcon, Danvers MA) (Figure 14). The GPS tags were programmed according to Chapter 1 and the Open Tags recorded continuously on all sensors at 100 Hz until the battery was exhausted (roughly 4-6 days). The Crittercams are capable of storing 8-10 h of video footage. In an effort to observe underwater behavior over the extent of a foraging trip, I programmed the Crittercams to record for 30 min of every 2 h cycle between the hours of 8:00 AM and 5:00 PM (HST), when the camera was wet. Night time recording was attempted, but the infrared lights used by the Crittercams were too dim to allow any visual window beyond the seals' head. Therefore, recordings were made during daylight hours only. Four to six days after deployment, the VHF transmitter and telemetry tags were used find the seals and recover the Crittercam and Open Tag; the GPS-GSM phone tag was left on the animal to collect long-term movement and summary dive data.

## **Data Processing**

I processed the GPS data using methods described in Chapter 1 to identify the date, time, and location of each dive. Only GPS data collected while both the Open Tag and Crittercam were recording are included in the present analysis. Open Tags were not attached to the instrument package in a 'North East Down' position (a geographical coordinate system for representing state vectors) so data for all sensors were rotated

prior to analysis to ensure that the x, y, and z planes were accurate. Open Tag, GPS, and Crittercam records were matched using the date/time stamps for each instrument and further refined by matching data records of the deepest dive in each trip. Crittercam video footage was examined manually to obtain the date/time at the start of each dive, the depth of the dive, the habitat visible to the seal, presence of potential prey, and seal behavior (searching, prey capture/attempted capture, resting, vocalizing, interacting with other seals, or being followed by competitors).

**Table 3: Description of tags deployed on Hawaiian monk seals as part of the instrument package.**

Instrument	Company	Data	Data Recovery Method	Deployment Duration
GSM-GPS phone tag	Sea Mammal Research Unit	Dive depth, duration, and location. Haul-out times and locations.	Transmitted through the GSM cell phone network	3-6 months
Crittercam	National Geographic	Video of prey and time of prey capture attempts and successes	Must be recovered	3-6 days
Open Tag	Loggerhead Instruments	Gyroscope, magnetometer, acceleration, and depth	Must be recovered	3-6 days

Open tag data were downloaded and analyzed using Humu (in development). I used a private beta-version of Humu, which is an online cloud-processing platform for analyzing high resolution accelerometer data. Within Humu, the full dive record was re-

constructed and the following parameters for each dive were described: dive depth and duration, pitch, yaw and roll, average stroke rate, the presence of active search events, proportion of dive spent searching, and bottom time. Monk seals typically target cryptic prey that hide in the sand or under rocks; when seals are searching for these prey they tend to invert their bodies in a head-down position in the water column. In the Crittercam footage I observed, I did not identify any prey captures or attempted captures during a dive that were not also accompanied by an inverted body position. Therefore, I defined an active search or feeding event when the pitch of the animal was between  $70^{\circ}$  and  $90^{\circ}$  at a depth greater than 3 m. This designation was verified within Humu by animating the pitch axis of the accelerometer and viewing the animation with concurrent video footage and by comparing the dives defined as 'feeding' dives within Humu to video footage of the same dive.



**Figure 14: Photo of the instrument package attached to a Hawaiian monk seal**

Environmental variables, including bathymetric depth, distance to shore, measures of bottom complexity, and habitat were assigned to each dive based on GIS

analysis and video observed during the dive. Bottom complexity was composed of four individual variables produced using the Benthic Terrain Mapping program in ArcGIS: slope, terrain ruggedness, and rugosity (Wright et al. 2012). Habitat was assigned by extracting the benthic habitat under each dive start location. The habitat data were taken from NOAA's Center for Coastal Monitoring and Assessment programs "analysis of shallow water benthic habitats of the MHI (2007)" (Battista et al. 2007). Most dives that occurred on Penguin Bank were in 'Unknown' habitat due to the depth and turbidity of the water so habitat for these dives was manually defined as 'Penguin Bank'. Dive characteristics and the above environmental variables were used to predict whether the seal was actively searching for prey on that particular dive. In Chapter 1 I showed that seals do not use diving bouts to forage on a particular prey patch or in a particular area, but that they search continuously for food while at sea. Consequently, dives were not partitioned into bouts and, instead, were analyzed individually.

## **Identifying Search Events**

My goal was to identify feeding events and then examine factors that might influence whether or not those events occurred during a dive. After watching over 40 hours of video footage I realized that pitch could be used to infer feeding and active search events for Hawaiian monk seals. Unfortunately, however, monk seals have a very steep descent at the start of a dive and swim in a near vertical position for the first couple of meters, which would trigger a search event if using pitch alone. To eliminate

the possibility of identifying the start of a dive as a search event, the metric was adjusted to include depth. Therefore, a search event was recorded when the pitch of the animal was between 70° and 90° and the seal was at a depth  $\geq 3\text{m}$ . Crittercam footage was matched to the Open Tag dives by comparing dive start times, surface events, and depth. Initial validation of the metric was done by comparing the pitch axis of the Open Tag data to concurrent video footage. The full pitch record was extracted for at least one dive per seal to validate every predicted search event on that dive (Figure 15). Search data were then summarized and dives were classified as search or not (1, 0). Secondary validation was done by comparing the observed (video) and predicted (from pitch) search dives for all of the dives that were matched to video footage.

## **Model Development**

I used behavioral and environmental variables to predict the occurrence of search events for monk seals. If a search event (with pitch between 70° and 90°) occurred during a dive, it was designated as a searching dive. My goal was to understand where and when seals were foraging and not to measure foraging success, so I did not distinguish between search events and captures. I used a Bayesian Generalized Linear Mixed Model (GLMM) with a binomial sampling distribution to determine which combination of predictors to use in the final model (Gelman et al. 2012). As described in Chapter 1, there was a considerable degree of individual variation in monk seal behavior, so each seal was initially modeled separately before adopting a mixed model.

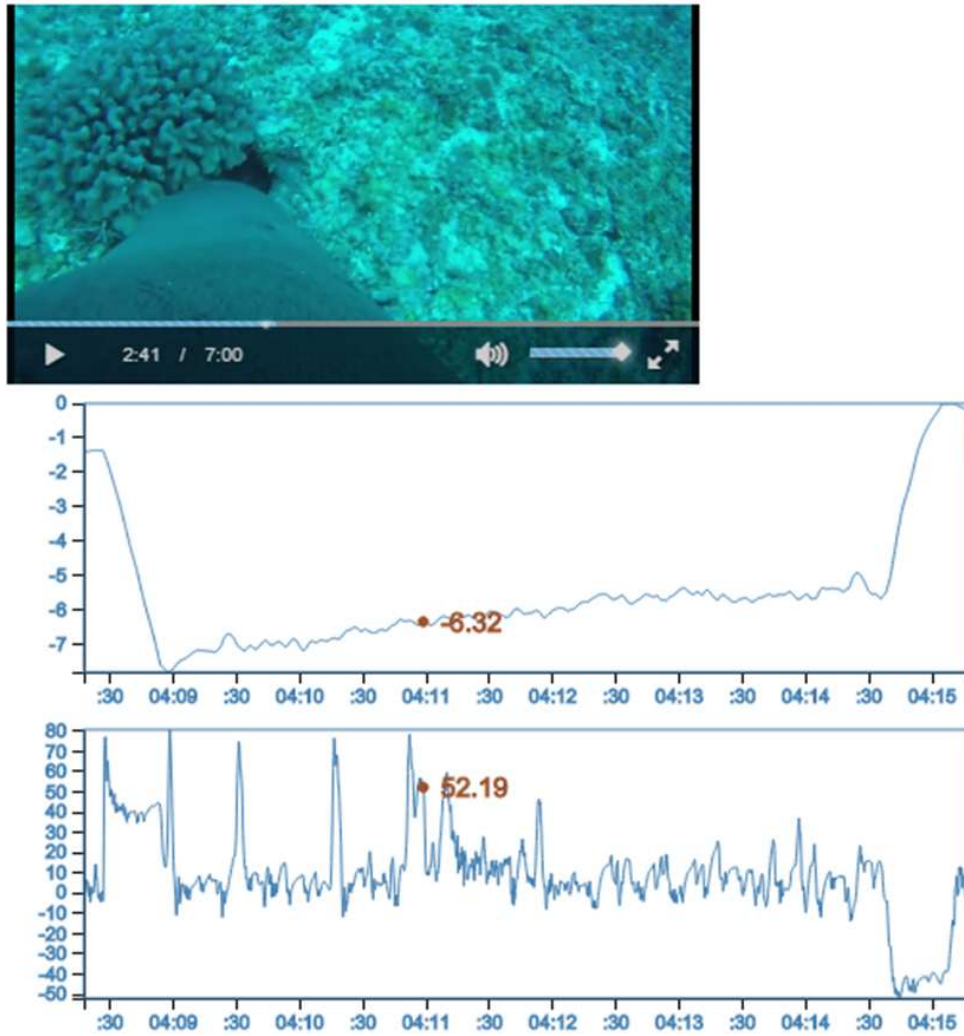


Figure 15: Movement axes from the Open Tag with concurrent video footage highlighting a peak in pitch as the animal searches for prey.

The fixed effects in the global models were: maximum dive depth; dive duration; stroke rate; overall dynamic body acceleration (ODBA); proportion of time spent at the bottom of the dive (bottom%); available bathymetric depth; the ratio of dive to available depth (dive ratio); distance to shore; bathymetric slope; terrain ruggedness, surface area to planar area (rugosity); and the habitat structure where the dive occurred (pavement, sand, aggregate reef, rock, boulder, pavement with channels etc.). For descriptions of the habitat structure see Battista et al. (2007). The standard deviation of the y-axis of the gyroscope was used to infer the stroke rate over the course of the dive, and bottom time was defined as the amount of time spent > 80% of the maximum depth of the dive. Variables were selected by comparing AIC, BIC, null and residual deviance values for a suite of models and the most parsimonious model with the lowest values was chosen as the best fit. The final models for all individual seals included some measure of depth (dive or bathymetry), duration, and movement (ODBA or stroke rate). This similarity suggested that a mixed model would be sufficient to account for the variation among individual seals. The data were then compiled and model selection was done again, using all of the previous variables. The chosen variables were then included in a final design matrix (X) with seal as a random effect. I used a Gibbs sampler to model the data using a binomial likelihood and uninformative priors on the predictors. The model structure was:

$$y_i \sim \text{Bernoulli}(\theta_i) \quad (1)$$

With an inverse link function to map the parameters:

$$\text{logit}(\theta_i) = X_i\beta + \alpha_j[\text{seal}_i] \quad (2)$$

$Y_i$  is the response variable representing whether or not a search was identified on a dive.

$\theta_i$  is the odds associated with a search event on dive  $i$ ,  $X$  is the design matrix of predictor variables,  $\beta$  are the coefficients associated with each fixed predictor, and  $\alpha_j$  is a vector of coefficients associated with the random effect (seal). The priors on  $\beta$ ,  $\alpha$  were normal distributions with starting values specified as:

$$\beta \sim \text{Normal}(\mu_\beta, \varphi_\beta) \quad (3)$$

$$\alpha_j \sim \text{Normal}(\mu_\alpha, \varphi_\alpha) \quad (4)$$

$$\mu_{\beta,\alpha} \sim \text{Normal}(0,0.001) \quad (5)$$

$$\varphi_{\beta,\alpha} = \frac{1}{\sigma_{\beta,\alpha}^2} \quad (6)$$

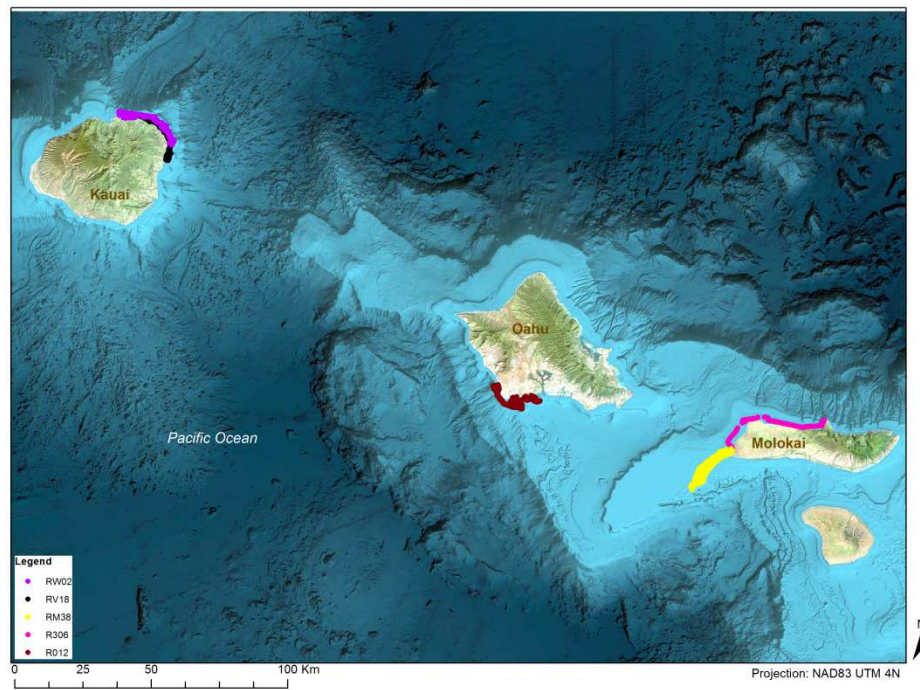
$$\sigma_{\beta,\alpha} \sim \text{Uniform}(0,10) \quad (7)$$

I let JAGS initialize the parameters and allowed the model to adapt during the initial sampling period. Gelman and Geweke diagnostics were used to assess convergence and stationarity in the chains (Plummer et al. 2006). All analyses were performed in R version 3.0.2, JAGS version 3.4.0, and Arc GIS version 10.2.

