

**THE HAWAIIAN MONK SEAL: ABUNDANCE ESTIMATION,  
PATTERNS IN SURVIVAL, AND HABITAT ISSUES**

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## DECLARATION

I declare that I composed this thesis and that it has not been submitted in any previous application for a degree. Some of the chapters have been published, submitted, or will be submitted for publication in peer-reviewed journals. Most were collaborative efforts with coauthors, and with the exception of the contributions listed below, the work presented in this thesis is my own. Further acknowledgement of others who contributed in a variety of ways is provided at the end of chapters.

*Chapter 3* was coauthored with Bert Harting and Thea Johanos. Bert wrote the computer code necessary for conducting simulations used in the analysis. Thea was instrumental in editing and preparing data sets used in the chapter. *Chapter 4* was coauthored with Paul Thompson. Paul provided extensive reviews of the manuscript, which made for a much more coherent and focused presentation. *Chapter 5* was coauthored with oceanographers Jeff Polovina and Evan Howell. The study was conceived in a discussion with Jeff, during which we generated the hypotheses to be tested. Evan provided the Transition Zone Chlorophyll Front positional data, as well as figures depicting the front. Both Jeff and Evan contributed to the writing, primarily the passages regarding oceanography. *Chapter 6* was coauthored with Thea Johanos, who flew most of the aerial surveys with me and had maintained records of monk seal births in the main Hawaiian Islands since the 1980s. Finally, *Chapter 7* was coauthored with Charles Littnan and Dave Johnston. Charles led the effort to map islands during a research cruise to the Northwestern Hawaiian Islands, and Dave conducted the GIS analyses.

Jason Baker, June 2006

## ABSTRACT

Conservation is facilitated by precise abundance trend monitoring, understanding what drives vital rates, and characterizing habitat use and threats. This thesis addresses Hawaiian monk seal abundance estimation, patterns in survival, and habitat issues. Various closed capture-recapture abundance estimates were evaluated and found typically to be negatively biased, suggesting the influence of individual capture heterogeneity. Through analysis of discovery curves, a criterion was derived to determine whether total enumeration had been accomplished at a given site and year. The potential for estimating abundance through extrapolation of non-linear asymptotic functions fitted to discovery curves was investigated through simulation analysis. When individual capture heterogeneity existed, fitted asymptotes tended to be biased. Age-specific survival rates of monk seals were relatively low from weaning to age 2 yr, intermediate to age 4 yr, then relatively high rates were sustained until age 17 yr, following which senescence was detected. Temporal trends in survival among subpopulations suggest regional structuring and connectedness within the archipelago. Survival rates were further analyzed in relation to the dynamics of the Transition Zone Chlorophyll Front (TZCF), a North Pacific oceanographic feature hypothesized to variably deliver relatively productive waters into monk seal foraging habitat, thereby influencing seal survival. For young monk seals at the most northerly atolls, survival was lower when the front remained further north. The relationship was strongest following a one- or two-year lag, perhaps indicating the time required for enhanced productivity to influence the food web and improve the seals' prey base. The first surveys of the main Hawaiian Islands (MHI) found a minimum 45 seals in 2000, and 52 in 2001. MHI births have evidently increased since the mid-1990s, and weaned pups in the MHI are larger than those in the species core range, the Northwestern Hawaiian Islands (NWHI). Seals may have recently re-colonized the MHI, which were

very likely part of their historic range. Most NWHI are low-lying and therefore potentially vulnerable to increasing global average sea level. The potential for habitat loss was explored by creating topographic models of several NWHI and evaluating the potential effects of sea-level rise under a range of passive flooding scenarios. Projected terrestrial habitat loss ranged from 3% to 65% under a median scenario (48-cm rise), and 5% to 75% under a maximum scenario (88-cm rise). Insights gained from syntheses of long-term Hawaiian monk seal datasets, augmented with new field studies, have altered some perspectives and priorities for conservation of the species. They have also led to more efficient field effort allocation, allowing for limited resources to be spent on more novel research and conservation efforts.

## TABLE OF CONTENTS

Author's Declaration	3
Abstract	4
Acknowledgements	7
Preface	10
Chapter 1.	11
General Introduction	
Chapter 2.	22
Evaluation of closed capture-recapture methods to estimate abundance of Hawaiian monk seals, <i>Monachus schauinslandi</i>	
Chapter 3.	51
Use of discovery curves to assess abundance of Hawaiian monk seals	
Chapter 4.	74
Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal	
Chapter 5.	96
Effect of variable oceanic productivity on the survival of an upper trophic predator, the Hawaiian monk seal, <i>Monachus schauinslandi</i>	
Chapter 6.	112
Abundance of the Hawaiian monk seal in the main Hawaiian Islands	
Chapter 7.	129
Potential effects of sea-level rise on the terrestrial habitats of endangered and endemic megafauna in the northwestern Hawaiian Islands	
Chapter 8.	150
General Discussion	
References	160

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I thank the Pacific Islands Fisheries Science Center (PISFC, formerly known as the Honolulu Laboratory) of the National Marine Fisheries Service for my own gainful employment to be sure, but also for its fantastic staff, upon whom I relied in many ways during my graduate project. Key among them were several members of the PIFSC Protected Species Division (staff and contractors), who have dedicated much effort to keeping the Hawaiian monk seal on earth: Bud Antonelis, Brenda Becker, Bob Braun, Suzanne Canja, Maire Cahoon, Robert Dollar, Carolyn Grant, Bert Harting, John Henderson, Thea Johanos, Liz Kashinsky, Charles Littnan, Jim Swensen and Chad Yoshinaga. Among this illustrious company, Thea Johanos deserves special recognition. Long-term datasets are rare and precious, requiring constant care, maintenance and grooming. Thea has overseen the Hawaiian monk seal demographic database since its inception in the early 1980s and has ensured its integrity to this day. She knows the data

better than anyone, and was the person I turned to countless times to find out if my ideas for analysis were realistic, and how to go about extracting the data I needed. Were it not for Thea, the analyses presented in this thesis would not have been possible.

I am also grateful for the contributions of others at PIFSC. Chapters 2 through 7 all were improved by the careful technical reviews of the PIFSC Publications Group, including Fran Fiust, Judy Kendig, Audrey Rivero and Jerry Wetherall. The PIFSC librarian, Ani Au, cheerfully provided me with access to literature, which I could not obtain on my own. I am indebted to Susan Kamei, friend and colleague, for her support and guidance. Susan and her administrative support staff have helped me navigate the sometimes daunting challenges of professional research within a US federal government institution, no doubt averting disaster and sparing me jail time more times than I know.

I owe a great debt to my supervisors, Paul Thompson and Bud Antonelis. These two, unbeknownst to me, cooked up the scheme by which I would become a Honolulu-based doctoral student of a Scottish university. When first confronted with this unique opportunity, I was both honored and a bit hesitant, but soon resolved that these guys must know what's best for me, so I signed on. Bud has been my professional supervisor at PIFSC during this project, and his support has been fantastic. He's allowed me to get away to Cromarty for significant periods to concentrate on research and made the studies that comprise this thesis a priority in my job. Paul has been the best kind of graduate advisor imaginable – never asking anything of me<sup>1</sup>, always responding promptly to my queries, and above all, serving as an exceedingly skilled reviewer. I once fancied myself a capable writer. But after having Paul go through six manuscripts that I had naïvely judged publishable, I have been humbled. Paul has a rare knack for seeing the essence of a study,

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<sup>1</sup> Except the one time when he tasked me with gutting and butchering a road kill roe deer we found on the way to Eynhallow.

and structuring its presentation in the most compelling way. Without his input, the chapters below would have suffered, and far fewer would be published.

While I am based in Hawaii, my most productive time in the past five years have been the weeks I've stolen away to the Lighthouse Field Station in Cromarty. There, I was able to focus solely on my research without the distractions of my job in Honolulu. This experience was further enhanced by the staff and students who populate the Lighthouse. I have enjoyed the Lighthouse's potent intellectual milieu, and even more so the kindness, hospitality and camaraderie extended by this wonderful group.

This thesis was squeezed into an already busy professional and personal life. Therefore, I pursued it in times and places which weren't already filled with other things – this often meant while I was away from home. I worked on this thesis in a myriad of locales besides Honolulu; those that I can recall include Midway Atoll, Tutuila, Seattle, the Pribilof Islands, London, Eynhallow, Cromarty, Lacoste, Washington, DC, and Newport, RI - and in all intervening airspace and airports. Along the way, I've benefited from the support, advice, scientific discourse and assistance of many fellow-travelers, colleagues, friends, and surf buddies, notable among them and in no particular order: Brent Stewart, Pam Yochem, Charles Littnan, Dave Johnston, Bert Harting, Tim Ragen, Daniel Goodman, Don Siniff, John Durban, Kim Parsons, Vladimir Groisbois, Helen Bailey, Tim Barton and David Lusseau.

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## **PREFACE**

This thesis is comprised of chapters that are, or hopefully soon will be, published in peer-reviewed journals. As such, each was designed to stand alone, and consequently some repetition is inevitable. For example, the same map of the Hawaiian Islands appears in several chapters, and was retained for ease of reading. Because many of the references appeared in multiple chapters, I created a reference list at the end of the thesis, which contains all the literature cited throughout. In Chapters 2 and 6 (the first two that I wrote), a total abundance of approximately 1400 monk seals is reported, whereas 1300 is the figure cited in other chapters. Regrettably, this difference reflects the decline in monk seal population abundance that has occurred during my studies. References for chapters already published appear as footnotes at the beginning of the respective chapters.

## Chapter 1. General Introduction

Monitoring population abundance, estimating demographic rates, and documenting habitat use and needs are all fundamental to the practice of conservation biology. Recognizing spatial, temporal and age-related variability in demographic rates (survival and reproduction) are especially useful for identifying critical life stages or individual populations at heightened risk. Further, analyzing such patterns in relation to covariates (natural or anthropogenic) is a key step in diagnosing declines and identifying measures that may foster recovery of endangered species (Caughley and Gunn 1996). Subsequent long-term monitoring then allows one to evaluate whether conservation measures have ultimately been successful.

The Hawaiian monk seal (*Monachus schauinslandi*) is among the rarest of marine mammals in the world. Approximately 1300 remaining individuals are scattered throughout the entire Hawaiian archipelago, but the core population consists of six main subpopulations in the remote Northwestern Hawaiian Islands (NWHI) (Figure 1.1) (Ragen and Lavigne 1999; Carretta *et al.* 2006). The Hawaiian monk seal is a relatively old species, having split from the Mediterranean monk seal lineage some 10-11.6 Ma (Fyler *et al.* 2005). It is the only extant phocid seal which lives in warm subtropical waters (the third member of the genus *Monachus*, the Caribbean monk seal, has not been sighted since the 1950s and is probably extinct (Kenyon 1977, but see Boyd and Stanfield 1998).