## **Results**

Sixteen instrument packages were deployed on monk seals between 2012 and 2014 with one adult male instrumented twice. I recovered data from all instruments (GPS, video, and Open Tag) for 6 of the 16 packages (5 males and 1 female). I recovered

Open tag data without concurrent Crittercam and GPS footage for one animal. Due to issues with depth sensor calibration and/or malfunction only six seals were included in the analysis (five with all data streams and one with just Open Tag data). Tracking duration ranged from 2 - 5 days, covering at least two foraging trips for each seal (Figure 16). Mean dive depth was  $18.03 \pm 16.99$  m with search events occurring, on average, at  $20.80 \pm 14.49$  m. An average of  $482.83 \pm 105.29$  dives were recorded per seal with an average of  $251.83 \pm 169.27$  search events detected per animal, so roughly half of the dives recorded in this study contained search events (Table 4).



**Figure 16: Movement paths of Hawaiian monk seals with concurrent Open Tag and Crittercam footage**

**Table 4: Tracking duration and mean summary data for Hawaiian monk seals equipped with an Open Tag and Crittercam**

SealID	Island	# dives	# trips	# days	Dive depth (m)	Dive duration	Bottom Time	Bathymetric Depth (m)
R012	Oahu	524	3	6	24.76 ± 13.96	6.93 ± 3.10	76.4%	62.78
RA50	Oahu	502		7	16.49 ± 15.71	4.3 ± 2.9	58.4%	NA
RV18	Kauai	575	8	6	7.6 ± 5.10	3.57 ± 2.59	54.9%	6.11
RW02	Kauai	554	5	2	11.23 ± 9.03	3.84 ± 2.36	56.5%	31.09
RM38	Molokai	457	17	5	25.24 ± 25.36	6.95 ± 3.35	72.8%	38.71
R306	Molokai	372	4	3	32.93 ± 17.32	5.54 ± 1.49	66.1%	14.22

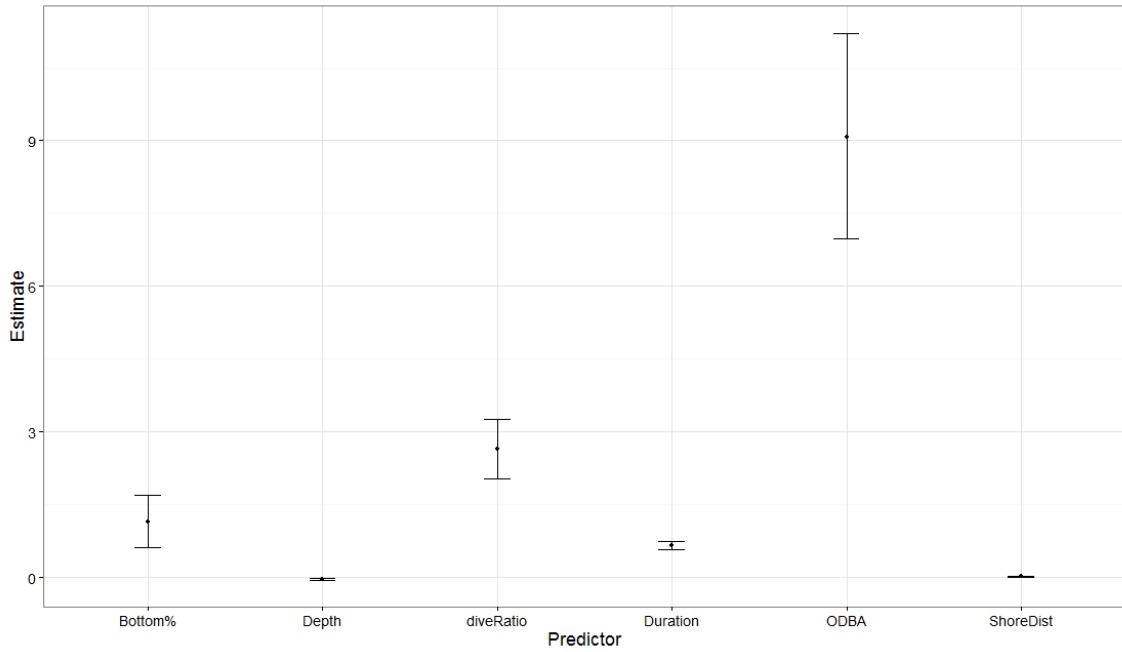
### Identifying Search Events

Within Humu, 3,138 dives were identified for the six seals. Of those seals, five had concurrent video footage, but the time stamps for one Crittercam malfunctioned so video matching was only possible for four of the seals. The Open Tag recorded on all sensors, continuously, until the battery died; the Crittercam recorded for 30 min of every 2 hr period, during daylight hours only. Ninety three dives (3%) were matched to concurrent Crittercam footage to validate the pitch metric. Two of the seals had almost perfect prediction with only one false positive prediction each. The other two seals had a large number of false negatives, but no false positives. Overall, the combination of pitch and depth was 78% successful at predicting search events for monk seals.

## Model Selection

Initially I used simulated data to verify model structure. Due to uncertainty about where to initialize the priors, the sampler was run multiple times to test for acceptable convergence. The final model was run using the entire dataset, initialized at the mean values from the previous run, and then run for 7,500 iterations with a burnin of 2,000. Convergence was confirmed visually and by using Gelman and Geweke diagnostics.

As noted above, each seal was initially modeled separately to ascertain the effect of each predictor without the confounding influence of individual seals. None of the individual models were identical in regards to predictors, but inference of the results was similar for all of the seals. For example, monk seals perform benthic dives almost exclusively, so depth was an important predictor of search events. In the models, depth, as related to foraging, was represented in two ways: via dive depth, or the combination of bathymetry and dive ratio (dive depth/bathymetry). Both metrics of depth represent the physical depth of the seal when search events occurred. In a similar vein, ODBA and stroke rate are both measures of body motion and were essentially interchangeable in the individual models. In general, the individual models for all seals included some measure of depth, duration, and motion as the best predictors of search events. None of the individual models retained any of the habitat variables.



**Figure 17: Coefficient estimates for the fixed effects used to model search events for Hawaiian monk seals.**

Variable selection in the mixed model supported the results of the individual models and excluded redundant variables, but also kept a number of the habitat variables. The final model included dive duration, mean ODBA, bathymetry, dive ratio, bottom %, and distance to shore. Seal was included as a random effect. None of the HPD intervals spanned zero indicating that all of the predictors significantly influenced search events for male Hawaiian monk seals (Figure 17). The coefficient estimates (Table 5) from the model output were used to estimate the probability of a search event occurring on a dive:

$$P(Y = 1|x) = \frac{e^{x\beta}}{1+e^{x\beta}} \quad (7)$$

Where;

$$\theta = \alpha[\text{seal}_j] + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_6 X_6 \quad (8)$$

Generally, the probability of a search event increased as dive duration, depth, and ODBA increased and when seals performed benthic, square-shaped dives.

Monk seals rarely pursue prey in the water column and, instead, prefer cryptic prey that hides in rocks or in the substrate. Therefore, I expected that some measure of rugosity or benthic complexity would be a good predictor of search events; however, none of the individual or mixed models included these variables. Similarly, habitat type was also excluded. Measures of bathymetry, dive ratio, and aspect were included in the mixed model, but the other measures of rugosity and bottom complexity were not. Light (whether it was day or night) was not a good predictor of feeding for any of the seals although, on average, 70% of all dives occurred during daylight hours.

**Table 5: Estimated coefficients for the fixed effects and corresponding interpretation.**

Covariate	$\beta$ estimate	S.E.	Explanation
Bathymetry	-0.038	0.007	Probability of searching increases at deeper depths
Shore Distance	0.016	0.0053	Probability of searching increases farther off shore
Dive Duration	0.66	0.041	Longer dives increase the probability of searching
ODBA	9.077	1.08	More body motion during a dive increases the probability of searching
Dive Ratio	2.65	0.31	Maximum depths closer to the sea floor increase the probability of searching.
Bottom %	1.15	0.28	Increased time at the bottom of the dive increase the probability of searching.

GPS data were not recovered for RA50, a sub-adult tagged on Oahu, so this animal was not included in the mixed model and was modeled separately. The results for this seal were similar to those of the mixed model, but without the predictors that required location information (bathymetry, dive ratio etc.). Search events occurred more frequently on deeper and longer dives. Stroke rate was not a significant predictor of search events for this animal, but including it in the model helped account for more of the residual deviance. Model output suggested that increasing stroke rate for this seal increased the probability of searching.

## ***Discussion***

Combining high-resolution behavior data with environmental variables provided insight into the fine-scale foraging behavior of monk seals in the MHI. The strongest predictors of foraging events in the mixed model were ODBA and dive ratio. In the individual models, maximum dive depth, dive duration, bottom time, and stroke rate were the most influential. Generally, the probability of searching increased on long, deep dives, with more time at the bottom and with increased stroke rate. Active search events seldom occurred near shore, in shallow water, or during short dives in which the seal did not reach the bottom. In general, few of the environmental variables, including habitat structure, rugosity, and slope, predicted monk seal search events, but depth, aspect, and dive ratio were useful parameters.

Many of these variables have been used to predict underwater behavior in a number of pinniped species including harbor seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*). However, they are most often used to aid in dive classification, which is then used to infer behavior (Frost et al. 2001, Lea et al. 2002, Austin et al. 2006b, Shepard et al. 2008, McIntyre et al. 2012). The collection of multiple high resolution and simultaneous data streams allowed direct visualization of the underwater behavior of monk seals. It quickly became apparent that these seals had one main dive type (square-shaped and benthic) and that statistical dive classification was unnecessary. My goal was to identify search events and then examine factors that might influence whether or not those events occurred during a dive. Using pitch to identify searching allowed me to classify dives as foraging or not-foraging without using traditional classification methods. There was still error associated with the prediction of searches, but I am more confident with this direct approach than with a statistical classification because I was able to validate a subset of the data and quantify the success of the approach. Additionally, because square-shaped, benthic dives dominate monk seal diving behavior, it is nearly impossible to separate dive types using statistical dive classification such as k-means. By using pitch instead of dive characteristics to classify dives, I was also able to investigate how behavioral and environmental variables influenced the probability of a search event instead of using behavior to classify the dives and thus being limited to environmental variables as predictors.

The pitch metric was not perfect, however, and I did identify a number of false negative search events for two of the seals. False negative prediction results in underestimation of search behavior for those individuals and thus this approach may be overly conservative. With > 75% prediction accuracy for this metric, I am confident that the overall effect of each predictor would remain the same even if the false negatives were removed. Additionally, I believe the false negatives were the result of issues with instrument placement and not the metric itself. The metric identifies a search event when the pitch axis of the accelerometer peaks above 70°. If the Open Tag was placed backwards on the seal, then the algorithm would need to be changed to identify a search event at -70°. Without visual confirmation of the direction of the tag, I had to manually go through and adjust the values if the data did not align correctly. The metric would also be faulty if the Open Tag was attached to the instrument package at an angle. With correct placement and known orientation of the Open Tag, I believe the number of false negatives would decrease dramatically and the accuracy of this metric would increase.

## **Depth**

Both dive depth and bathymetric depth were good predictors of search events for monk seals in the MHI. It is interesting to note that dive depth was included in models for four of the six individual models and that bathymetric depth was used for one seal but was and not included in the previous four. In the mixed model, dive depth was excluded and bathymetric depth was retained as the best representative of depth for

all the individuals. Crittercam footage has revealed that monk seals swim near the bottom almost exclusively while at sea (Parrish et al. 2005, Parrish et al. 2008). Thus, these two depth variables are functionally redundant and it makes sense that one or the other was included, but not both. Additionally, dive ratio (the ratio of dive depth to bathymetric depth) was included only for models of seals that included bathymetry as a predictor (including the mixed model). By combining dive ratio with bathymetric depth, I essentially used the same metric as dive depth, but was able to account for more variation in the data. The probability of a search event decreased as dives became shallower.