Adult Hawaiian monk seals are approximately 2m in length (Reif *et al.* 2004) and weigh approximately 200 kg. The mating system is not well known, but the species does not exhibit sexual dimorphism and is likely promiscuous (Stirling 1983). Females typically mature between 5 and 9 years of age. They give birth to a single pup, which they nurse for 5-6 weeks, fasting all or most of that time. The average interval between

consecutive births is 381 days, such that individuals tend to give birth later in the year as they age (Johanos *et al.* 1994). This also leads to asynchronous pupping and breeding among individuals, such that births can occur in any month, but most are born March to August (Johanos *et al.* 1994). Hawaiian monk seals appear to be primarily benthic

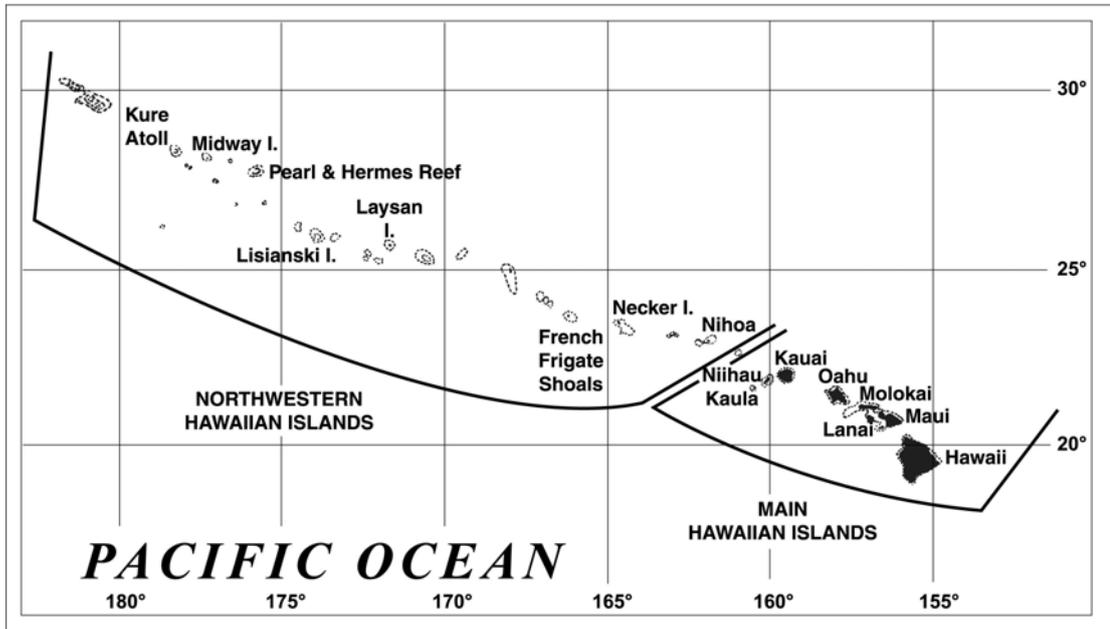


Figure 1.1. The Hawaiian archipelago, indicating the location of the six main Hawaiian monk seal subpopulations in the Northwestern Hawaiian Islands – French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll and Kure Atoll.

foragers, using diverse habitats including shallow reefs, atoll slopes, sand fields, banks and seamounts throughout the NWHI (Parrish *et al.* 2000, 2002, 2005, Stewart *et al.* 2006). Their diet includes reef fishes, cephalopods and crustaceans (Goodman-Lowe 1998).

Due to steep declines in abundance following surveys in the late 1950s, the species was listed as endangered under the United States Endangered Species Act (ESA) in 1976. Efforts to monitor the species and foster its recovery began in the early 1980s, led by the U.S. National Marine Fisheries Service (NMFS) as prescribed by the ESA. Monk seal population monitoring research at each NWHI subpopulation has focused on

determining abundance, age and sex structures, survival rates, reproductive rates, and causes of injury and mortality. This effort has been both long term and intensive, with annual field seasons typically ranging from 2 to 5 months. A primary focus of the program has naturally been to discover and, when possible, mitigate natural and



Figure 1.2 An adult female Hawaiian monk seal resting at Kure Atoll, 2003.

anthropogenic threats to the species, such as human disturbance, fisheries interactions, entanglement in marine debris, intraspecific aggression, shark predation, starvation, and clustered mortality events (Gerrodette and Gilmartin 1990, Hiruki *et al.* 1993*a,b*, Starfield *et al.* 1995, Craig and Ragen 1999, Lavigne 1999, Ragen 1999; Donohue *et al.* 2001; Henderson 2001, Bertilsson-Friedman 2002, Carretta *et al.* 2006). Yet, despite many successful management interventions and regulations which protect monk seals and their habitat in the NWHI, the Hawaiian monk seal's future is not secure. When this thesis was

begun in 2001, overall monk seal abundance had begun a renewed decline after an approximately 8-year period of relative stability.

The Hawaiian monk seal has the distinction of being the subject of a long-term and thorough demographic study on a par with that undertaken for any large, free-ranging mammal in the world. A suite of demographic parameter estimates have been updated annually for each NWHI subpopulation, and these are typically available for review within a few months after annual field seasons have ended. This near real time information on population status and trends is scrutinized and considered in the context of evaluating past recovery efforts and designing future measures.

When this thesis was undertaken, the Hawaiian monk seal population assessment system had matured, was functioning well and providing high quality, timely information



Figure 1.3. Hawaiian monk seal field research camp at Southeast Island, Pearl and Hermes Reef, in 2003.

to scientists and managers. The project was now poised to make significant advances in broader analysis and synthesis of the accumulated demographic data. Some outstanding progress in these areas had already been achieved (Johanos *et al.* 1994, Ragen 1999, Craig and Ragen 1999, Antonelis *et al.* 2003). In addition, the development of a simulation model for the monk seal was an invaluable achievement. This had its roots in a relatively simple model designed to evaluate whether and when management intervention to reduce male aggression should be undertaken (Starfield *et al.* 1995). The model was next expanded to a spatially implicit deterministic metapopulation model (Ragen, unpublished). More recently, Harting (2002) built upon Ragen's work and completed a fully stochastic metapopulation model. The primary use of this highly flexible model is to project future scenarios, especially to explore a variety of management options. This has proven a valuable tool for forecasting using current population status and distributions of observed demographic parameters. However, great potential remained to achieve further insights into monk seal population biology and conservation through synoptic analyses of the wealth of data collected over the past two decades.

Good population monitoring programs have momentum. This helps maintain consistency in methods, comparability of data collected, and dogged commitment to the long-term time series so rarely available to practitioners of conservation biology. Even so, the business of collecting new field data, maintaining the integrity of databases, and generating the latest up-to-date analyses, can be all consuming. It then becomes difficult to step back and evaluate field and analysis methods, research priorities, and to recognize emergent patterns in the accumulated data. This thesis represents an effort to take such a broader view in three areas germane to Hawaiian monk seal assessment and conservation: abundance estimation, patterns in survival and issues relating to habitat.

Precise and unbiased abundance estimates are invaluable for early detection of declines in endangered species, and for timely evaluation of the efficacy of recovery efforts. Further, when protective measures for declining species restrict economic activity (*e.g.*, development projects, commercial fisheries, etc.), claims regarding trends in abundance may come under considerable scrutiny. For the Hawaiian monk seal, abundance has traditionally been characterized with an index known as “beach counts”, which are tallies of all seals on land at a given time (Kenyon and Rice 1959). Substantial declines in these counts led to the species being listed under ESA (U.S. Department of Commerce 1976*a,b*). The mean beach count index is useful because it is relatively easy to obtain and provides a comparable measure available over several decades. Beach counts only account for the fraction of the population on land during a census, and this is a variable which fluctuates considerably. A disadvantage of beach counts, then, is that while they seem to provide a good indication of long-term trends, they poorly reflect year-to-year changes in abundance (Eberhardt *et al.* 1999).

Clearly, it would be preferable to obtain estimates of total abundance rather than an index. Hawaiian monk seal subpopulations are relatively small, numbering up to a few hundred individuals. Indeed, in some cases, field staff suggested that they had exhaustively identified all individuals present in a subpopulation, thereby achieving a total count. In other cases, sampling was clearly not sufficient to achieve total enumeration, as new individual seals continued to be identified throughout the field seasons. In all cases, sighting histories of individual Hawaiian monk seals were collected at each site throughout field seasons of varying length. However, because no quantitative methods had been developed to determine whether total enumeration was achieved, nor had modern capture-recapture methods been evaluated for their applicability to the Hawaiian monk seal, the beach count index remained the favored indicator of monk seal

abundance. However, it seemed promising that better methods of tracking monk seal abundance could be developed.

Sophisticated analytical techniques have been developed that use sightings of identified individuals within a capture-recapture framework to estimate abundance (*e.g.*, Otis *et al.* 1978, Seber 1982, Schwarz and Seber 1999). These models involve a suite of assumptions, including population closure, no loss of marks, and homogeneity of individual capture probabilities (Otis *et al.* 1978). While more recent models have been designed to account for capture heterogeneity, their performance has only rarely been tested in free-ranging populations with known abundance. Chapter 2 evaluates the applicability of a variety of capture-recapture methods for estimating Hawaiian monk seal abundance. Because in many cases total or minimum abundance was known, this analysis is of broad interest to those who estimate abundance using capture-recapture methods.

The shape of “discovery curves,” the number of individuals identified plotted against search effort, is often used in studies of cetaceans and nesting marine turtles to judge whether total enumeration has been achieved or to indicate whether a population is open or closed (*e.g.*, Williams *et al.* 1993; Karczmarski *et al.* 1999; Wilson *et al.* 1999; Limpus *et al.* 2001). This approach is especially applicable to relatively small, localized populations comprised of readily identifiable individuals. However, evaluation of discovery curves tends to involve non-quantitative, subjective, “by eye” judgments. An analogy appears in the species accumulation and species-area literature, where more quantitative techniques have been used to assess the form of curves representing the discovery of new species within an area, or the relationship between the number of species and area sampled (Fisher *et al.* 1943, Good and Toulmin 1956, Flather 1996, Tjørve 2003). Using such relationships to extrapolate an estimated total number of

species has also been investigated (Soberon and Llorente 1993; Colwell and Coddington 1994; Ugland *et al.* 2003).

Chapter 3 focuses on the use of discovery curves to evaluate when monk seal subpopulations have been completely enumerated. Further, the potential for extrapolating discovery curves to reliably estimate asymptotes representing total abundance is investigated. This is accomplished using both real monk seal data and simulations, where the effects of incomplete sampling and capture heterogeneity can be assessed.

Survival was another area where synthesis of the accumulated Hawaiian monk seal data had not been fully explored. Each year, after new field data arrive, Jolly-Seber estimates of subpopulation-, age-, and cohort-specific survival are generated (Jolly 1965, Seber 1965). These have proven valuable for detecting the proximate causes of declines (Craig and Ragen 1999) and for generating distributions of parameter estimates to be sampled in a simulation model (Harting 2002). The primary conclusion of these analyses has been that juvenile survival is highly variable both spatially and temporally.

However, many questions about monk seal survival remained largely unexplored. For example, do female monk seals have higher survival than males? This is a common pattern in mammals (Ralls *et al.* 1980), but whether it occurs in the monk seal was not known. In mammals, survival theoretically follows a pattern of relatively low juvenile rates, improved survival in adulthood, followed by a senescent decline (Caughley 1966). Field studies rarely confirm these patterns, especially in long-lived species. Do monk seals exhibit these features, and if so, at what age does senescence begin? It is clear that juvenile survival varies considerably over time, but what about older animals? What about spatial variability? Do survival rates vary independently among all six subpopulations throughout the NWHI, or do some co-vary in time? All of these questions can have significant influence on future prospects for conservation of the species.

The monk seal data present a rare opportunity to evaluate survival patterns in a free-ranging large mammal. The usual concerns about whether the sampled population is representative of the species, and how to distinguish apparent survival (survival confounded by migration) from actual survival are negligible in the monk seal case. Individuals have been marked and resighted for more than 20 years at all six main subpopulations spanning the core range of the species. Additionally, most of the offspring born into the species over the past two decades have been marked. Chapter 4, then, presents a comprehensive treatment of spatial and temporal variability in monk seal survival.

While characterizing variability in vital rates is important, conservation biologists and managers really want to know what *drives* this variability. In Hawaiian monk seals, fluctuating juvenile survival appears to be the primary proximate cause for declines in abundance. Moreover, food limitation appears to be associated with a sustained period of chronic low juvenile survival at the largest subpopulation (Craig and Ragen 1999). Since 2000, several years of high post-weaning monk seal mortality have been observed at many sites throughout the NWHI. No clear anthropogenic cause can apparently explain this decline in survival. In fact, it has occurred during a time when the already low level of commercial fishing in the NWHI has been further reduced (Carretta *et al.* 2006). Thus, it seems likely that other factors must influence monk seal survival. The Transition Zone Chlorophyll Front is a large-scale oceanographic feature separating relatively oligotrophic subtropical waters from the more productive North Pacific Transition Zone waters. This front migrates seasonally and its southern extent in winter varies annually, providing a potential source of variable productivity in monk seal foraging habitat. Chapter 5 investigates the relationship between this front and monk seal survival rates.

Caughley and Gunn (1996) made the prescient observation that “remnant populations of an endangered species often end up not in the habitat most favorable to it but in the habitat least favorable to its agent of decline.” As noted above, the Hawaiian monk seal’s primary range is in the remote NWHI, and consequently, virtually all research and recovery efforts have been focused on that area. The original Hawaiian Monk Seal Recovery Plan (Gilmartin 1983), the blueprint for restoring endangered species under the ESA, made no mention of seals in the main Hawaiian Islands (MHI, the 8 large islands one usually thinks of as “Hawaii”). However, in the 1990’s, some evidence pointed to an increase in the number of seals in the MHI. Research on MHI monk seals was minimal, consisting only of documenting sightings reported by a variety of sources (mostly the public), and tagging and measuring a few known pups each year. Though these were highly non-systematic and opportunistic data sources, they seemed to suggest that monk seals in the MHI may have been on the rise in the 1990’s. To address the lack of any systematic evaluation of seals in the area, the first aerial surveys for monk seals were conducted along all MHI shorelines in 2000 and 2001. The results of these surveys, along with information on the condition of MHI pups, is presented in Chapter 6. That chapter also addresses the likely distribution of monk seals in Hawaii prior to the arrival of man, and the prospects and challenges for future monk seal conservation in the main islands.

The Intergovernmental Panel on Climate Change (IPCC) predicts that global average sea level will rise during the next century, providing a median estimate of a 48 cm rise by 2100 (Church *et al.* 2001). The uncertainty of predictions increases over time, but sea level will likely continue to rise beyond 2100. Recent evidence suggests that the world’s oceans may rise even more rapidly than previously predicted, as the rate of ice loss from the Greenland Ice Sheet has accelerated (Rignot and Kanagaratnam 2006).

As has been noted, the Hawaiian monk seal population is concentrated in the NWHI. These islands are small and low-lying, potentially making them especially vulnerable to rising sea level. In addition to monk seals, a variety of other megafauna (Hawaiian green sea turtles, several seabirds and endemic land birds) rely upon the NWHI for their continued existence. Given this situation, it is remarkable that no elevation maps of the islands were available when this thesis project was begun. Chapter 7, the final of this thesis, addresses the potential effects of sea level rise on several of the islands that represent key habitat for the persistence of the monk seal and other species. Island elevations were surveyed and topographic models were created to evaluate how much land area might be lost under a variety of plausible sea level rise scenarios.

Long-term research should ideally involve a judicious balance between maintaining consistency while shifting priorities and adapting protocols as demanded by new circumstances and the insights provided by novel data or synthesis of information collected thus far. When the research subject is an endangered species, the need to tread this way wisely is especially critical. The aim of this thesis was to improve our chances of getting this right for the Hawaiian monk seal, with a focus on three areas: sharpening the tools used for tracking abundance trends, evaluating patterns and drivers of variable survival, and revealing both an opportunity for expansion into under-occupied habitat in the MHI, and identifying a potentially severe threat to core habitats in the NWHI.

## Chapter 2. Evaluation of closed capture-recapture methods to estimate abundance of Hawaiian monk seals, *Monachus schauinslandi*<sup>2</sup>

### ABSTRACT

Numerous capture-recapture methods have been developed to estimate abundance, yet the performance of these models is only rarely judged by comparison with true abundance. This study presents a rare opportunity to assess capture-recapture estimates in a free-ranging population with known minimum abundance. Hawaiian monk seal abundance has historically been characterized using a trend index or has been estimated using simple enumeration. Here, I evaluate the applicability of various closed population capture-recapture models to estimate Hawaiian monk seal abundance and its associated error. Twelve data sets (two years from each of six subpopulations) representing a wide variety of sampling and logistical scenarios were analyzed using models that explored effects of animal size class (juvenile, subadult, or adult), tag status, and sighting location on initial capture and recapture probabilities. Various models were also explored to account for capture heterogeneity among individuals. Size and sex effects always significantly improved model fits, and tag status and location effects were also frequently influential. In most cases, abundance estimated from capture-recapture models was substantially lower than known minimum abundance, suggesting the influence of individual capture heterogeneity. Attributes of individuals known to be alive, but not captured during systematic surveys, did not reveal patterns that explained sources of capture heterogeneity. In some cases, mixture models produced less-biased estimates but were associated with very large confidence intervals. Among the model types examined, those

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<sup>2</sup> This chapter published as: Baker JD (2004) Evaluation of closed capture-recapture methods to estimate abundance of Hawaiian monk seals, *Monachus schauinslandi*. Ecological Applications 14:987-998.

available in Program CAPTURE performed best and, while still prone to negative bias, may nevertheless prove useful in characterizing population trends in Hawaiian monk seals. This study demonstrates that selection of appropriate closed capture-recapture models can be substantially improved by independent validation.

## INTRODUCTION

Precise and unbiased estimates of abundance are a fundamental requirement when managing exploited or endangered populations. Both applied and natural marks have long been used to facilitate individually-based behavioral and demographic studies. This has led to the development of sophisticated analytical techniques that use sightings of identified individuals within a capture-recapture framework to estimate abundance (*e.g.*, Otis *et al.* 1978, Seber 1982, Schwarz and Seber 1999). These studies require consideration of the potential for, and ramifications of, violating various assumptions of capture-recapture methods, including population closure, loss of marks, and heterogeneity in individual behavior leading to unequal capture probabilities (*e.g.*, Otis *et al.* 1978). While more recent models have been designed to account for such capture heterogeneity, their success in reducing negative bias in abundance estimates can be difficult to determine. Only rarely have capture-recapture estimates been tested against known population sizes (Edwards and Eberhardt 1967, Strandgaard 1967, Mares *et al.* 1981, Greenwood *et al.* 1985, Boulanger and Krebs 1994, Manning *et al.* 1995, Koper and Brooks 1998, Cross and Waser 2000), and their performance when applied to wider-ranging or socially complex mammals remains unclear. The consequences of bias in abundance estimates for managers of such populations could be severe. Inadequate consideration of positive bias could lead to over-exploitation in harvested species. Alternatively, negative bias might result in economic consequences for industries such as

fisheries, where take limits can be influenced by the abundance of endangered populations.

Potential to explore these biases is likely to be greatest in endangered species, where low numbers and restricted range provide opportunities for alternative techniques to provide comparative data on abundance. The Hawaiian monk seal (*Monachus schauinslandi*) is one such endangered species, which primarily inhabits the remote Northwestern Hawaiian Islands (NWHI), where approximately 1,400 seals reside predominately in six main subpopulations (Figure 2.1) (Ragen and Lavigne 1999, Carretta *et al.* 2002). Early efforts to characterize abundance involved using counts on land as an index of population size (Kenyon and Rice 1959), and steep declines in these counts led to the species being listed as endangered under the U.S. Endangered Species Act in 1976 (U.S. Department of Commerce 1976*a,b*).