## **Duration**

Dive duration is a common metric used to classify and analyze foraging behavior in a number of diving predators (Coltman et al. 1997, Lesage et al. 1999, Costa and Gales 2000, Baechler et al. 2002, Austin et al. 2006b). As dive duration increased, the probability of a search event also increased. Monk seals swam in a near-vertical orientation as they descended to the seafloor, with little horizontal movement in the descent and ascent phases of the dive. Therefore, very little time was spent diving and not searching/traveling along the sea floor where prey might be encountered. This strategy not only increases the likelihood that a seal will encounter potential foraging habitat, but also increases the amount of time a seal can spend traveling along the sea floor looking for prey. Consequently, an increase in dive duration should also result in

an increase in bottom time. For the two seals for which dive duration was not included in the model, bottom time was included as a predictor of search events. Due to the dive strategy employed by monk seals, these predictors essentially produce the same result and all of the seals had one or both of these predictors in the final model. Thus, longer dives would expose seals to more potential prey and the probability of searching and/or feeding would increase.

### **Proportion of the Dive Spent Foraging**

I considered foraging behavior to include both searching for and consuming prey. Crittercam footage and analysis of dive data revealed that most dives performed by male Hawaiian monk seals would be considered foraging dives. The proportion of time that a seal spends at the 'bottom' of a dive (bottom %) has long been considered a metric of 'foraging effort' (Austin et al. 2006b). This variable measures the amount of time (effort) a seal expends in the search for potential prey. The more time a seal spends at the bottom of a dive the more likely it is to encounter prey. Consequently, bottom % was a good predictor of active search events. Predictably, an increase in effort resulted in an increased probability of a search event.

### **Body Motion**

Gyroscopes measure the rotational velocity of an object in three dimensions. When a monk seal swims, it strokes its hind flippers in a semi-circular, rotational manner, with concurrent movement of the head that is apparent on the Crittercam. The

standard deviation of this rotational velocity in the horizontal axis was, therefore, a good indicator of stroke rate over the course of a dive. Initially, stroke rate was included as an indirect measure of speed. If the overall stroke rate was lower, the seal was likely swimming more slowly along the bottom and was more likely to encounter prey or areas to investigate for prey. This would suggest that an increase in stroke rate (faster movement along the bottom) should decrease the probability of a search event. However, for all the seals for which stroke rate was a significant predictor, the effect was the opposite. As stroke rate increased, the probability of a search event on that dive also increased. This may seem counter-intuitive, but validation using the Crittercam footage helped explain the result. When a seal stopped to search for potential prey (inverted body position) and did not find a prey item, the movement was very smooth and the seal quickly continued along its path. However, if the seal attacked a potential prey item or expended effort into searching at that location, it increased the stroke rate and made changes in orientation to maintain a body position capable of grasping and removing the prey from its hiding place. This increase in stroking during prey capture attempts helps to explain why the probability of a search event increased with an overall increase in stroke rate and suggests that body motion is a better indicator of prey capture than speed. As an alternative to stroke rate, acceleration can be used as a proxy for speed in some instances, but it is often difficult to tease out the effect of gravity on the resulting calculations and, at least for monk seals, stroke rate is not the way to accomplish this

type of inference. More work is needed to develop a reliable estimate of speed from accelerometers before the results can be applied in this type of scenario.

ODBA is often used as a link to energy expenditure in animals fitted with accelerometers (Wilson et al. 2008, Gleiss et al. 2011, Halsey et al. 2011, Qasem et al. 2012), but it is also a metric of an animals' overall body movement. I used the mean ODBA over the course of a dive as a potential predictor of foraging behavior, assuming that increased energy expenditure would be linked to an increased probability of active search events over the course of a dive. As noted above, stroke rate increases during prey capture attempts, so there is movement in all three axes. These events are visible in just one axis (pitch, Figure 3), but ODBA is capable of measuring this change in all dimensions. When a seal is attempting to capture or is handling prey, ODBA increases with stroke rate. These two variables were highly correlated (0.816). Consequently, one or the other predictor was included in all of the models. In this application ODBA, like stroke rate, is a better indicator of total body motion and capture events than as a metric of energy expenditure and actually had the strongest influence on the probability of a search event.

### **Time of Day**

Light was not a good predictor for any of the seals. I expected to see some diel pattern for individuals and observed that most (70%) of the dives occurred during daylight hours (between 0800 and 1800). However, the fact that light was not a good

predictor of search events, although a significant proportion of dives occurred during the day, suggests that there are a number of reasons why a seal may leave the beach, including disturbance or thermal regulation, which are not directly related to foraging or an increased likelihood of searching for prey.

## **Habitat**

In the Crittercam footage I observed seals digging in the sand or turning over rocks and coral heads to find cryptic prey, so some level of benthic rugosity or sand is necessary for them to find prey. However, the probability of foraging success may decrease if the habitat is too complex and the seal has no way to find or capture the prey, for example, within a complex reef habitat. Near-shore habitats in the vicinity of tagging locations generally included 'pavement' or 'aggregate reef'. 'Pavement is defined as flat, low-relief, solid carbonate rock with coverage of macroalgae, hard coral, zoanthids, and other sessile invertebrates that are dense enough to begin to obscure the underlying surface' (Battista et al. 2007). This type of substrate is likely too dense for prey to burrow into, and lacks relief such as large coral heads for prey to hide in or under. 'Aggregate Reef is defined as an area of high relief that lacks sand channels of spur and groove' (Battista et al. 2007). This habitat would provide more hiding places for potential prey, but the complexity of the habitat may require too much effort for the location and capture of prey to make it worthwhile for monk seals. Therefore, neither of these habitats are ideal for monk seal foraging and perhaps explains why search events and

feeding occurred farther offshore, in deeper waters. The benthic habitat classes used in this study were derived from Lidar data, which limits the classification to water depths  $\leq$  30 m. This type of data is also limited in its fine-scale classification. Most of the dives in this study occurred on 'pavement', a habitat classification that does not appear conducive to monk seal foraging. Monk seals likely forage on 'pavement', but without a way to sub-classify this substrate to identify areas with higher relief or coral heads where prey can hide, it is less-useful in the prediction of monk seal search events. Habitat structure was not a significant predictor in the models, likely because the seals foraged within only one or two of the structure types during this study.

### **R306**

R306 is an adult male seal tagged on Molokai. He made multiple foraging trips during the study, but none to Penguin Bank. As described in Chapter 1, every other seal I instrumented on Molokai ( $n = 7$ ) made trips to the Bank. Most animals tagged on Molokai spend most of their time foraging on the Bank, but this seal preferred to stay closer to shore, moving around the west and north ends of the island. R306 captured several types of prey including snapper (*Lutjanidae spp.*) and unicorn fish (*Naso brevirostris*) so this near shore behavior included foraging activity. He also had the simplest individual model, which included only bottom time and stroke rate as predictors. Strikingly, bottom time had the opposite effect on predicting a search event than for all the other seals. The probability of searching decreased as bottom time

increased. In addition, this model included no measure of depth. All models for the other seals included some measure of depth to predict search events. R306 remained near shore, within a narrow depth range (less than 60 m), for the duration of the study. Thus, depth was likely not a good predictor of foraging behavior for this seal because there simply was not sufficient variation in this parameter to affect the likelihood of a search event.

These results, when combined with the overall movements of the animal, suggest that R306 pursued a foraging strategy that differed from the other seals instrumented in this study. Penguin Bank is a relatively large area with fewer than 30 seals known to forage there regularly. Seals that forage on the Bank are usually Molokai residents for at least part of the year. R306 is considered a Molokai seal, but exhibited a different foraging strategy than the other seals from the island. Over the course of the entire tracking duration with the GPS tag (2 months), only 5.9% of his foraging trips were made to Penguin Bank compared to 79% for RM38, another male seal tagged on Molokai and tracked for over 4 months. R306 preferred to forage near shore and rarely ventured to the Bank where most of the other seals forage. This behavior has been observed in one other monk seal. RE70, an adult male from Molokai, was instrumented twice with a GPS phone tag, once in 2011 and then again in 2014. In 2011, he had very similar foraging patterns to R306 and rarely ventured onto Penguin Bank. However, in 2014, RE70 made significantly more trips onto the Bank and actually ventured to Oahu

on one trip. During the second deployment, RE70 did not spend a lot of time along the north shore of the island like he did in 2011; all near shore foraging was focused around the south west corner of the island, closest to Penguin Bank. It is interesting to note that the tracking period for RE70 in 2011 was very similar to that of R306 in this study (March – May vs February – May), and that the tracking period in 2014 was much longer (January – May). While more long-term tracking must occur in order to fully understand these results, the data suggest that R306 was implementing a different foraging strategy than the other Molokai seals, and based on the Crittercam footage, appears to be very successful. These different strategies may suggest some level of diversification of foraging behavior or a partitioning of foraging habitat for monk seals in the MHI, or at least on the island of Molokai. Conversely, it could also suggest some seasonal variation in the foraging patterns of Molokai seals. Both R306 and RE70 foraged near shore and on the north and west ends of the island during the early spring, but RE70 showed different behavior when instrumented during the winter months. This change could represent inter-annual variation similar to that described for R012 in Chapter 1, or an underlying seasonal influence on the foraging behavior of monk seals. There are no known seasonal increases of prey species for monk seals, so what could drive this seasonal change is unknown. It is more likely that different foraging strategies are emerging for monk seals in the MHI, but until more long-term monitoring data is collected, and more seals are

instrumented from the same island in the same year, it will be difficult to quantify the different strategies or determine the drivers behind the diversification.

## **Conclusions**

In summary, adult male Hawaiian monk seals in the MHI were more likely to search for prey on longer dives in which they exhibited an increase in body motion. Five of the six seals searched for prey primarily in deeper waters farther offshore, but one animal employed a different foraging strategy. The probability of a search event for the five similar seals could be predicted with some measure of dive depth, dive duration, and body motion. The remaining seal (R306) employed a different foraging strategy for which depth was not a predictor of search events.

Diversity in foraging behavior within a population should increase as food becomes limiting. Tinker et al. (2008) defined two processes through which this is manifested in the wild. The within-individual diversity hypothesis (WIDH) assumes that individuals within a population respond to changes in prey availability in similar ways; and the among-individual diversity hypothesis (AIDH) suggests that increased dietary diversity occurs via individual diversification. For California sea otters (*Enhydra lutris*), dietary diversity between locations of low and high prey abundance was more consistent with the AIDH. In California sea otters, when resource availability decreased, dietary diversity increased as predicted, driven principally by increasing variation among individuals. It has been suggested that the MHI were originally part of the range

of monk seals before they were extirpated, with a remnant population restricted to the NWHI (Baker and Johanos 2004). Increased survival and fecundity rates, better body condition, and decreased competition in seals that are now re-colonizing the MHI all support this hypothesis (Baker et al. 2011). Under this scenario, one would assume that prey abundance is not (yet) limiting in the MHI, so the foraging behavior of the population would be similar among individuals. My results suggest that either diversification of foraging behavior has already begun for some individuals, or that the baseline level of individual variation in foraging behavior is quite high. It is possible that the differences observed for R306 could be caused by social or territorial behavior rather than mediated by foraging preferences, but it is difficult to identify the driver without a better understanding of the social structure of monk seals in the region, or without extensive and simultaneous instrument deployments for seals in overlapping areas.

## **Future Directions**

The overarching goal of the present study was to identify a reliable metric of feeding for Hawaiian monk seals. Due to their benthic foraging strategy and preference for cryptic prey, the pitch axis of the accelerometer was an ideal indicator of when monk seals were actively searching for or consuming prey. The next steps in this approach are best illustrated by analysis of data from seal RA50. Due to camera and GPS tag malfunctions, I was unable to recover any video or location data for this animal, but I was able to obtain multiple days of Open Tag data. This allowed me to test whether data

from an Open Tag alone would provide similar insight to that obtained from animals from which I obtained the full suite of data. After watching the Crittercam footage for all of the other seals I was confident that pitch was a reliable metric of search events and that this could be applied to an animal without concurrent video. Additionally, the lack of GPS locations only excluded two variables from the model for RA50, which were present for the other seals: bathymetry and dive ratio. As mentioned above, dive depth was a good predictor when both bathymetry and dive ratio were excluded so the dive depth recovered from the open tag could serve as a substitute for bathymetry and dive ratio. In summary, analyzing the foraging behavior of individual adult male Hawaiian monk seals in the MHI could be performed with just the Open Tag.