Subsequent efforts to monitor and foster the recovery of Hawaiian monk seals have resulted in an extensive research program in the six main NWHI subpopulations for over two decades. In recent years, monitoring effort has been so intensive that almost all individual seals using most of these sites are likely to be identified through resights of tags, recognition of permanent natural marks or applied temporary pelage bleach marks. This enumeration process provides a known minimum abundance (Carretta *et al.* 2002), but it is a point estimate lacking an estimate of associated error, such that the potential number of uncounted seals cannot be assessed. Because sightings of marked seals are collected in a systematic manner, on repeated censuses through each season, the application of capture-recapture techniques to these data could overcome this problem and provide both a point estimate and an estimate of error. In this paper, I investigate whether applying capture-recapture models to existing Hawaiian monk seal data can

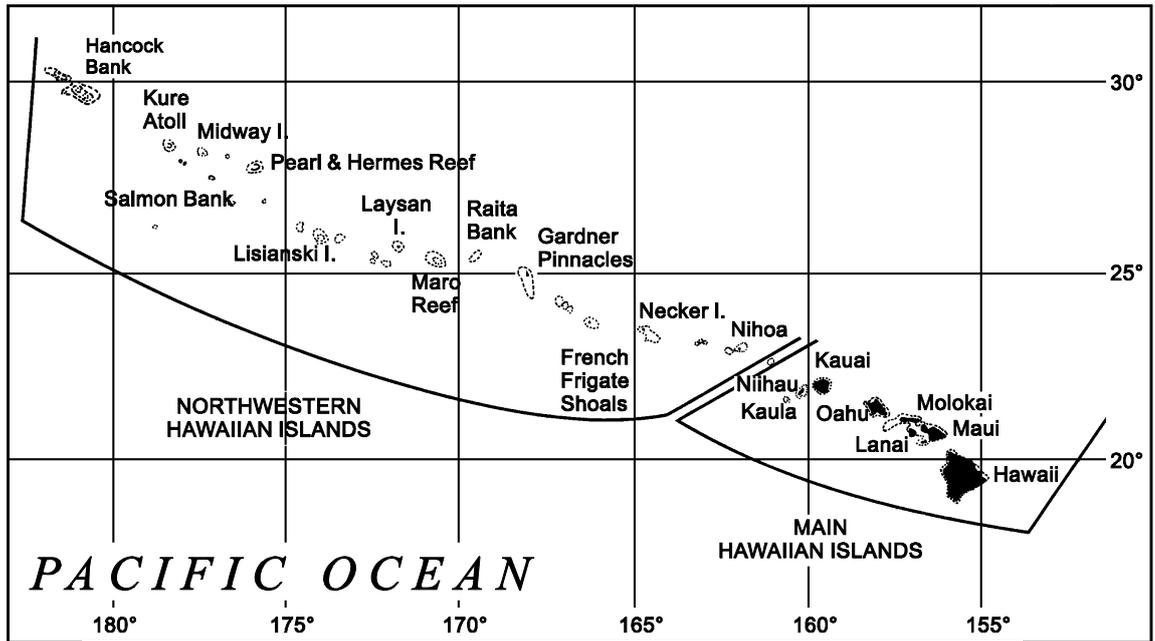


Figure 2.1. Location of the six main subpopulations of Hawaiian monk seals in the Northwestern Hawaiian Islands.

generate abundance estimates that represent an improvement over both the beach count index and simple enumeration. This database of individually-based sightings presents a rare opportunity to independently evaluate the capture-recapture abundance estimates, specifically with respect to the influence of capture heterogeneity among individuals. The six monk seal populations studied vary in terms of their physiography, population size and logistic challenges that constrain sampling effort. Thus, they represent a diversity of scenarios in which the performance of the capture-recapture models can be evaluated. Furthermore, seals were identified both during systematic censuses (which conformed well to capture-recapture methods) and during non-systematic and opportunistic sightings (which did not). Thus, some seals were known to be present in the population, even though they were not seen on any systematic census. The total number of individuals identified during both types of sampling constitutes a known minimum population size, which is compared to estimates derived from capture-recapture analysis using only the systematic data.

## METHODS

Capture-recapture data analyzed here were extracted from the Hawaiian monk seal sighting databases from six locations: French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll (Figure 2.1). The fundamental methods employed were consistent among all sites and years. However, varying physiography among the sites and logistical constraints led to variability in the timing, duration and frequency of sampling occasions. General methods will be described first, followed by salient site-specific characteristics. Because unequal capture probabilities tend to result in biased abundance estimates (Otis *et al.* 1978), efforts were

made to sample available data in such a way as to minimize known sources of heterogeneity introduced through the design of resighting studies.

### *Marking*

Since the early 1980s, all or nearly all pups were marked on each hind flipper with a unique colored plastic tag. Many older animals, which had either never been tagged or whose tags required replacement, were also captured and tagged opportunistically. As a result, the majority of seals bear tags. In addition, photographic and hand-drawn records of natural markings (shark bite and other scars, permanent natural pelage patterns) were collected and updated annually for all seals. Finally, to facilitate resighting seals and provide a unique mark for seals without tags or distinguishing natural marks, most seals were given temporary pelage bleach marks.

### *Recaptures*

Presence of individual seals was recorded during both complete systematic surveys (hereafter referred to as censuses) of all landing areas, as well as during incidental sightings or partial censuses of beaches (hereafter referred to as non-census sightings). For capture-recapture analysis, individual capture histories were constructed only from complete censuses. Censuses were conducted by walking the entire perimeter of all islands within an atoll and systematically searching for and identifying as many seals encountered as possible. This tended to equalize the probability that individuals would be identified given that they were present on land. Seals seen in the water were excluded from the capture histories, as identity of these seals could be less certain and capture probability would vary dependent on the nature of the distinguishing mark (*e.g.*, bleach mark versus flipper tag).

During censuses, seal identity, sex, size class (pup, juvenile, subadult, and adult size) (Stone 1984), and location were recorded. Censuses at multiple-islet atolls were

completed within at least a 2-day period. Censuses of single island subpopulations began at 1300 and were always completed within the day.

Some animals counted on censuses were not identified. Care was taken to avoid disturbing seals, such that alert and aware animals were not always approached closely enough to identify. Also, even approachable seals sometimes could not be identified on each sighting. The number of seals present but not identifiable on a given census was recorded.

Non-census sightings were collected on surveys that did not cover all island perimeters, were focused on particular age/sex groups, or were simply sightings recorded incidental to other activities. These sightings were excluded from capture-recapture analysis because their inclusion would certainly introduce capture heterogeneity through unequal effort. For example, on multiple-islet atolls, seals which frequented the islet where researchers were based were more likely to be resighted than those that favored distant islets, which researchers visited less often. Likewise, nursing mothers were more closely monitored than other sex and age groups, giving them higher non-census capture probabilities.

The duration of field seasons and the number of censuses completed per season varied among sites and over time, although they usually occurred during the main period of pupping and breeding (March-August, Johanos *et al.* 1994). Atoll physiography, weather conditions and other factors variably influenced the census schedule. Conducting censuses was but one of many research objectives with which field teams were charged. Often, researchers were at their field sites for several weeks or more prior to conducting the first census and also remained after the final census. Thus, the census period constituted a subset of the full field season, and non-census sightings occurred both prior

to, and after, the census period. Below, site-specific details of field methods are discussed.

*Single Islands - Laysan and Lisianski*

Laysan and Lisianski are relatively large (11 and 5 km perimeter, respectively) islands, where field seasons were approximately 5 months duration. All locations where seals land were readily accessible to researchers each day, and weather conditions rarely affected the schedule of surveys. Typically Laysan and Lisianski field teams spent approximately the first month of each field season identifying seals and applying bleach marks to most of the population. Subsequently they began conducting censuses every few days, usually completing 20-30 per season. During the past decade, the number of seals (excluding pups) identified at these sites ranged from 206 to 272 at Laysan and 143 to 197 at Lisianski. Long before the end of each field season, sightings of seals not yet seen that year almost completely ceased, suggesting the entire population had been identified.

*Multiple-islet Atolls*

The remaining four sites consist of coral atolls of varying size, with varying numbers of islets. Seals frequently move among the islets within atolls. Researchers were stationed at one islet at each atoll, and travelled by small boat to the various islets to conduct census- and non-census-related research. Islets range from substantial vegetated islands to small sand spits only a few tens of meters in diameter. Ability to reach all the islets was highly dependent on weather, sea state, and distances between islets.

*French Frigate Shoals.*--The largest of the NWHI atolls, it consists of a 36-km diameter lagoon enclosed by a fringing reef and dotted with 9 islets where seals land. Weather and sea conditions had to be favorable to achieve a full census of all islets within 2 days. Because the population is relatively large (240-351 non-pups identified per year during the past decade) and spread among the variably accessible islets, little bleach marking

was done, making repeat identification within a season more difficult. This site has recently harbored the largest subpopulation of Hawaiian monk seals, which has steeply declined for more than a decade (Craig and Ragen 1999, Carretta *et al.* 2002). Field seasons have tended to be 4-5 months long, typically with 8-10 censuses conducted.

*Pearl and Hermes Reef*.--Another large atoll (diameter 32 km) with 8 islets, the monk seal population here has been growing since the early 1970s (number of non-pups identified ranged from 198 to 227 during the past decade). Like French Frigate Shoals, conducting censuses at Pearl and Hermes Reef is highly weather dependent. Research at this atoll typically occurs over a 7-10 week period, within which 8-10 censuses are conducted.

*Midway Atoll*.-- This relatively small (11 km in diameter) atoll is quite tractable for monitoring, consisting of two primary islands and one small spit, all within 2 km of one another. The monk seal population here has grown from just a few individuals in the 1980s to approximately 50-60 animals (excluding pups) recently. Very little research effort was expended until the population began to grow, following which field seasons extended from 9 to 12 months. Up to 50 censuses have been conducted in some years.

*Kure Atoll*.--This small atoll (9 km diameter) has only two permanent islands. In recent years, field season durations are usually 9-12 weeks, during which 10-15 censuses were completed. The number of seals older than pups identified at this site increased from 64 in 1990 (Van Toorenburg *et al.* 1993) to approximately 100 in recent years.

#### *Data Analysis*

Data sets from two years from each of the six subpopulations were selected for analysis. Years representing ‘best-case’ scenarios were chosen with the rationale that if the results were not satisfactory, less ideal data sets would yield no better results. Several elements constituted best-case data sets. First, a relatively large number of censuses were

desirable to reduce the error of abundance estimates. Further, because monk seals alternate time on land with trips to sea, it was desirable to have censuses relatively evenly spread over most of the field season so that each animal in the population would likely be available for capture on several occasions. To further minimize capture heterogeneity, years with a relatively low proportion of unidentifiable seals encountered per census (*i.e.*, the population was well-marked), and low variability in total number of seals identified per census, were chosen.

Capture-recapture histories from censuses were analyzed using closed population maximum likelihood estimators (MLE) in Program MARK<sup>1</sup> and various other estimators available through Program CAPTURE (Otis *et al.* 1978, White *et al.* 1982, Rexstad and Burnham 1991). Open models using multiple capture events both within and between consecutive years (*e.g.*, Kendall *et al.* 1995) were not appropriate because some individuals had temporary bleach marks not maintained between years. The first time a seal was identified during a field season was treated as the initial capture (analogous to marking), and any subsequent resightings were treated as recaptures. Variables thought to potentially affect capture probabilities were used to subdivide populations into strata ('groups' in Program MARK parlance), the parameters of which were fitted separately. Models (see below) were used to explore effects of size class (adult, subadult, or juvenile), sex, and tag status (presence or absence of flipper tags). At multi-islet atolls, geography might have influenced capture probability; thus, the islet of initial sighting was used as a proxy location effect to further distinguish groups. Time (capture occasion) dependence of capture probabilities was also explored.

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<sup>1</sup>White GC Program MARK. <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm> (16 Dec. 2002).

When the number of individuals in a group (*i.e.*, a particular sex, size, and location combination) was either zero or very low, nonsensical parameter estimates with enormous variances resulted. In such cases, individual islet locations were collapsed until adequate cell counts were achieved. To the degree possible, adjacent islets with similar physiography were combined. Most untagged animals were either adults that had never been tagged or those that had lost their tags. The effect of tag status therefore was analyzed only for adults. When all variables of interest (size, sex, location, and adult tag status) were considered simultaneously, the number of animals in one or more groups was typically too low to obtain identifiable parameter estimates. To avoid this problem, separate analyses were done for each data set; one involving location, sex and size and the other exploring adult tag status, sex, and size.

Fundamental assumptions for capture-recapture abundance estimation are presented in Otis *et al.* (1978). Populations were assumed to be closed during the study, *i.e.*, there were no additions (births or immigration) nor losses (mortality or emigration) during a field season. Because censuses were conducted within the periods when most births occur, only non-pup abundance was estimated. Field seasons were of sufficient duration that mortality could have occurred during the census period. Likewise, some movement between subpopulations occurs, which constitutes emigration/immigration (Harting 2002). Finally, seals alternate time ashore with time at sea, a form of temporary emigration. The implications of violating the closed population assumption will be discussed.

Other assumptions were that marked animals did not lose their marks during the study and that all marks were correctly recorded (Otis *et al.* 1978). These assumptions were well adhered to. The redundant identification system involving tags, bleach marks, and natural marks makes it very unlikely that an animal ‘loses its mark’ during a season.

Further, data were collected on standardized forms, which allow for notation of any uncertainty in the field identification. Data were checked manually, and quality control checks involving cross-referencing of tag numbers, bleach marks, size, and sex of animals were employed to find mis-identifications. Only sightings recorded as absolutely certain were used in this study.

Simple closed capture models in Program MARK assume no capture heterogeneity within groups. Capture heterogeneity was explored using mixture models, where initial capture probability and recapture probability parameters are modeled as mixtures of values (Norris and Pollock 1995, Pledger 1998, 2000). This allowed for estimated proportions of groups to be subject to different capture and recapture probabilities independent of any identified characteristic (*i.e.*, sex, size, location). Additional estimators for treating capture heterogeneity were analyzed using Program CAPTURE.

Models in Program MARK were fitted beginning with a saturated closed capture model (no individual heterogeneity) including all variables of interest and their interactions. Subsequently, terms that appeared insignificant based upon examination of parameter estimates were eliminated one at a time beginning with interactions followed by main effects. The results were ranked and evaluated using the small-sample Akaike's information criterion (AICc, see Anderson *et al.* 2000). The total abundance estimate from the model with the lowest AICc was considered best. In cases where two or more models were roughly equally supported according to AICc, parsimonious models (those with fewer estimated parameters) were preferred (Burnham and Anderson 1998).

Next, the best fitting model for each data set was re-parameterized to allow for two mixtures within each group in order to further explore unequal capture probabilities. A "null" mixture model was also fitted with two mixtures and no group distinctions.

Additional abundance estimates were generated using the model selection procedure available in Program CAPTURE (Otis *et al.* 1978, Rexstad and Burnham 1991), whereby a testing algorithm determines which of a suite of models involving combinations of time, behavior and heterogeneity effects is most appropriate for a given set of capture histories. Estimates were obtained using the model type assigned the highest rank by the algorithm. When the chosen model included all three effect types ( $M_{tbh}$ ), which has no estimator in Program CAPTURE, the second highest rank model was used. When two estimators of the indicated model type were available, both were run.

Parameters estimated in closed-capture models are discussed using the following nomenclature:

$p_i$  is estimated initial capture probability for group  $i$

$c_i$  is estimated recapture probability for group  $i$

$N_i$  is estimated abundance of group  $i$

$M_i$  is the total number of unique individuals in group  $i$  captured during all capture events combined, and

$f_{0,i}$  is the estimated number of individuals of group  $i$  not seen during any capture event, such that:

$$N_i = M_i + f_{0,i}.$$

For this study,  $N$  was of primary interest. Probabilities  $p$  and  $c$  drove the estimation of  $N$ , but were of little interest. Separate estimates of  $N$  are obtained for each of the  $i$  modeled groups. The  $N_i$  are the sum of  $M_i$  and  $f_{0,i}$ , as above, with the  $f_{0,i}$  fitted using the log link function. The  $f_{0,i}$  on the log scale are referred to as  $\beta_i$ , and Program MARK provides variance estimates for the  $\beta_i$ . Estimated variances for the real-scale  $f_{0,i} = e^{\beta_i}$  were calculated using the delta method (Seber 1982). Thus:

$$\text{var}(e^{\beta_i}) = \left( \frac{\partial e^{\beta_i}}{\partial \beta} \right)^2 \text{var}(\beta_i)$$

or

$$\text{var}(e^{\beta_i}) = (e^{\beta_i})^2 \text{var}(\beta_i)$$

Expanding this calculation to the variance of the total estimated abundance,  $\sum N_i$ , the row vector of  $e^{\beta_i}$ 's was multiplied by the variance-covariance matrix of  $\beta_i$ 's, and the product post-multiplied by the column vector of  $e^{\beta_i}$ 's:

$$\text{var}(\sum N_i) = [e^{\beta_i}]^T \bullet [\text{var cov}] \bullet [e^{\beta_i}].$$

Having obtained estimates of total abundance and its variance, 95% confidence intervals were calculated following Rexstad and Burnham (1991).

Abundance estimates from systematic censuses were compared with the total number of seals identified from all (including non-census) sightings within a season. Discrepancies between the two could occur if some animals were present only during the portion of the season when censuses were not conducted. The census period was defined as the dates between the first and last census in a given field season. Sightings of seals never seen during any census were examined to determine whether they suggested the populations were not closed during the entire field season. For each data set, these seals were categorized as seen only before the first census, seen only after the last census, seen only before and after the census period, and seen at least once during the census period (though only during a non-census sighting).

To investigate possible sources of capture heterogeneity, logistic regression analysis of the binary response “seen” or “not seen” during censuses was used to investigate whether size, sex, location, adult tag status, and interactions among these variables significantly influenced which seals were never seen during census. Each of the

12 data sets was analyzed separately because differing site physiography and year-specific patterns in sighting effort could influence individual capture heterogeneity. Data from the same site in different years were not combined, as many individuals were present both years, and their observations would likely be non-independent. Fisher's exact test was used when the number of seals not seen on census was sufficiently small that expected values in simple contingency tables were less than 1, or when 20% of expected values were less than 5 (Zar 1984).

## RESULTS

### *Data sets*

A variety of scenarios is represented in the selected data sets (Table 2.1, Figure 2.2). These include single island subpopulations (Laysan and Lisianski) with 3-5-month-long field seasons and a large number of censuses (capture occasions), small atolls (Midway and Kure) usually with long seasons and many censuses, and finally large complex atolls with numerous islets (French Frigate Shoals and Pearl and Hermes Reef), either short or long field seasons but a relatively low number of census. The number and distribution of censuses over time within the total period of field effort also varied (Figure 2.2).

### *Best fitting models from Program MARK*

The parameters found to significantly influence  $p$  and  $c$  varied substantially among the data sets (Table 2.1); however, some patterns emerged. First, models with time-dependent capture probabilities had the worst AICc values among all models fitted for all data sets. A second feature was that for all but one of the 12 data sets, models with distinct parameters for initial capture ( $p$ ) and recapture ( $c$ ) probabilities performed better than those with equal initial and recapture probabilities. However, there was no

discernable pattern in these differences. In some data sets,  $c$ 's tended to be greater than  $p$ 's, in others the opposite was found. Even within data sets there was variability such that some size/sex groups had higher  $p$ 's and others had higher  $c$ 's at the same location and year.

Accounting for size and sex improved fits to every data set (Table 2.1). This did not necessarily mean that each size (juvenile, subadult, adult) and sex combination had different capture probabilities, rather that at least one size/sex group differed from the others. In half the data sets, tagged animals had significantly higher estimated capture probabilities. Finally, for most of the multi-islet atoll data sets, first capture location influenced capture or recapture probabilities for some groups of animals, though not consistently. That is, there were often size  $\times$  location and sex  $\times$  location interactions in capture probabilities.

For each data set, numerous models with a wide variety of parameters were evaluated, and the quality of the fits differed greatly as assessed by AICc. However, each model tended to produce very nearly exactly the same estimate of total abundance. Thus, while one could definitively determine which of a suite of models fit best, this selective process had no real bearing on the parameter of ultimate interest,  $N$  (a typical example is presented in Table 2.2).

#### *Abundance estimates*

Total estimated abundance from all types of capture-recapture models examined were compared to the total number of seals identified during systematic census, and the total number identified during both census and non-census observations (Figure 2.3). In the majority of cases, capture-recapture analysis underestimated true abundance, and the estimated population size was equal to, or just slightly larger than, the total number seen on census. This was typically much lower than the total number of individual seals known