I programmed the Open tag to record at 100Hz, but search events could be identified using a much lower sampling rate, which would also allow for a longer deployment period. Sampling at 100 Hz allowed for 4 -6 days of data collection before the battery died. Search events were also identified after thinning the data to 50 Hz. If the sampling rate were cut in half, or even to 25 Hz, the deployment duration could increase from less than 1 week to at least 2 weeks. Additionally, other studies have shown that long-term deployment of single or small instruments, and short term deployments of large instrument packages do not affect the long-term survival or behavior of Hawaiian monk seals (Littnan et al. 2004), but the effects of deploying multiple instruments for longer durations have not been tested for this species. There

has been a considerable degree of failure in the recovery of location data for this species (~ 60%), so deploying GPS tags will always be a priority. A package with the Open Tag and GPS tag, without including a camera, would substantially decrease the mass and volume of the instrument package. In the future, therefore, it should be possible to reduce the sampling rate of the Open Tag and deploy it with a GPS tag to facilitate long-term monitoring of monk seal foraging behavior while retaining the benefits of high-resolution data collection and the ability to identify search events in the MHI.

## Chapter 3. Linking Individual Variability to Habitat Preferences in Hawaiian Monk Seals

### *Introduction*

The foraging behavior of marine predators can be broken down into four components: vertical movement (diving), horizontal movement (space use), habitat use, and prey capture (Austin et al. 2006b). In recent years, biologging has increased our understanding of each of these individual components, but the *integration* of these components should lead to a better understanding of foraging behavior as a whole. In Chapter 1 I addressed the horizontal component and described a high level of individual variability in the movements and space use of monk seals in the main Hawaiian Islands (MHI). In this analysis I also demonstrated the limits of GPS data for interpreting fine-scale behavior. The addition of accelerometer data in Chapter 2 provided the resolution needed to identify foraging dives and the factors that influenced foraging behavior, addressing both the vertical and prey capture components, but lacking the habitat component and long-term descriptions of foraging behavior. Both previous chapters addressed important aspects of monk seal ecology and highlighted the importance of considering scale in the interpretation of foraging behavior. The lack of (spatial) resolution in Chapter 1 and (temporal) scale in Chapter 2 left questions unanswered regarding larger influences of the environment on monk seal foraging behavior, and did not address the broad-scale patterns of behavior and habitat use in this species. My results, however, did indicate that most dives performed by monk seals contained

search events and could be considered foraging dives, and that a considerable level of variation was present among individuals. The goal of this chapter, therefore, was to build from the previous work and develop a model, using long-term telemetry data, to describe the influence of habitat on the foraging behavior of monk seals in the MHI. Given the results of the previous chapters, I was particularly interested in examining the role of individual variation in such a model.

## **Habitat Modeling**

Conservation of endangered species often requires the prediction or identification of habitat used by the species of interest. Numerous types of mathematical models have been developed and applied to animal movement data to understand space use and the influence of underlying habitat preferences. These models range in complexity from descriptions of the distribution of discrete step lengths and movement directions; to simulations of a single probability density function of all possible movements and directions; step-selection functions; Brownian motion (Horne et al. 2007); and state-space models (Jonsen et al. 2005, Johnson et al. 2008, Patterson et al. 2008). However, local environmental conditions, including terrain or prey, will influence movement rules for all of these models (Potts and Lewis 2014). Some models are able to account for these influences within the model framework (Moorcroft and Barnett 2008, Potts and Lewis 2014), but having a basic understanding of the effect of the environment on movement, *a priori*, can be beneficial.

Numerous statistical approaches can be used to model habitat use for both terrestrial and aquatic species. Generally, habitat models can be separated into two broad categories: descriptive techniques and modeling approaches (Redfern et al. 2006). The descriptive approach ranges from overlaying sighting and/or relocation data on a map that contains habitat variables, to correlation analysis, goodness-of-fit metrics, analysis of variance, and ordination. Each of these methods helps explore the empirical associations between the location of the animal and the environmental features in the study area, and helps identify important habitat variables; but they are generally employed when little information is known about the ecology of the species *a priori* (Redfern et al. 2006). When more knowledge exists, statistical modeling approaches are more beneficial. The most basic of these models are environmental envelope models, which quantify large-scale relationships between a species and its environment, but are not applicable for data on small spatial or temporal scales. Regression models and classification and regression trees are better suited to analyze fine-scale, high-resolution data for individual animals. Consequently, regression is one of the most commonly used methods for modeling the relationship between different animals and their environment (Redfern et al. 2006).

## **Monk Seal Behavior**

The results of Chapter 2 suggested potential differences in the foraging strategies between individual seals. R306, an adult male seal from Molokai, had different model

results than the other individuals and also appeared to utilize different foraging habitats than the other Molokai seals. This fine-scale analysis identified potential differences in foraging behavior but larger patterns of habitat use were not visible due to the short duration of instrument deployments. In order to identify larger patterns of behavior and habitat use for monk seals, I needed to examine the long-term telemetry records. As Austin et al. (2006b) suggested, integration of all components of foraging behavior are necessary to fully understand the behavior of individuals and the role of predators in the ecosystem. The goal of this chapter was, therefore, to integrate all four components foraging: diving (Chapter 2), space use (Chapter 1), prey capture (Chapter 2), and habitat use, to develop a better understanding of monk seal foraging behavior in the MHI. To accomplish this, I first needed to examine habitat use for seals in this region and then integrate the results with those from the previous two chapters.

## ***Methods***

### **Instrument Deployment**

Due to the size of the instrument package, only sub-adult and adult seals were captured on Oahu, Molokai, and Kauai following the methods of Baker and Johanos (2002). Both males and females were initially targeted, but due to strict capture guidelines (Baker and Johanos 2002), I was only able to instrument four females during the first two years of deployments. For the remainder of the study, I targeted only sub-adult and adult males. Seals that met the capture guidelines were captured with a hoop

net and then sedated with Diazepam (5mg/ml at 0.1-0.25 mg/kg IV). Weights were visually estimated prior to sedation and biomedical samples including blood and blubber biopsies were taken along with swabs of all orifices prior to instrument attachment. Two instrument packages were deployed, one including just a GPS-GSM phone tag and the other including a National Geographic Crittercam, Loggerhead Instruments Open Tag (3-axis accelerometer, magnetometer, gyroscope, and pressure sensor), a GPS-GSM phone tag (TDR), and a VHF transmitter (Table 3). The package was glued to the pelage of the animal, along the dorsal midline between the shoulder blades using 10 min epoxy (Devcon, Danvers MA). The GPS tags were programmed according to the methods described in Chapter 1 and the Open Tags and Crittercams were programmed according to methods described in Chapter 2.

## **Dive Classification**

GPS data were processed using the methods described in Chapter 1 to identify the date, time, and location of each dive. In Chapter 2 the Open Tag data were merged with concurrent GPS locations and video data and were successfully used to identify search events and classify dives into searching and non-searching categories. Monk seals are benthic foragers, and although a number of behavioral and environmental variables were important in predicting foraging events with Open Tag data, in all search events the seal positioned itself near the seafloor. Consequently, dive ratio (the ratio of dive depth to bathymetry) was one of the dominant predictors of search events in the Open

Tag analysis. I considered foraging behavior to include both searching for and consuming prey, but for ease of interpretation, for the rest of this chapter a ‘foraging’ dive is one that contains, or potentially contains, an active search event as predicted by the Open Tag data in Chapter 2.

One of the goals of this chapter was to integrate the results of the previous two chapters. Long-term collection of accelerometer data to identify foraging dives was not feasible, but extrapolation to the TDR record was possible using data collected by both instruments. In Chapter 2, validation of the pitch metric used to identify foraging dives was high (78%), so when using the open tag data to identify foraging dives in the TDR record, I considered the behavior assigned by the pitch metric as the true behavior of the seal in the open tag record. I then used Bayesian logistic regression to identify predictors of foraging using variables also recorded by the TDR. Model set up was:

$$y_i \sim \text{Bernoulli}(\theta_i) \tag{1}$$

$$\text{logit}(\theta_i) = X_i\beta \tag{2}$$

$Y_i$  is the response variable representing dive type (foraging or not) as predicted from the pitch metric.  $\theta_i$  is the odds associated with foraging on dive  $i$ ,  $X$  is the design matrix of predictor variables,  $\beta$  are the coefficient estimates associated with each predictor. The fixed effects in the global model were: dive ratio, dive duration, dive depth, and dive shape. Variables were selected by comparing AIC, BIC, null and residual deviance values of all combinations of predictors. The resulting predictors from the best model

were included in the final design matrix and used to classify foraging dives in the entire TDR record. I used the `bayesglm ()` function in R to run the models using an uninformative, default prior on  $\beta$  (Gelman et al. 2012).

## **Habitat Model**

Due to the basic nature and limitations of regression habitat models, prediction was not a primary goal for these data. Consequently, when developing the habitat model, I was not seeking the most parsimonious model to identify foraging habitat but, instead, wanted to incorporate all of the variables I suspected to influence monk seal foraging to develop the best description of foraging habitat for the seals tagged in this study. I performed basic model selection using AIC and BIC, but chose to keep all of the predictor variables: bathymetry, slope, terrain ruggedness, rugosity, distance to shore, and distance to the shelf. Analysis of the GPS data in Chapter 1 revealed a high level of individual variation in the movements and space use of the seals; consequently, prediction using these data was difficult and limited. In Chapter 2, although the influences on dive behavior were similar among seals, I was able to identify variation in the foraging behavior of at least one seal. My goal in the present chapter was to investigate these potential differences through an analysis of habitat use, investigate the drivers behind the variability observed in Chapter 1, and develop a way to quantify or summarize variation among individuals. Therefore, instead of including year, island, and individual seal as fixed or random effects within one habitat model, I ran multiple

models to identify ‘foraging habitat’ for monk seals under a number of different scenarios. All seals were grouped together with ‘foraging habitat’ identified for each year of data collection (2007, 2008, 2010, 2011, 2012, 2013, 2014), and for each island (Kauai, Oahu, and Molokai). Foraging habitat was also identified for each seal individually, lumping all years together if the animal was instrumented multiple times.

## Model Development

The final habitat model was run using the `MCMClogit()` function in R with dive type (foraging or not foraging ) as predicted from the dive classification above as the response variable (Martin et al. 2011). This function generates a sample from the posterior distribution of a logistic regression model using a random walk Metropolis algorithm. The model structure was:

$$y_i = \text{Bernoulli}(\theta_i) \quad (3)$$

With the inverse link function:

$$\theta_i = \frac{e^{X_i\beta}}{(1+e^{X_i\beta})} \quad (4)$$

$y_i$  is the response variable representing dive type,  $\theta_i$  is the odds of a foraging on dive  $i$ ,  $X$  is a design matrix of predictor variables (chosen from previous model selection method), and  $\beta$  refers to the coefficients associated with each predictor (the effect of each

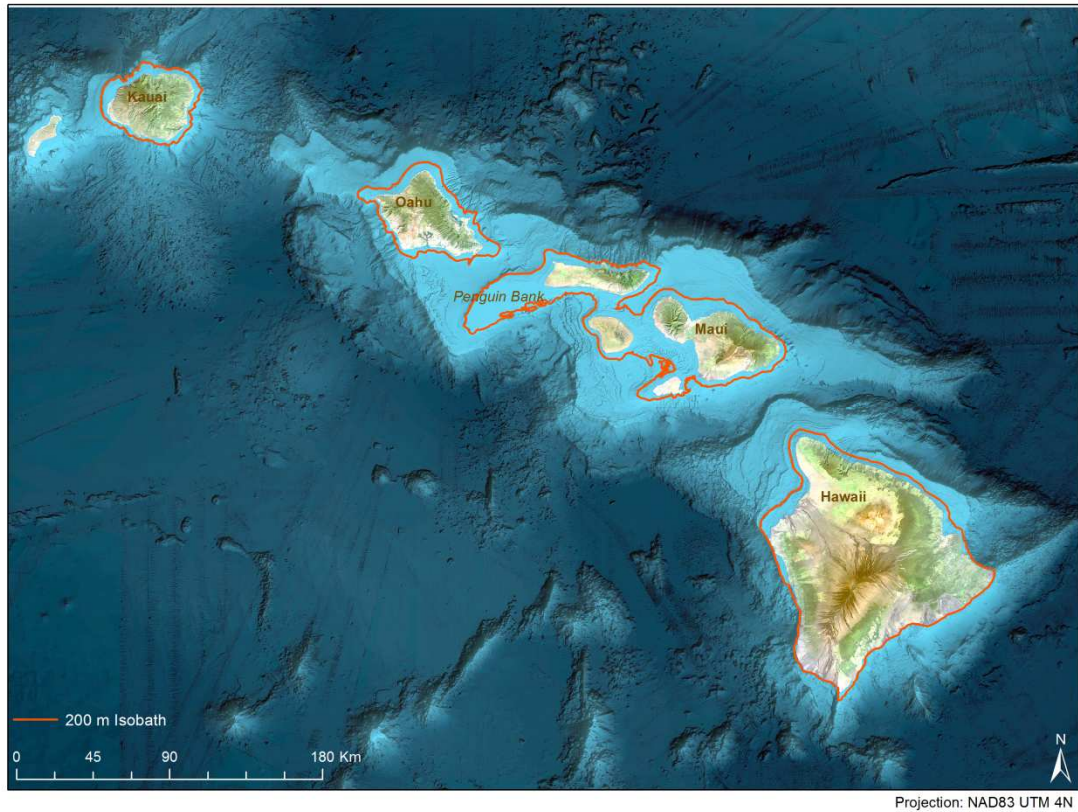
predictor in determining dive type). A multivariate Normal prior was placed on the fixed effects parameters with starting values specified as follows:

$$\beta \sim \text{Normal}(b_0, B_0^{-1}) \quad (5)$$

The beta vector was initialized using the coefficient estimates from the model selection and the hyper-parameters used to initiate the priors were:  $b_0$  = (mean of the starting beta values),  $B_0$  = (precision of the starting beta values). Vague priors were used to allow the data to dominate the analysis and dictate the shape of the posterior distribution, while still accounting for the high levels of variability. The simulation was run for 100,000 iterations with a burnin of 10,000.