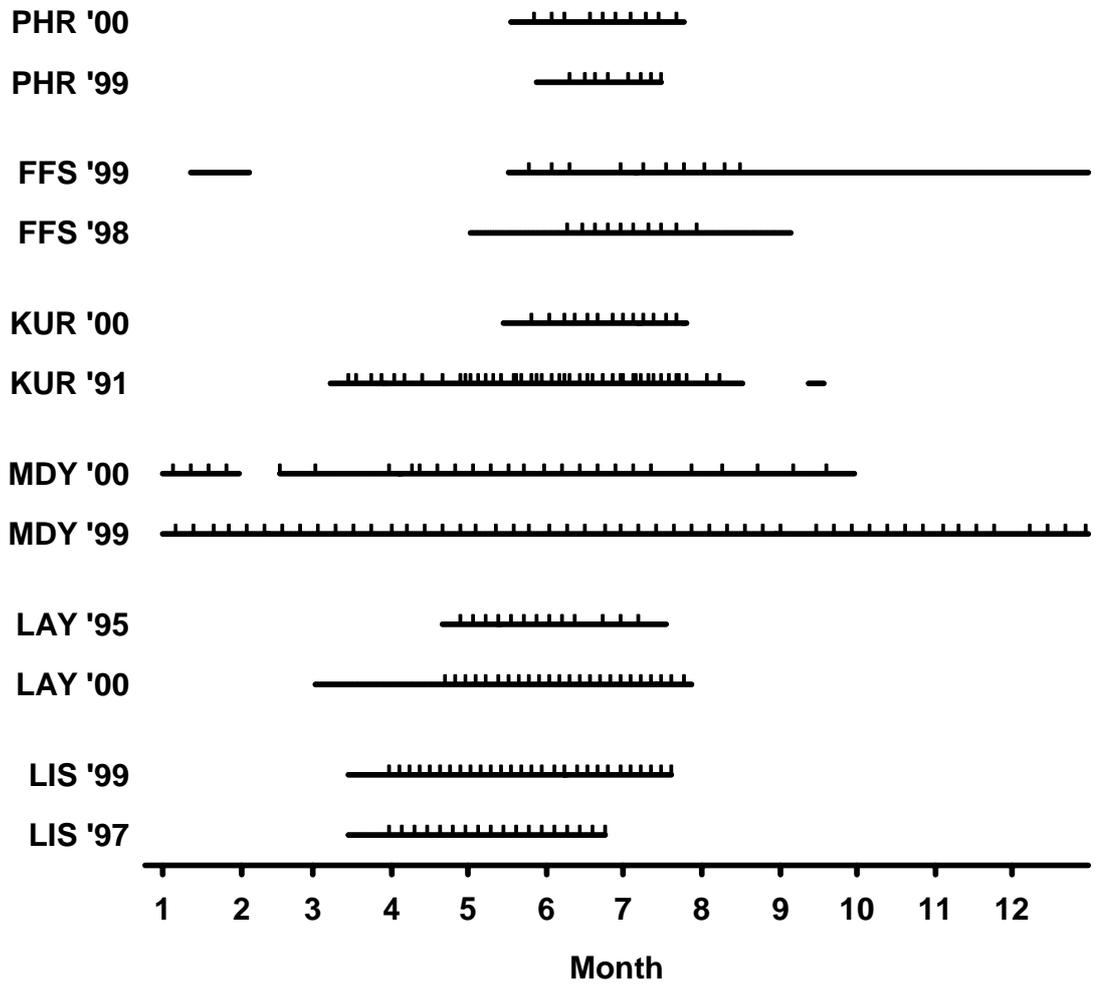


Figure 2.2. Duration of field effort (solid lines) and timing of systematic census (vertical marks) of Hawaiian monk seals for 12 analyzed datasets. PHR = Pearl and Hermes Reef, FFS = French Frigate Shoals, KUR = Kure Atoll, MDY = Midway Atoll, LAY=Laysan Island, LIS = Lisianski Island.

Table 2.1. Data sets selected for capture-recapture estimation of monk seal subpopulation abundance. “X’s” indicate that the factor in the column heading was found to significantly influence either initial capture probability ( $p$ ), recapture probability ( $c$ ), or both in Program MARK closed capture models.

Subpopulation	Year	Site description	Field effort (d)	Number of censuses	Size	Sex	Tag status	Location
Lisianski	1997	single island	102	18	X	X		N/A
Lisianski	1999	single island	128	28	X	X		N/A
Laysan	2000	single island	149	24	X	X	X	N/A
Laysan	1995	single island	89	13	X	X		N/A
Midway <sup>3</sup>	1999	3-islet atoll	365	50	N/A	N/A	N/A	N/A
Midway <sup>4</sup>	2000	3-islet atoll	258	27	X	X	N/A	N/A
Kure	1991	2-islet atoll	170	44	X	X	X	X
Kure	2000	2-islet atoll	73	13	X	X		X
French Frigate Shoals	1998	9-islet atoll	127	10	X	X	X	
French Frigate Shoals	1999	9-islet atoll	253	10	X	X	X	X
Pearl and Hermes Reef <sup>5</sup>	1999	8-islet atoll <sup>6</sup>	50	8	X	X	X	N/A
Pearl and Hermes Reef	2000	8-islet atoll <sup>6</sup>	69	10	X	X		X

<sup>3</sup> All groups were combined together (any subdivision of groups precluded model convergence).

<sup>4</sup> Only analyzed sex and size groups (distinction of tag status and location groups precluded model convergence).

<sup>5</sup> Only analyzed sex, size, and tag status (location could not be analyzed due to low sample sizes in certain size-sex-location groups).

<sup>6</sup> At Pearl and Hermes Reef there are seven permanent islets and a small number of scattered ephemeral sand spits sometimes used by seals.

Table 2.2. Sample of several models fitted to the French Frigate Shoals 1998 monk seal capture histories using Program MARK. Groups consisting of combinations of size (juvenile, subadult, or adult), sex, and two within-atoll location categories were examined. Model parameterization is denoted for  $p$  (initial capture probability), and  $c$  (recapture probability). The symbol “\*” (*i.e.* size\*sex) denotes all additive and interaction terms. AICc and  $\Delta$ AICc are ranked with the best model on top. Note that while model performance based upon AICc varied widely with a simple model being clearly best, the estimated total abundance ( $N$ ) varied little.

	Model				
$P$		$C$	AICc	$\Delta$ AICc	$N$
adult males vs all others	adult males vs all others		1702.06	0	279.8
size*sex	size*sex		1712.00	9.94	280.0
size*sex	size*sex*loc 2-way interactions only		1714.73	12.67	280.0
size*sex*loc 2-way interactions only	size*sex*loc 2-way interactions only		1722.43	20.37	280.8
size*sex*loc w/ 3-way interactions	size*sex*loc w/ 3-way interactions		1726.23	24.17	281.6
time dependence and additive size, sex, location effects	time dependence and additive size, sex, location effects		1861.13	159.07	267.0

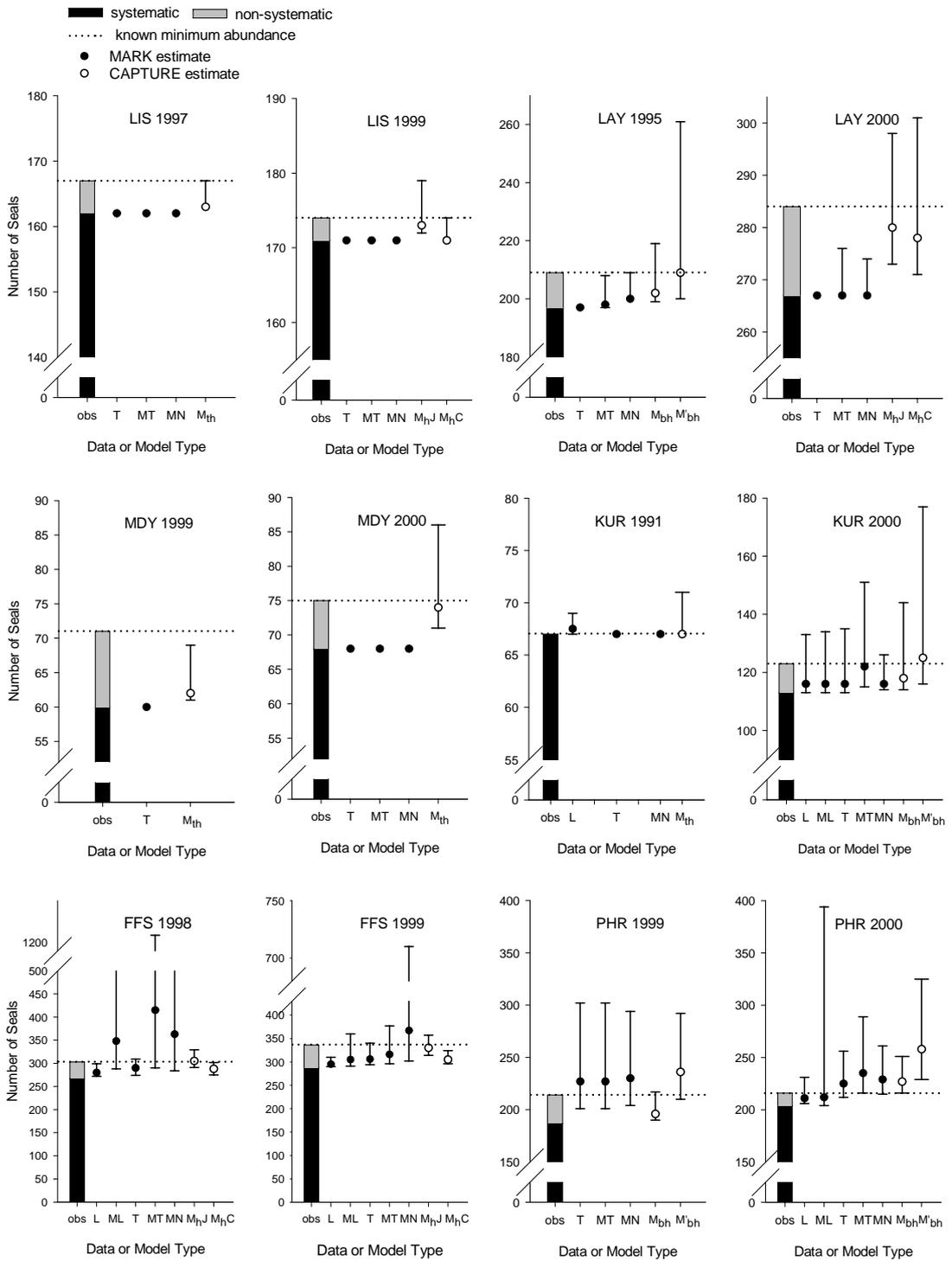


Figure 2.3. Comparison of capture-recapture estimates with known minimum population abundance of Hawaiian monk seals for 12 datasets. Observed number of animals seen during census (black bar), plus those seen during non-census activities (grey bar), constitute known minimum abundance (dotted line). Estimated abundances from various Program MARK models are indicated by solid circles with 95% confidence intervals. Lack of confidence intervals indicates the estimated error was essentially zero. Model types are: L = Location (grouped according to islet where first sighted), ML = Mixture model with location, T = adults grouped according to tag status, MT = Mixture model with tag status, MN = Null mixture model. Open circles and 95% confidence intervals indicate Program CAPTURE estimates. Model types are coded:  $M_{hJ}$  = jackknife estimator with individual heterogeneity,  $M_{hC}$  = Chao's heterogeneity estimator,  $M_{th}$  = time dependence and heterogeneity,  $M_{bh}$  = removal method behavioral response and heterogeneity, and  $M'_{bh}$  = Pollock and Otto behavior response and heterogeneity.

to have been present when non-census sightings were included. In about half of the Program MARK models, the upper 95% confidence limits for total abundance were lower than the known minimum abundance (Figure 2.3).

In particular, analysis of the single-island and small-atoll subpopulations (Laysan, Lisianski, Midway and Kure) produced negatively biased estimates of abundance. Also, because of the large number of censuses conducted at these sites, the estimated variance of abundance was small, often essentially zero. Mixture models did not correct the negative bias in abundance for these data sets, rather they tended to produce larger variance estimates.

Models fitted to the data from large multi-islet atolls with relatively few (8-10) censuses, produced somewhat varying results (Figure 2.3). At French Frigate Shoals, the simple closed-capture models produced negatively biased abundance estimates. Several of the mixture models produced point estimates greater than the known minimum abundance, and all had upper confidence limits exceeding that number. However, the width of the confidence intervals was often very large (*e.g.*, French Frigate Shoals, 1998 in Figure 2.3). Estimates for Pearl and Hermes Reef differed in that most models produced point estimates of abundance that exceeded known minimum abundance. Again, many of the estimates were imprecise with extremely high upper confidence limits.