## **Habitat Identification**

Telemetry data were combined with environmental data based on GPS location. Environmental variables including bathymetry, slope, terrain ruggedness, rugosity, and distance to shore were calculated according to the methods described in Chapter 2. All benthic habitat variables were constructed using a 50 m grid, the highest resolution bathymetry data available for the region. An additional variable, distance to the shelf-break was also included. The 'shelf' was defined using the 200 m isobath (Mathewson 1970) (Figure 18). Benthic habitat type was only available for near-shore regions. A large portion of dives occurred outside this region and habitat type was not an important variable in the analysis described in Chapter 2, so I excluded it from this analysis.



**Figure 18: Main Hawaiian Island archipelago. The shelf break at the 200 m isobaths is indicated in orange.**

The coefficient estimates from the habitat model were used to input the results into a GIS and identify foraging habitat under each of the following scenarios: by year (2010, 2011, 2012, 2013, and 2014), by island (Oahu, Kauai, and Molokai), and by seal (all 19 individuals). Each habitat variable was converted into a raster and then added together using the results from the logistic regression. The format was:

$$\begin{aligned} \text{logit}(\theta_i) = & \beta_0 + \beta_1(\text{bathymetry}) + \beta_2(\text{terrain Ruggedness}) + \beta_3(\text{slope}) \\ & + \beta_4(\text{rugosity}) + \beta_5(\text{shore distance}) + \beta_6(\text{shelf distance}) \end{aligned}$$

The log odds of the resulting raster were then converted to probability using equation (4). To optimize identification of foraging 'habitat', instead of using a probability of 50%, I used receiver operator characteristics (ROC) curves (Pearce and Ferrier 2000). ROC curves allow selection of a cut-off value that maximizes true positives while minimizing false positives (maximizing true negatives). The area under the ROC curve (AUC), and Phi correlation were used to measure model performance. AUC ranges between 0 – 1, with 1 being perfect prediction. Phi ranges from -1 – 1; Phi = 1.0 also suggests perfect prediction, Phi = 0 suggests the output is no better than a random guess, and a value less than 0 represents inept prediction (worse than guessing) (Dean Urban, pers comm). The resulting cutoff values were used to define foraging habitat. All analyses were performed in R version 3.0.2 and ArcGIS version 10.2.

## **Results**

I deployed 40 instruments from 2007 – 2014 (4 females and 25 males), with most seals tagged in 2010-2014. Seven animals were instrumented twice and one animal was instrumented three times over the study duration. Due to instrument and/or epoxy malfunction, I recovered data from 27 of the 40 TDR tags, representing a 68% recovery rate, 19 individual seals (4 females and 15 males), and 1,505 days of data. The average tracking duration was  $151.89 \pm 78.99$  days, with GPS locations received roughly every 20 min. All haul-out locations were removed from the data along with any dives that lacked concurrent environmental data (i.e. if there was a gap in the bathymetry layer).

This resulted in 355,266 dives for 19 seals; an average of  $18,698 \pm 9149$  dives per seal. I ran 29 habitat models to identify foraging habitat by island, year, and seal. Rugosity did not significantly influence the probability of foraging in all of the models, but was retained during model selection to maintain consistency. Model convergence was confirmed visually and by using Gelman and Geweke diagnostics (Plummer et al. 2006). Only five models had AUC values  $< 0.65$  and no models had values  $< 0.58$  suggesting good model performance (Table 6).

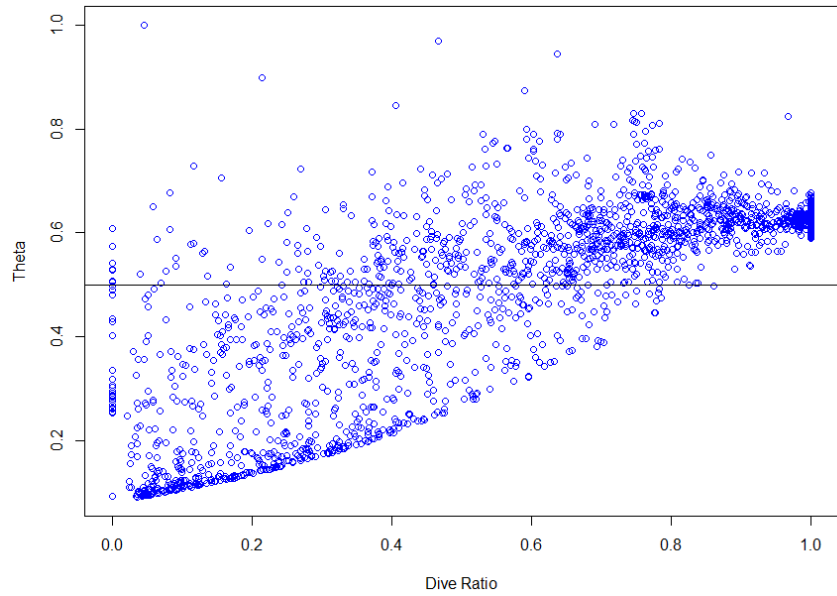
## **Dive Classification**

The interaction of dive duration and dive ratio was the best predictor of foraging in the Open Tag data. I plotted the probability from the model output against each predictor to determine an appropriate cut-off value to separate foraging from non-foraging dives using just dive ratio and dive duration. Just over half (52%) of the Open Tag dives were considered foraging dives; of those, the mean dive ratio was  $0.749 \pm 0.265$ . Model results suggested a dive ratio cutoff near 0.80 to have  $> 50\%$  probability of being a foraging dive (Figure 19). The mean dive duration of foraging dives in the open tag data was  $359.09 \pm 134.05$  sec. Model results suggested that dives with duration longer than 375 sec had  $\geq 50\%$  probability of being a foraging dive (Figure 20). Therefore, I initially defined foraging dives as those with a dive ratio  $\geq 0.80$  and a duration  $\geq 375$  sec and then I compared confusion matrices for a range of cutoff values based on model results. Changing the cutoff for duration or dive ratio did not improve classification

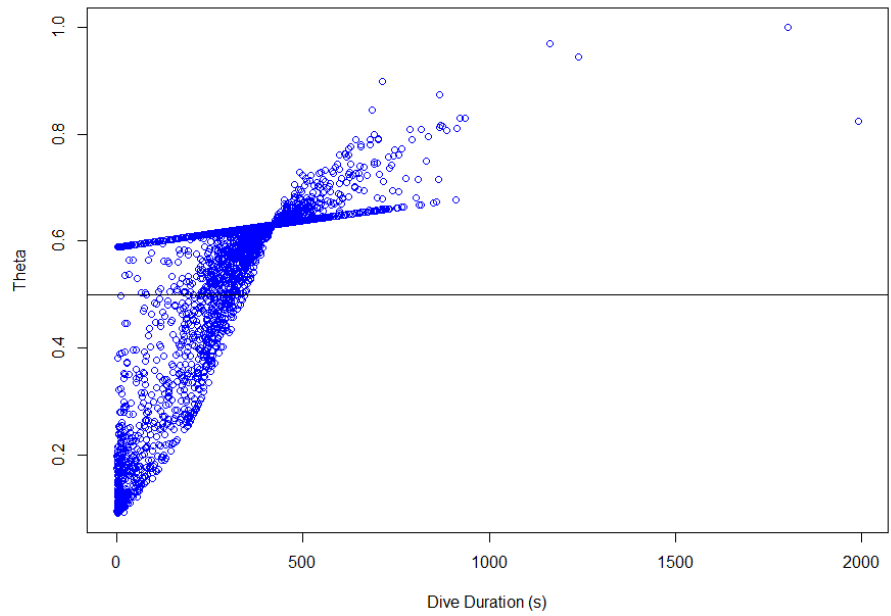
accuracy, but removing duration altogether decreased the false positive prediction by roughly 5%. Therefore, to be conservative and decrease the number of false positive predictions in the TDR record, I identified foraging dives as those with a dive ratio  $\geq 0.80$ . This classification resulted in 77% of the TDR record being classified as foraging dives with an average of  $77\% \pm 0.08$  foraging dives classified per seal record.

**Table 6: Model performance for classification of foraging habitat**

Model	AUC	Phi	Model	AUC	Phi
Year			Seal		
2010	0.734	0.765	RB02	0.705	0.687
2011	0.626	0.789	RB24	0.739	0.755
2012	0.664	0.793	RE70	0.571	0.756
2013	0.670	0.815	RI11	0.630	0.777
2014	0.642	0.805	RK05	0.672	0.756
Island			RK35	0.676	0.827
Oahu	0.625	0.827	RK36	0.695	0.750
Kauai	0.689	0.798	RM38	0.598	0.753
Molokai	0.610	0.787	RR70	0.676	0.847
Seal			RS00	0.691	0.898
R012	0.826	0.881	RV18	0.745	0.792
R018	0.748	0.660	RW02	0.613	0.788
R1KK	0.749	0.885	T21M	0.799	0.887
R306	0.618	0.698			
R4DF	0.759	0.873			
RA12	0.654	0.647			



**Figure 19: Output from logistic regression to identify foraging dives using dive ratio. The 50% probability is marked with the black line.**



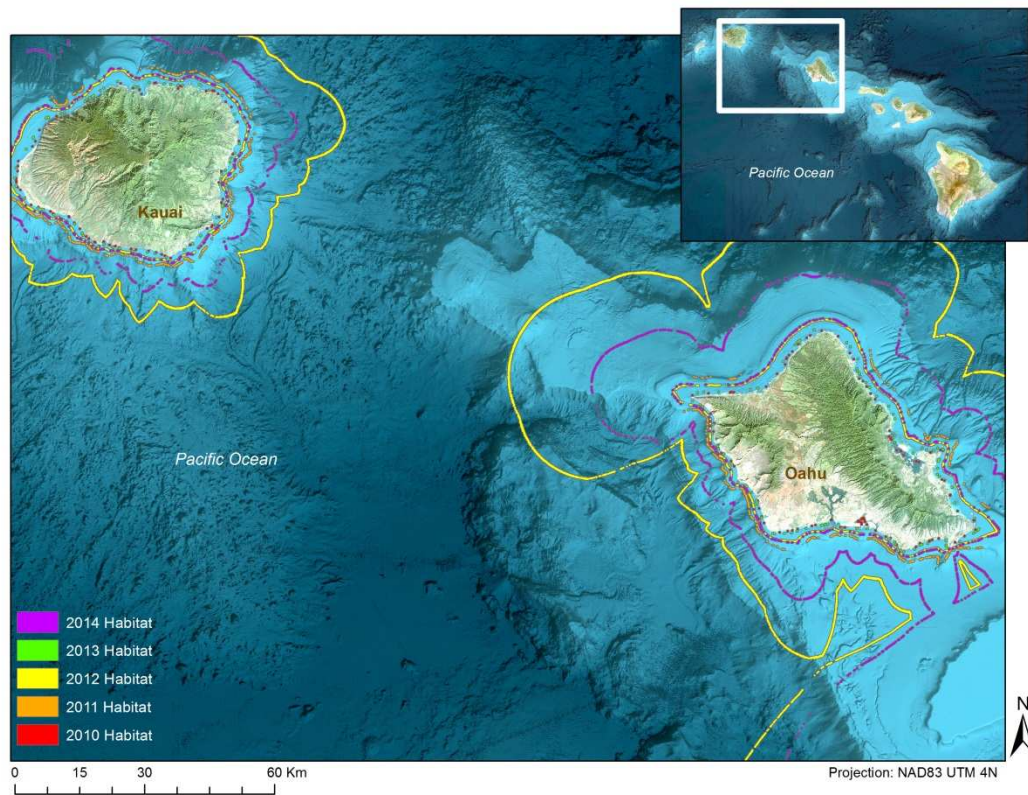
**Figure 20: Output from logistic regression to identify foraging dives using dive duration. The 50% probability is marked with the black line.**

## Foraging Habitat by Year

The first two years of data collection, 2007 and 2008, represent data from one animal and therefore represent only the behavior of that individual (RK35). The first year of multiple tag deployments for this study was in 2010. Bathymetry, aspect, slope, and distance to the shelf significantly influenced foraging during all years of data collection (Table 7). Rugosity was only significant in 2012, 2013, and 2014, but had a value that was essentially zero for all of the models. Distance to shore and terrain ruggedness were significant in all years, except 2011. Across all years, the probability of foraging increased in shallower depths and as aspect, slope, and distance to shore increased. In every year except 2011, as distance to the shelf increased, the probability of foraging decreased. Terrain ruggedness had a more variable influence on foraging behavior across years. The influence was negative in 2011 and 2014, and positive in all other years. Spatially, foraging habitat was variable across years (Figure 21). In 2010, 2011, and 2013, foraging habitat was near shore, but in 2014 it was farther offshore. In 2012, both near shore and offshore foraging habitats were identified.

**Table 7: Coefficient estimates for models of foraging habitat by year.**

	Bathymetry	Terrain Ruggedness	Slope	Rugosity	Shore Distance	Shelf Distance
2010	0.0069	0.77	0.0035	-3.4 e <sup>-7</sup>	5.51	-9.09
2011	0.0063	-0.23	0.0043	-6.8 e <sup>-7</sup>	-0.32	0.98
2012	0.011	0.67	0.0028	1.3 e <sup>-6</sup>	1.37	-2.79
2013	0.033	0.27	0.0032	-3.7 e <sup>-5</sup>	47.65	-15.96
2014	0.011	-0.03	0.0030	-1.5 e <sup>-5</sup>	5.68	-9.85



**Figure 21: Foraging habitat for Hawaiian monk seals by year.**

### **Foraging Habitat by Island**

Similar effects were observed by island as by year (Table 8). For all islands, the probability of foraging increased as slope, terrain ruggedness, aspect, and distance to shore increased, and as bathymetry decreased. Distance to the shelf negatively influenced foraging on Kauai and Molokai, but had a small positive effect for seals from Oahu. Again, the effect of rugosity was essentially zero for all the islands, but it was still

a significant factor for both Oahu and Molokai. Surprisingly, distance to the shelf was not a significant predictor of foraging for seals on Molokai although animals from this island spent most of their time on Penguin Bank, near the shelf break. Foraging habitat predicted for Kauai and Oahu was located near shore on all the islands, but habitat for Molokai was more variable and also included a band of habitat farther offshore (Figure 22).

**Table 8: Coefficient estimates for models of foraging habitat by island.**

	Bathymetry	Terrain Ruggedness	Slope	Rugosity	Shore Distance	Shelf Distance
Oahu	0.007	0.030	0.0051	-1.36 e <sup>-6</sup>	1.28	-0.09
Kauai	0.009	0.64	0.0048	2.06 e <sup>-7</sup>	19.90	-3.73
Molokai	0.018	0.52	0.0054	-2.11 e <sup>-5</sup>	5.53	-1.23

### **Foraging Habitat by Seal**

Differences between individual seals likely drove the differences observed by both year and island. Bathymetry was the only consistent variable across all seals, with the probability of foraging increased in shallower depths. Distance to shore had a positive effect for all but one individual, R018, which was instrumented twice and traveled extensively between Oahu, Kauai, and Niihau. Terrain ruggedness, slope, rugosity, and distance to the shelf were not as consistent across individuals. For each of these variables, most seals had similar results, but at least 30% of the seals were different. The seals with different results for one variable were not necessarily the same

animals that differed for another (Table 9). The effects for all but the distance variables were similar among seals, but the signs of each were different. Consequently, when examining the effects more closely, it appears that distinct habitat preferences exist but are shared by some of the seals.

**Table 9: Coefficient estimates of foraging habitat for individual seals.**

	Bathymetry	Terrain Ruggedness	Slope	Rugosity	Shore Distance	Shelf Distance
R012	0.020	-1.05	0.0024	5.5 e <sup>-7</sup>	49.42	-11.83
R018	0.0041	0.34	0.0015	9.4 e <sup>-7</sup>	-0.95	-7.55
R1KK	0.013	-0.47	0.0045	8.3 e <sup>-5</sup>	8.05	-0.034
R306	0.0047	0.88	0.0041	-8.3 e <sup>-5</sup>	5.97	-0.45
R4DF	0.26	-0.012	0.0033	-2.2 e <sup>-6</sup>	18.49	-18.85
RA12	0.0093	2.33	-0.0027	-1.2 e <sup>-5</sup>	9.13	-12.27
RB02	0.032	0.38	0.0059	2.3 e <sup>-6</sup>	12.59	4.35
RB24	0.11	0.051	0.0057	-6.3 e <sup>-5</sup>	67.88	0.28
RE70	0.0066	0.88	0.0081	-2.4 e <sup>-5</sup>	1.82	-0.15
RI11	0.0024	1.28	0.00063	-3.6 e <sup>-5</sup>	4.52	-4.89
RK05	0.035	0.64	-0.0081	-2.1 e <sup>-6</sup>	80.65	-22.46
RK35	0.021	2.94	0.0067	-1.1 e <sup>-6</sup>	52.33	-36.57
RK36	0.016	-0.16	0.0034	2.8 e <sup>-6</sup>	42.46	0.012
RM38	0.0093	0.25	0.0060	-6.6 e <sup>-5</sup>	3.43	-0.42
RR70	0.034	0.68	-0.0076	-1.4 e <sup>-5</sup>	22.86	-9.72
RS00	0.15	-0.71	7.66 e <sup>-5</sup>	-5.1 e <sup>-5</sup>	134.4	-31.73
RV18	0.175	0.98	-0.0016	-1.6 e <sup>-5</sup>	237.8	-15.06
RW02	0.026	0.067	-0.0028	-3.7 e <sup>-5</sup>	56.8	-6.51
T21M	0.013	-3.98	0.019	7.7 e <sup>-6</sup>	11.35	2.23

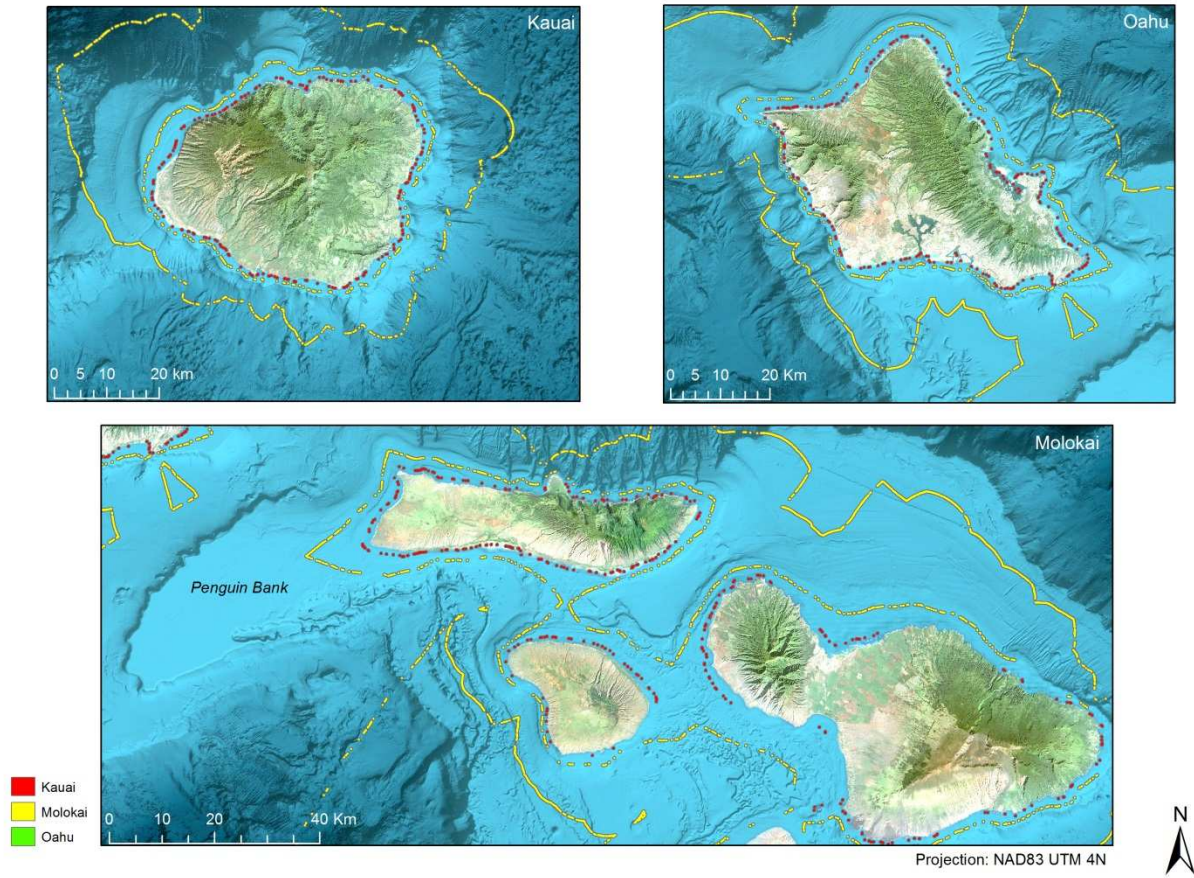


Figure 22: Foraging habitat for Hawaiian monk seals by island.