Program CAPTURE tended to produce more useful results. Estimates were frequently less negatively biased and confidence intervals were by and large better behaved (*i.e.*, neither unrealistically small nor too large to be practically useful). Notably, the algorithm always selected model types that included heterogeneity effects. These models and their usual abbreviations in the capture-recapture literature include two

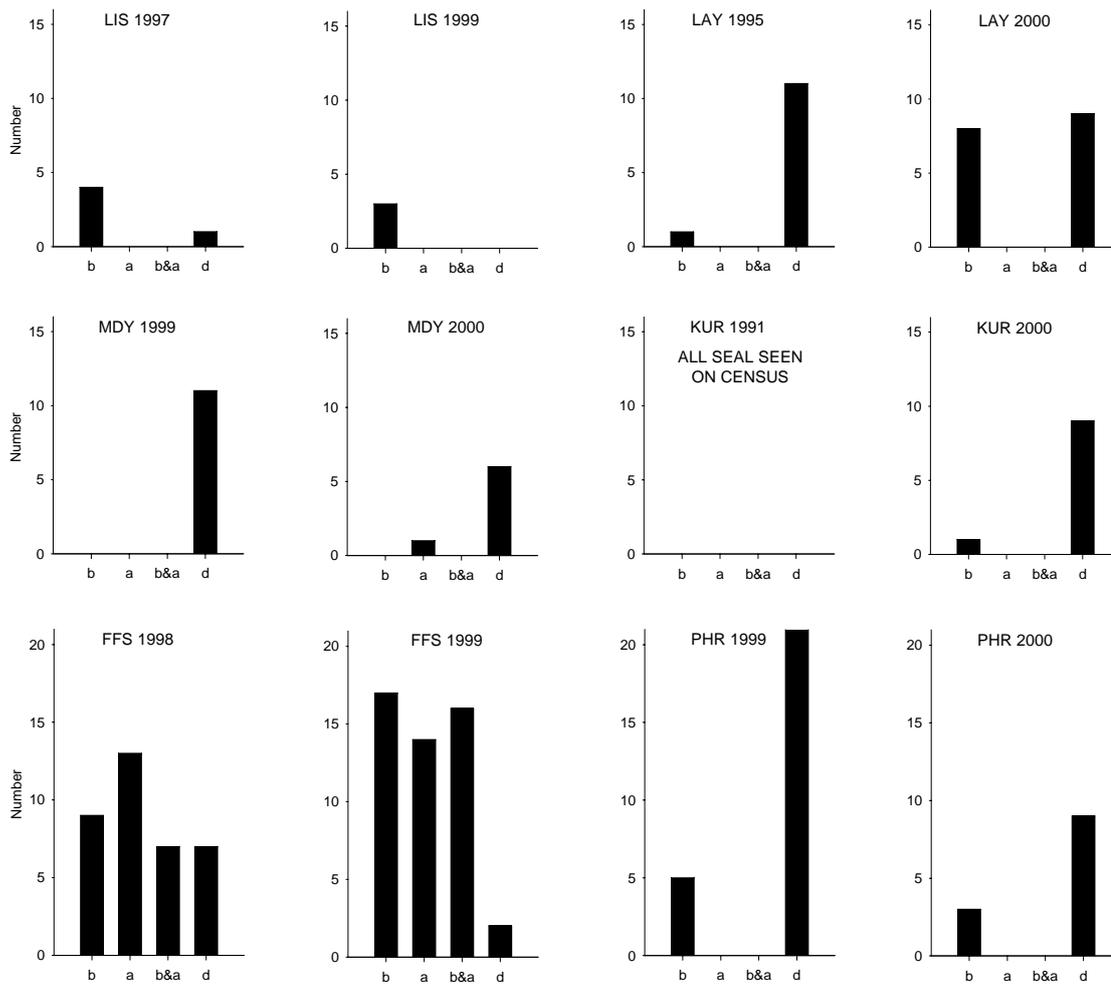


Figure 2.4. For 12 modeled data sets, the number of individuals seen only during non-census activities, according to the timing of their sightings relative to the census period: b = only before, a = only after, b and a = only before and after, but not during, and d = during the census period but not during any actual census survey.

involving individual heterogeneity (jackknife estimator  $M_h$ , Burnham and Overton 1978, 1979; and Chao's  $M_h$ , Chao 1989), one with time and heterogeneity effects ( $M_{th}$ , Chao *et al.* 1992) and two with behavioral response to capture and heterogeneity (removal  $M_{bh}$ , Otis *et al.* 1978, and Pollock and Otto 1983  $M_{bh}$ ).

*“Un-captured” individuals*

With the exception of those at French Frigate Shoals, most seals sighted only during non-census activities were seen at least once between the first and final census (Figure 2.4). Thus, they were alive and present at least some of the time when systematic censuses were being conducted, but they were not captured during those events. In some cases the census period encompassed virtually the entire field season (*i.e.*, at Midway Atoll), leaving little opportunity for sighting outside that period. In other cases significant non-systematic sighting effort before or after the census period occurred (*i.e.*, French Frigate Shoals, Figure 2.2). Even at French Frigate Shoals, most of the seals missed on census were seen either during, after, or only before and after the census window. These seals were alive during the census period, but some may not have been present at the site during the systematic surveys. The few seals seen only before the census period might have died prior to the census period.

No individual characteristics were found to consistently explain why certain individuals were “trap shy” (not sighted during census). Logistic regression analysis of the 12 data sets examined found that adult tag status and islet location had no significant influence on whether seals were seen on systematic surveys. For both years at Lisianski Island and Kure Atoll in 1991, too few seals were unseen on censuses to allow statistical analysis. At Laysan Island (both years) and Kure Atoll in 2000, no significant effects were detected.

At the remaining sites, age and sex class were sometimes related to whether seals were seen on census, but no consistent pattern emerged. At Midway Atoll, there was some suggestion that juveniles were more likely to be seen during census than adults or subadults. All Midway juveniles were sighted on at least one census, while 20% in 1999 and 12% in 2000 of older animals were not seen on any census (1999,  $p = 0.06$ ; 2000,  $p = 0.33$ ). In contrast, at Pearl and Hermes Reef, juveniles tended to be less likely seen on censuses than older seals in 1999 ( $p = 0.06$ ). In 2000, specifically juvenile females were less likely to be seen compared to all other groups ( $p = 0.004$ ). Finally, at French Frigate Shoals in 1999, there was a strong tendency for males to be missed on census compared to females, without regard to size class ( $p = 0.008$ ). At the same site in 1998, no significant effects were found.

## DISCUSSION

All data sets examined involved small populations (< 500 individuals) with ample capture occasions, and analyses were stratified with respect to characteristics believed likely to influence capture probability (*i.e.*, sex, size, etc.). It is notable that even under these seemingly favorable conditions, the capture-recapture abundance estimates obtained were quite often poor, mainly due to negative bias. Eberhardt *et al.* (1999) applied a relatively simple capture-recapture method (Manly-Parr, Seber 1982) to Hawaiian monk seal census data from Laysan Island and also obtained estimates that were negatively biased.

Two assumptions, population closure and homogeneity of capture probabilities, were most likely subject to violation. Because young-of-the-year were excluded from the analyses, lack of population closure could involve only death, immigration, or emigration during the capture period, all of which could have occurred to some extent. However,

lack of population closure within the census period will tend to negatively bias capture probability estimates, thereby causing an overestimation of abundance (Otis *et al.* 1978). Thus, violation of population closure could not account for the pattern of underestimation found in the present analysis. If a significant number of animals had been identified on non-systematic sightings then subsequently died prior to the systematic capture period, this could indeed lead to capture-recapture estimates lower than the known minimum abundance. However, the number of animals seen only before the census period could account for only a relatively small portion of the negative bias (Figure 2.4).

In contrast, individual capture heterogeneity leads to negative bias in population estimates (Otis *et al.* 1978). It is clear from the significant effects of sex, size, tag status, and location (Table 2.1) that all individual monk seals did not have equal capture probabilities. Yet estimates remained negatively biased even after stratification, indicating that individual capture heterogeneity likely existed that could not be ascribed to these characteristics. It is possible that the particular habits of seals coming and going to land and sea, individual daily activity patterns, etc., yielded individual capture heterogeneity.

In some cases, mixture models (Norris and Pollock 1995, Pledger 1998, 2000) yielded upper confidence limits that included the known minimum abundance (Figure 2.3). However, the reduction in bias came at a high cost in terms of precision. Estimates from most of the mixture models were so uncertain that they would be virtually useless for monitoring trends over time.

Program CAPTURE performed best among the model types examined and, while still prone to negative bias, may nevertheless prove useful in characterizing population trends in Hawaiian monk seals. Notably, the model selection algorithm always gave highest rank to estimators involving capture heterogeneity (sometimes with time

dependence and/or behavioral response). Thus, varying combinations of factors seemed to influence the capture histories observed in different years at various sites, while individual heterogeneity was always present.

Because they partition their time between land and sea (and can typically only be captured on land), pinnipeds may exhibit especially high levels of capture heterogeneity compared to either entirely terrestrial or aquatic animals. Nevertheless, other studies which appraised capture-recapture estimates relative to known abundance suggest that heterogeneity is common and failing to validate model performance or assumptions may lead to incorrect inference. Even in a very controlled experimental situation, Edwards and Eberhardt (1967) found that capture-recapture estimates of a known number of cottontails in an enclosure were negatively biased. Pledger (2000) re-analyzed Edwards and Eberhardt's cottontail data using a two-mixture heterogeneity model and found that while estimated  $N$  was close to the known value, the upper confidence limit was very high.

While rare relative to the overall application of capture-recapture methods, researchers have found various clever ways to evaluate abundance estimators for their particular species of interest under natural conditions (Boulanger and Krebs 1994, Cross and Waser 2000, Greenwood *et al.* 1985, Koper and Brooks 1998, Manning *et al.* 1995, Mares *et al.* 1981, and Strandgaard 1967). All of these studies save one (Cross and Waser 2000) found evidence for capture heterogeneity which led to negative bias among estimators. The studies which evaluated Program CAPTURE along with other methods, found that CAPTURE performed best (particularly heterogeneity models,  $M_h$ ,  $M_{bh}$ ,  $M_{th}$ ). This pattern is consistent with the monk seal results. Authors often, though not always (Koper and Brooks 1998) concluded that they had identified an estimator that, though to some degree biased, was adequate for their purposes. Universally, it was clear that without independent validation, there would have been little basis for model selection.