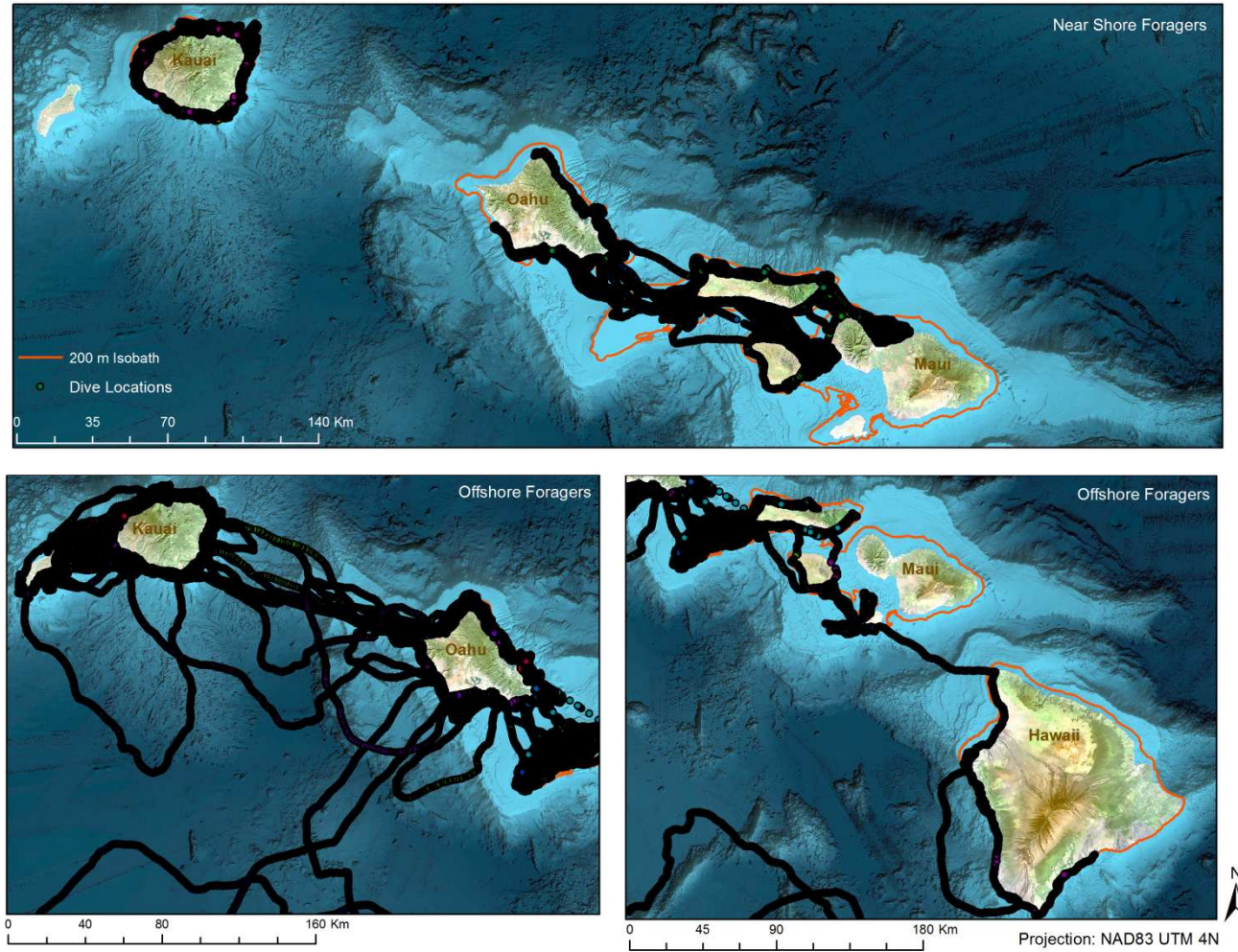


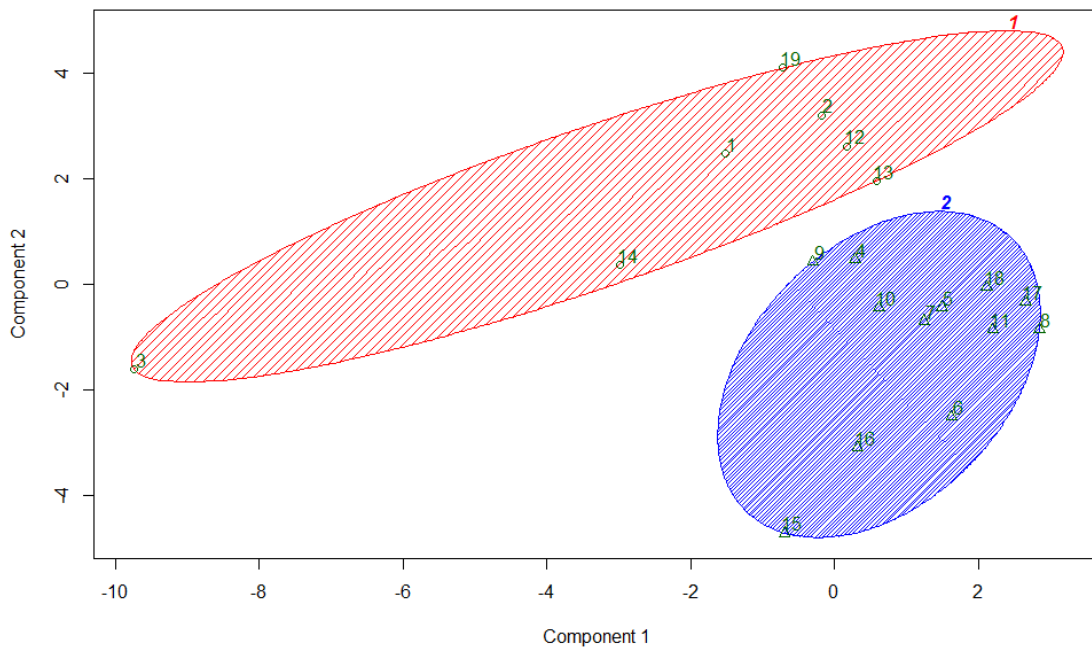
Figure 23: Movements of Hawaiian monk seals in each behavior mode. The bottom two panels show all offshore foragers.

## **Integrating the Components of Foraging**

Preliminary integration of the vertical and horizontal components and the feeding component was done to classify foraging dives in the TDR record, for use in the habitat models. The habitat use component was then addressed in the results of the habitat models listed above. In the final integration step I examined the results of the habitat models for individual seals in combination with their general movements and space use. This last step was necessary for understanding monk seal foraging behavior on a large-scale and to quantify the level of individual variation between the seals.

Two of the 19 seals tagged in this study were unique in the influence of habitat on their foraging behavior, but the other 17 had model results that were the same as at least one other individual. When the general movements of the seals were integrated with the results of the habitat models it became apparent that at two different movement modes exist for monk seals foraging in the MHI: near shore foragers and seals that moved between the islands and foraged in multiple regions (Figure 23). These groupings were initially defined by visually examining the results from the habitat models concurrently with the movement paths of each seal. To quantitatively validate the groups I did a *post-hoc* k-means cluster analysis. For each seal, the factors included in the cluster analysis were the mean habitat variables for each seal and characteristics that described the horizontal and vertical foraging behavior for each seal: mean and median foraging trip distance, mean dive depth while foraging, mean dive duration while

foraging, and the mean and median inter-trip duration. I compared the results for a range of different clusters, but  $k = 2$  revealed the best fit (Figure 24). Increasing the number of clusters did not account for more point variation in the analysis and also identified clusters that contained only one individual. The results of the cluster analysis were similar to my manual classification, particularly in the behaviors they represent, but some individuals were misclassified (Table 10).



**Figure 24: Cluster plot against the 1<sup>st</sup> and 2<sup>nd</sup> components. Clusters define behavior modes for individual Hawaiian monk seals.**

**Table 10: Classification results for Hawaiian monk seal foraging behavior.**

Seal	Classification		Seal	Classification		Seal	Classification	
	Manual	Cluster		Manual	Cluster		Manual	Cluster
R012	1	1	RB24	1	2	RR70	2	2
R018	1	1	RE70	1	2	RS00	2	2
R1KK	1	1	RI11	1	2	RV18	2	2
R306	2	2	RK05	2	2	RW02	2	2
R4DF	1	2	RK35	2	1	T21M	1	1
RA12	2	2	RK36	1	1			
RB02	2	2	RM38	1	1			

## ***Discussion***

This is the first study to simultaneously record movement, diving, and foraging in free-ranging Hawaiian monk seals in a manner that could be translated to long-term telemetry data. My findings indicated that pitch was a reliable metric for identifying most foraging events and could be translated to TDR data via dive ratio. Several habitat variables were significantly associated with foraging in monk seals, but two distinct movement modes appear to exist in the MHI: near shore and offshore/inter-island. The strongest predictors of these two modes were slope and distance to the shelf break.

The ability to identify feeding events in pinnipeds has already been established using stomach-temperature transmitters (Gales and Renouf 1993, Hedd et al. 1996, Andrews 1998, Austin et al. 2006b) and more recently, with concurrent video and

accelerometer recording (Davis et al. 2003, Ydesen et al. 2014). However, these metrics have seldom been applied to long-term datasets. I was able to use short-term, high-resolution data to classify foraging dives and then use this metric to extrapolate to long-term, low-resolution telemetry data to examine foraging behavior and habitat use in Hawaiian monk seals. My results indicate that long-term monitoring of behavior is necessary to understand the foraging behavior of monk seals in the MHI and that short-term data collection, even of a very high resolution, does not identify broader patterns in foraging behavior among individual seals.

Dive shape analysis is a widely used approach for inferring behavior associated with individual dives in pinnipeds (Le Boeuf et al. 1988, Austin et al. 2006b) and seabirds (Wilson et al. 1996), but direct evidence of this inference remains limited unless other methods are used to link feeding events to individual dives (Austin et al. 2006b). I used accelerometers to identify a body position specific to benthic foraging, which allowed me to identify events in which seals searched for and/or consumed prey on individual dives. My definition of foraging behavior, including both searching for and consuming prey suggests that most monk seals forage on most dives. However, when I defined foraging to be an active search, triggered by the presence of appropriate habitat or prey, then I was able to classify foraging/searching dives using a very simple metric: pitch. I used dive ratio to integrate the vertical and horizontal components of foraging with feeding events and translated this metric to long-term TDR data. Validation with

the Open Tag data showed a classification accuracy of 57%. Dive ratio is an imperfect method to identify foraging dives, but in the absence of long-term accelerometer data, it is a useful method of classifying dive behavior from long-term telemetry records. Dive ratio is essentially describing how close to the seafloor an animal was swimming during a dive. Monk seals forage almost exclusively in the benthos and forage on most dives, so identifying when the seal was close to the seafloor was a good indicator of when they were foraging. This extrapolation was successful for monk seals in the MHI primarily because their dive and foraging behavior was so consistent. Nearly all of the dives recorded in this study were square-shaped and near the seafloor, and all capture attempts were targeted towards cryptic or benthic species. For pinnipeds that exhibit more variation in their foraging behavior and incorporate both benthic and pelagic hunting, this type of extrapolation would be less successful. For example, harbor seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) are opportunistic predators that have been known to switch foraging strategies both seasonally and annually, depending on prey availability (Tollit et al. 1998, McConnell et al. 1999, Baechler et al. 2002, Thomas et al. 2011, Lance et al. 2012). Dive ratio and pitch would therefore not be successful methods to identify foraging in these species. However, this integration method may be very successful for other benthic-foraging species including bearded seals (*Erignathus barbatus*) or walrus (*Odobenus rosmarus*).

There was high value in integrating multiple high-resolution data streams, but in practice, this approach is difficult. Instrument failure reduced my sample size from 16 seals to only 5 for which all three types of data were available. I had success integrating each of the data streams, but multiple instruments increase the possibility of instrument failure and it was difficult to program, record, and recover all of the data for every animal. Additionally, comparisons of foraging using pitch and dive ratio within the Open Tag data indicated that this method was effective, but I was able to achieve a classification accuracy of only 57%. The failure to improve this accuracy may be related to the false negative predictions from the Open Tag data described in Chapter 2. When validating the pitch metric, I discovered a number of false negative predictions for two of the seals. Video footage showed search events that were not detected with the pitch metric, which resulted in under-predicting foraging events for those animals; however, as I mentioned in Chapter 2, I believe the false negatives were the result of tag placement and not an issue with the metric itself. The dive ratio metric in the present study would have identified missed dives as foraging dives, even though the pitch metric did not. The lower classification accuracy for dive ratio (57% compared to 78%) was due to validation against Open Tag data that contained false negative predictions from the pitch metric. The accuracy of the dive ratio metric would likely improve with fewer false negatives in the Open Tag record. Additional instrument deployments using both the Open Tag and TDR would validate this hypothesis and provide additional data

to quantify the error associated with this type of extrapolation. The dive ratio metric is likely imperfect and may identify more dives as ‘foraging’ dives, but it has the advantage of relating directly to my initial definition of foraging. When monk seals swim along the sea floor, they are likely both searching for and detecting prey, which would be identified using the dive ratio metric. The difference in accuracy with the pitch metric comes at a much finer scale, the identification of active search events triggered by the potential presence of prey in certain areas. This difference is important for fine-scale behavior analyses, but when looking at foraging on a much larger scale dive ratio provides an important and useful link and is likely more accurate than suggested by the pitch metric-comparison.

## **Movement Modes**

Interpretation of monk seal foraging behavior differed dramatically with the scale and resolution of the data. Combining high-resolution, short term behavior analysis with long-term low resolution dive data revealed two distinct movement modes for monk seals: near shore and offshore/inter-island. Seals in both groups foraged predominantly within the shelf break, but the ‘near shore’ foragers were the most faithful to the islands where they were instrumented and foraged almost exclusively between the shoreline and the 200 m isobath. The ‘offshore’ seals also foraged predominantly near shore, but moved between neighboring islands and also made longer foraging trips outside the shelf break. This group also included the Molokai seals

that foraged predominantly on Penguin Bank, and seals that made extensive movements between islands and those that performed multi-day trips out to the open ocean. This broader pattern of behavior among individuals was not apparent over short temporal scales (less than a week) or without dive classification. These two modes of behavior account for the individual variation that was observed in Chapter 1 and also helps explain the different foraging strategies observed in Chapter 2.

Five of the ten 'near shore' foragers from Oahu and Kauai exhibited identical model results. For all these seals, the probability of foraging increased farther from shore, in areas of increased terrain ruggedness, and in shallower water. The probability decreased as distance to the shelf increased and slope became steeper. Combining the habitat results with general movement activity added an additional four animals to this 'near shore' strategy. The differences in the model results for these seals suggest additional partitioning within the 'near shore' strategy as a result of the seals' response to slope and distance to the shelf break. Additionally, the movements of the seals suggest that they are much more focused in their space-use than the other 'near shore' foragers and remained either on the north or south sides of their respective islands for the entire deployment period.

The 'offshore' foragers differed from the 'near shore' foragers in their relationship with both distance to terrain ruggedness. Both groups had a positive relationship with distance to shore and distance to the shelf break, but the probability of

foraging increased for the 'offshore' seals in areas with less terrain ruggedness. This suggests foraging in mostly flat, sandy habitats with occasional coral heads and rocks as opposed to more complex reef habitats that exist closer to shore. All of these animals did forage near shore as well, but either made multiple trips onto Penguin Bank or between the islands (between Kauai and Niihau, or Oahu-Kauai-Niihau). This behavior mode also includes seals that made multi-day, exploratory trips out to sea. All of these seals exploited both the near shore and offshore environments regularly, suggesting that they are adaptable enough to continue exploiting whatever is available, or that these are still exploring the area. Consequently, it appears that the habitat preferences, when combined with patterns of space-use, can elucidate larger patterns of foraging behavior for monk seals.

## **Habitat Response**

Large animals can traverse many habitats within a single foraging trip. Consequently, it is often difficult to determine which habitat associations are related to particular behaviors, like foraging (Austin et al. 2006b). My integration of behavior and location data largely overcame this problem. Results from all the habitat models showed that the probability of foraging decreased with increasing water depth, suggesting that monk seals were more likely to forage in shallower water. This is the opposite of what was expected given the results of Chapter 2, although even though depth was a significant predictor in all of the models, its influence on the probability of foraging in

the present study was minimal. For most of the models (individuals, years, and islands) the probability of foraging increased  $\leq 0.8\%$  with a decrease of a meter in depth. This is a very small influence when compared to the effect of the other predictors. My study included data from 19 seals, 9 of which were 'near shore' foragers. The other behavior mode contained near shore foraging events, but also contained a number of dives that occurred in deeper water. The prevalence of near shore foraging likely explains why depth was retained in all of the models, but the large number of foraging dives that occurred in deeper water, highlighting variability both among and between individuals, may explain why the effect itself was so small.

Distance to shore and distance to the shelf break were the most variable predictors for all of the models. Distance to shore was positive for all islands, and for all but one year (2011), and one seal (R018). This animal, that was instrumented in 2011, routinely traveled between Oahu and Kauai, and while on Kauai, made numerous trips to forage at Niihau. For this animal, an increase in the distance to shore decreased the probability of foraging. Seals that move between islands may have distinct modes of behavior; as they move farther offshore, between the islands, they may perform traveling dives and do not resume foraging until they are closer to shore and/or over the shelf area.

The effect of distance to the shelf break was different that of from distance to shore because the 200 m isobath meanders between the islands in some locations (Figure

18). On Kauai and Hawaii, the shelf break acts as more of a perimeter around the islands and is likely correlated with distance to shore, but for the other islands, the shelf area is larger and connects some of the islands under water. Consequently, the correlation between the two distance measures was very low (0.23). Distance to the shelf break was the only predictor that varied signs among both years and individuals. On all of the islands, an increase in the distance to the shelf resulted in a decrease in the probability of foraging, suggesting that seals prefer to forage closer to, or on the shelf break itself. The tracking data mostly supports these results with most foraging trips occurring within the 200 m isobath contour. Four animals, all of which were instrumented in 2011, showed the opposite response to shelf distance. As shelf distance increased, the probability of foraging increased. For these animals, there was a positive effect for distance to shore. This has some interesting implications regarding habitat use and prey availability for these seals in 2011. This combination of distance predictors suggests that these seals were more particular than the others in regards to where on the shelf they were foraging. The positive response of shore distance suggests that the probability of foraging increased as they moved farther offshore, but if they moved too close to the shelf break (farther offshore) the probability of foraging decreased. These individuals were foraging between the shore and the shelf break, while the other seals were foraging farther from shore and closer to the shelf break itself. Four of the six seals instrumented in 2011 had this response, suggesting that changes in prey location or availability, or

environmental conditions that occurred that year may have influenced the foraging behavior of the seals.

## **Conclusions**

This chapter highlights the importance of simultaneously recording and integrating multiple types of information to understand the drivers of foraging in Hawaiian monk seals. It also underscores the importance of considering scale in the interpretation of monk seal dive behavior and the influences of habitat on foraging events. Using both high- and low-resolution data I was able to identify broader foraging patterns that would otherwise have been missed. My results suggest that the collection of high resolution data, on a small temporal scale, can be translated with some accuracy, to lower resolution data and applied to long-term monitoring programs. This method is widely applicable to other benthic foraging species, especially those with behavior similar to that of monk seals in the MHI.

Individual variation has been identified as an important factor in the behavior of monk seals since they were first instrumented in the NWHI (Parrish et al. 2005, Parrish and Abernathy 2006, Stewart et al. 2006). However, my study is the first to group this variation into broader movement modes: near shore and offshore/inter-island. These modes account for most of the behaviors observed for monk seals in this region and captured a considerable amount of the individual variation described in the previous two chapters. Changes in behavior over time, as described for R012 in Chapter 1, have

already been documented for some seals in the MHI. Continued monitoring of this population and re-tagging individuals in multiple years will provide additional insight into the development and adaptation of these behaviors. In the future, it will be interesting to see how movement modes change over time and to investigate the potential drivers of this change. Whether these differences are related to age, sex, or life history is still unknown, but could be addressed with additional monitoring as the population in the MHI continues to grow.

## General Conclusions

Overall, my results illustrate the value of integrating multiple technologies to better understand the foraging behavior of Hawaiian monk seals. I used several high-resolution data streams to identify foraging events for monk seals in the main Hawaiian Islands (MHI). These high-resolution data allowed interpretation of fine-scale foraging behavior and the identification of individual foraging events.

My analysis of GPS data without accelerometers revealed that monk seals in the MHI performed shorter foraging trips and traveled shorter distances than their counterparts in the Northwestern Hawaiian Islands (NWHI). Additionally, I was able to show that broad generalizations of monk seal behavior were accurate even though there was considerable variation in the behavior of individual seals. The addition of accelerometer data, with concurrent video footage, enabled me to identify specific foraging events and develop a consequent link (dive ratio) to examine foraging behavior on a larger scale. Extrapolating this metric from the high-resolution data to the larger GPS dataset allowed me to examine the foraging behavior of monk seals on a much broader scale. This analysis provided a large step forward in our understanding of monk seal foraging behavior and habitat use in the MHI. Nearly all variation observed by island and year could be attributed to variation at the level of individual animals. By modeling foraging with respect to habitat use, I was able to categorize two different movement modes for monk seals foraging in this region: near shore and offshore/inter-

island. Near shore foraging was a dominant strategy for both categories, but the amount of movement around and travel between the islands differed. Using the results of this study, it should be possible to extend my findings (using pitch and dive ratio to predict foraging) to a much larger sample of monk seal data, thereby predicting where and when foraging might have occurred. Future models of behavior and habitat use will benefit from this ability to predict and identify foraging in Hawaiian monk seals.

Diversification of foraging strategies is typically observed if prey is limited and individual animals begin to specialize or develop preferences for foraging in a particular location of on a particular prey type (Roughgarden 1972, Bolnick et al. 2003, Tinker et al. 2008). According to the among-individual diversity hypothesis (Tinker et al. 2008), if prey abundance is not limiting in the MHI, one would assume that the foraging strategies among individuals would be similar. Near shore foraging was present for all of the seals, which supports this hypothesis, but the distinct separation in overall foraging strategy suggests that monk seal foraging behavior has already begun to diversify in this region. Additionally, if diversification in foraging is occurring in the MHI, where prey is not limiting, it poses some interesting hypotheses regarding the foraging behavior of monk seals in the NWHI. Starvation of juvenile seals in the NWHI suggests that prey availability *is* a limiting resource for monk seals in that region (Craig and Ragen 1999, Baker et al. 2007). If diversification is already apparent in a non-limiting environment (MHI), then the level of behavioral diversification in the NWHI should be

much higher than what I observed in the MHI. Previous studies in the NWHI (Curtice et al. 2011) suggest variation in behavior between islands, age and sex classes, but these behaviors have not been described in a quantitative manner. If similar resolution data were available from the NWHI it would be possible to test this hypothesis and to help explain how foraging behaviors adapt and change for monk seals on a broader scale. Prey may not be a current limiting factor in the MHI, but the tropics are a difficult place to be a seal, hence the lack of other extant tropical seal species. The North Pacific subtropical gyre, which encompasses the entire Hawaiian archipelago, is described as an oligotrophic environment because there are very low levels of surface chlorophyll and other nutrients required by plankton and ocean productivity. Diversification of foraging behavior for monk seals may simply be a consequence of being a successful seal in an oligotrophic tropical environment. The ultimate driver of this diversification is unknown, but if prey and environment are not limiting, then other drivers, including age, sex, social cues, or predation likely influence monk seal behavior.

Numerous studies have documented age and sex differences in the dive behavior of pinnipeds (Merrick and Loughlin 1997, Frost et al. 2001, Baechler et al. 2002, Lea et al. 2002, Burns et al. 2005). The sex differences in most of these studies were related to different energetic requirements for pregnant or nursing females and sexually dimorphic males that needed to maintain and defend a territory. Hawaiian monk seals are not sexually dimorphic and males do not defend terrestrial territories, so sex

differences may not be driving this behavioral diversification. Most age-based differences that have been observed in other species compared the dive behavior of pups and juveniles to adult animals. I have been unable to find a study that examined changes in behavior among adults, as individuals reach old age. Senescence has been documented in adult female monk seals (Johanos et al. 1994) so at least some female seals survive past their reproductive years. How the foraging behavior of an individual changes after their reproductive years is unknown. R012, an adult male tagged in this study showed a distinct switch in foraging strategies in just four years. When first instrumented in 2010, he was an offshore forager making multiple trips between Oahu, Kauai, and Niihau in addition to a 36 day trip to the open ocean. In 2014, he was a 'near shore' forager and did not leave the west side of Oahu. R012 is now an older male ( $\geq 20$  yrs), and it has been suggested that he is no longer a dominant male capable of competing for females (Tracy Wurth pers. comm.). The behavioral change I observed between 2010 and 2014 could be attributed to a change in dominance status, or to his age. It could also represent underlying changes in the environment or habitat specialization over time. Either way, it will be interesting to continue monitoring seals in the MHI, instrumenting individuals in multiple years, to see if other seals follow a similar pattern and change strategies over time.

Unlike many other pinniped species, monk seals do not aggregate on rookeries or breeding colonies to pup or breed, and they do not haul-out in large social groups.

However, monk seals interact with each other both at sea and on land, and social cues or territorial behavior may play a role in influencing the patterns of behavior and space use I observed for these animals. Unlike most phocids, monk seals forage almost exclusively in the benthos. They are opportunistic predators, but they do not benefit from dynamic and seasonal prey pulses and the ability to switch between benthic and pelagic foraging strategies. Most of the prey targeted by monk seals is relatively stationary, not dynamic or schooling like that of other phocid seals (Longenecker 2010, Cahoon 2011). The cryptic and stationary nature of their prey could allow monk seals to identify the habitat types preferred by their prey and return to the same location multiple times. In turn, this could lead to underwater territories or defensive behavior. Territorial behavior has not been documented in Hawaiian monk seals, and would be difficult to identify without long-term video monitoring of individuals. However, there is a distinct separation of foraging regions between the near shore and off shore foragers, especially on Molokai, and the potential influence of a social driver for this diversification should be considered.

### ***Instrumentation to infer foraging behavior***

Accelerometers are being used with increasing frequency to understand the foraging behavior of marine mammals. Previous studies have used acceleration itself and jerk signals to identify prey capture attempts with large whales (Simon et al. 2012, Goldbogen et al. 2013) and pinnipeds, including harbor seals, which feed on prey within

the water column (Ydesen et al. 2014). However, due to the increase in body motion associated with benthic foraging, jerk signals are not a precise metric for animals, like Hawaiian monk seals, that forage almost exclusively in the benthos. Pitch, instead of a jerk signal, was a simple metric that accurately identified an inverted body position, a behavior exhibited by benthic foragers searching for and capturing prey. This proved very effective for identifying search events for monk seals in the MHI and was readily verified with video footage. An added benefit of extracting foraging events using pitch is that it requires a relatively low sampling rate, which then allows for a much longer sampling duration. It was also possible to extrapolate foraging events from low-resolution data by translating the pitch metric to TDR data, suggesting that short-term studies that integrate multiple technologies can therefore lead to a better overall understanding of foraging behavior at sea.

### ***Data Gaps and Future Work***

My dissertation was able to develop a baseline of foraging behavior and habitat use for monk seals in the MHI, but a number of future analyses would improve this understanding of their overall foraging ecology. First, it would be useful to gain an improved understanding of the prey requirements of monk seals in this region. Juvenile monk seals in the MHI are more successful, with higher rates of survival, than their counterparts in the NWHI, but we still do not know how these fitness parameters are linked to foraging behavior. Additionally, female seals in the MHI wean larger pups and

also begin breeding at a younger age than females in the NWHI. Seals foraging in the MHI do not have to travel as far or stay at sea as long as seals in the NWHI, but we do not know how this affects juvenile survival or maternal investment in offspring. The next step would be to make this connection. Captive studies to investigate the metabolic rates of monk seals are currently underway at the University of California, Santa Cruz. The results of these studies could be combined with the accelerometer data from my wild seals to infer a metabolic cost of foraging in the MHI. Once it is possible to estimate these metabolic costs, we could determine whether different movement modes have different costs, and investigate ecological drivers behind such variation in behavior.

Additionally, once metabolic costs of foraging are determined, we could start to assess the impact of monk seal foraging on local prey populations. The Crittercam footage revealed that only a very small proportion of all potential prey were consumed by monk seals. Furthermore, this footage suggested a higher reliance on octopus than previously assumed, and documented depredation of commercially important bottom fish. Combining the caloric density of the prey observed in the monk seal diet with the metabolic cost of foraging and maintenance would allow estimation of the actual impact of monk seals on prey populations. This information is vital to determining the role of monk seal on the MHI ecosystem. The more we can understand monk seal foraging behavior, the better the information we can share with the public and, consequently, the better our chances of fostering the recovery of this species.

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### Publications

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### Fellowships and Awards

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### Professional Affiliations

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