The Hawaiian monk seal data are quite unique in that it has been possible to obtain good minimum abundance estimates for some subpopulations and years. Without this information, one would have been tempted to erroneously conclude that various estimates were reliable. While such reference points are rarely available, a practical general approach (used here and in the validation studies described above), is to select representative, tractable demographic units for which simultaneous capture-recapture sampling and exhaustive enumeration can be accomplished. The model or models that perform best can subsequently be applied to the broader population of interest with greater confidence and justification. Dorazio and Royle (2003) similarly suggest that prior knowledge about sources of heterogeneity is desirable to help select among classes of mixture models. This seems especially germane when one is keenly interested in why a certain model is best. In the practice of conservation and management, it may frequently be that determining which model type produces the most reliable inference is paramount, regardless of the underlying dynamics. In such circumstances, the approach offered above may be helpful.

New capture-recapture methods are continually developed and added to a long list of abundance estimators designed to better address heterogeneity and other issues (*e.g.*, Schwarz and Seber 1999, Yip *et al.* 2000, Durban 2002, Dorazio and Royle 2003). The capture-recapture literature is replete with numerous simulation and fewer empirical studies confirming that valid inference can be quite sensitive to model selection. Yet, in practice, the choice is all too often made in the absence of corroborating information.

#### ACKNOWLEDGEMENTS

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## Chapter 3. Use of discovery curves to assess abundance of Hawaiian monk seals<sup>7</sup>

### ABSTRACT

We investigated the pattern of first sighting of individual seals over the course of a field season, or the “discovery curve,” as a means for estimating abundance of the endangered Hawaiian monk seal, *Monachus schauinslandi*. We empirically derived a criterion to determine whether or not total enumeration had been accomplished at a given site and year. When greater than 100 h field effort was expended without a new individual being identified, we concluded that total enumeration was likely achieved. To evaluate the potential for estimating abundance through extrapolation of non-linear asymptotic functions fitted to discovery curves, we conducted simulations under a range of capture probability scenarios, including some based on observed individual variability in monk seal sighting frequencies. We demonstrated that if capture heterogeneity existed among individuals, the fitted asymptotes tended to yield biased estimates of abundance. Moreover, the levels of bias and uncertainty tended to decrease with the proportion of the population identified. While extrapolation shows little promise for generating unbiased abundance estimates, discovery curves have practical appeal for determining whether total enumeration has been achieved, and for optimizing field effort allocation. This is especially true for relatively small, closed populations of marked individuals.

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## INTRODUCTION

Reliable abundance information is critical for the conservation and management of rare species. Precise estimates of abundance reduce the time required to detect population declines and allow more powerful evaluation of management interventions. Furthermore, the factors that drive population trends may be more readily detected when trends in abundance are better characterized.

Populations consisting, at least in part, of individually identifiable animals are especially well suited for abundance estimation. Typically, some form of capture-recapture method is used to estimate population size based on individual sighting histories (e.g., Otis *et al.* 1978, Seber 1982, Schwarz and Seber 1999). Additionally, examination of “discovery curves,” the number of unique individuals identified plotted against some measure of search effort, is often used in studies of cetaceans and nesting marine turtles to judge whether total enumeration has been achieved or to indicate whether a population is open or closed (e.g., Williams *et al.* 1993, Karczmarski *et al.* 1999; Wilson *et al.* 1999; Limpus *et al.* 2001). This approach is especially applicable to relatively small, localized populations comprised of readily identifiable individuals.

The Hawaiian monk seal (*Monachus schauinslandi*) is an endangered species, primarily inhabiting the remote Northwestern Hawaiian Islands (NWHI) and predominantly distributed among six subpopulations each composed of up to a few hundred seals (Figure 3.1) (Ragen and Lavigne 1999). Abundance trends have historically been characterized using an index of population-size termed “beach counts,” tallies of all seals on land at a given time (Kenyon and Rice 1959). Substantial declines in these counts led to the species being listed as endangered under the U.S. Endangered Species Act in 1976 (U.S. Department of Commerce 1976*a,b*).

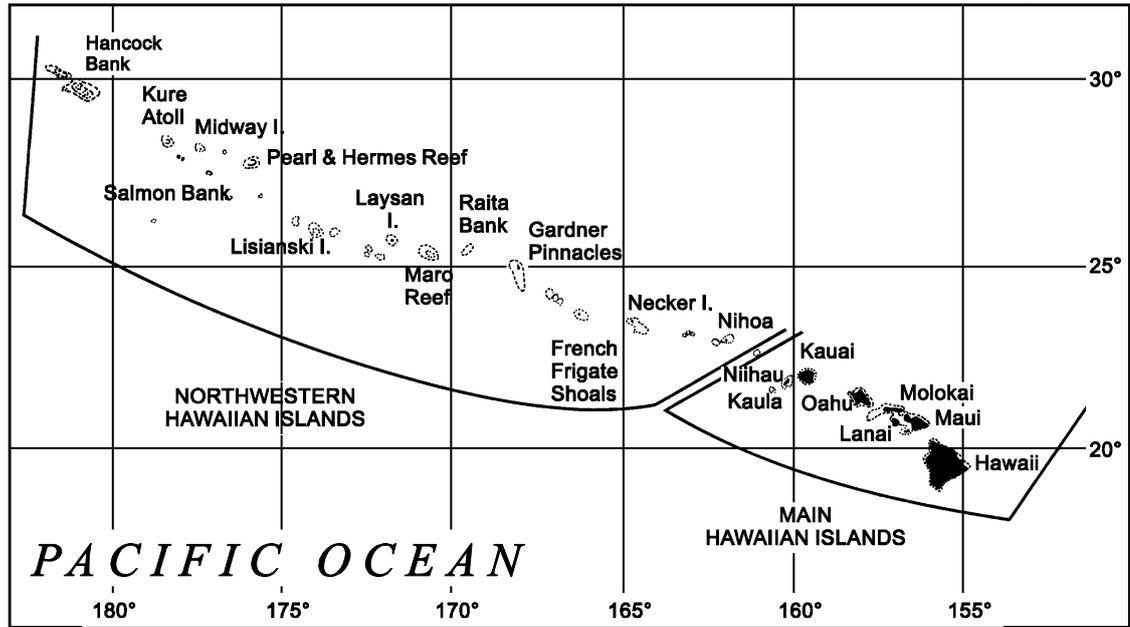


Figure 3.1 The Hawaiian Archipelago, showing the main Hawaiian Islands and the monk seal populations in the Northwest Hawaiian Islands.

The mean beach count index is useful because it is relatively easy to obtain and provides a comparable measure available over several decades. However, while beach counts seem to provide a good indication of long-term trends, they poorly reflect year-to-year changes in populations (Eberhardt *et al.* 1999). Also, total abundance information is preferable to indices for various applications, including estimating sustainable incidental take levels in commercial fisheries (*e.g.*, under the Marine Mammal Protection Act, Wade 1998), and providing input to demographic (*e.g.*, Harting 2002) and bioenergetic models (Polovina 1984).

Chapter 2 evaluated a variety of closed capture-recapture estimation methods and determined that they generally produced negatively biased estimates of Hawaiian monk seal abundance, likely due to capture heterogeneity. Among the models examined, the estimators available in Program CAPTURE (Otis *et al.* 1978, White *et al.* 1982, Rexstad and Burnham 1991) tended to be least negatively biased.

Total enumeration is a possible alternative to estimating abundance using capture-recapture methods. Individual monk seal subpopulations are relatively small, and field seasons last for several months. Throughout the field season, effort is made to identify individual seals using natural and applied marks, generating an accumulating list of identified animals. At some sites and years, continued effort no longer results in the sighting of individuals not previously identified in that season at that site, suggesting that all animals in the subpopulation may have been counted. Yet, no criteria exist for distinguishing with confidence when total enumeration may have been achieved.

The species accumulation and species-area literature addresses issues relating to the form of curves representing either the discovery of new species with field effort within a designated area, or the relationship between the number of species and size of area sampled. Fisher *et al.* (1943) and Good and Toulmin (1956) are classic papers in this

area, and Flather (1996) and Tjørve (2003) examine a suite of non-linear functions proposed to represent species accumulation and species-area relationships. Others have specifically focused on using such relationships to estimate the total number of species by extrapolation (Soberon and Llorente 1993, Colwell and Coddington 1994, Ugland *et al.* 2003).

In this paper, we develop an empirically derived criterion based on discovery curves to determine whether a population has been fully enumerated. We also explore the potential for estimating abundance of partially enumerated populations using observed patterns of accumulation of new individuals within field seasons. Specifically, we test whether models used in species accumulation analyses can produce reliable estimates of population abundance through extrapolation.

## METHODS

### *Individual Identification*

The six main Hawaiian monk seal subpopulations in the NWHI are either single islands (Laysan and Lisianski) or atolls containing two to nine islets where monk seals come ashore to rest and rear offspring (French Frigate Shoals, Pearl and Hermes Reef, Midway Atoll and Kure Atoll, Chapter 2, Figure 3.1). This study focuses on the six NWHI subpopulations where most of the species occurs and where, throughout field seasons typically lasting from 2 to 5 months or more, seals were identified during shoreline surveys. Most of these seals were identifiable by unique alphanumeric colored plastic tags on each hind flipper. Photographic and hand-drawn records of natural markings (shark bite and other scars, permanent natural pelage patterns) were also collected and updated annually (Harting *et al.* 2004). Finally, to facilitate resighting seals

and to provide a unique mark for those without tags or distinguishing natural marks, most seals were given temporary marks by bleaching their pelage.

As field seasons progressed, the list of uniquely identifiable individual seals was incremented. This process was straightforward for tagged seals and untagged seals once they were bleach-marked but is more complicated for others. Unknown seals were often assigned 'temporary' identities during individual surveys to facilitate their ultimate identification, and sometimes an individual seal received more than one temporary identifier. Thus, the number of unique seals in a subpopulation is less than the total number of identifiers assigned. For this investigation, we used only data from years and sites where rigorous protocols were followed to determine the unique status of seals with temporary identities.

True population abundance is variable as animals are born and die so that the time period to which an abundance estimate is being ascribed should be explicit. For example, the total number of individuals alive in a calendar year is greater than the highest number alive at any one time. Because it is impossible to instantaneously estimate abundance in the field, we designated a time period during which animals had to have been alive to be considered part of the population. We have adopted the convention that only seals seen during March to August were considered members of a Hawaiian monk seal population. Most field effort has historically occurred within this period, so this criterion could be consistently applied to all years and sites, while taking advantage of as much available data as possible. The few pups born outside March to August and their mothers were also counted. Additionally, some individuals moved between subpopulations and were identified at more than one site per year. To avoid double-counting individuals when subpopulation abundances were tallied, each seal was assigned to a single subpopulation in a given year using the following conventions. Adult females were assigned to the

subpopulation where they gave birth, if known. Pups were assigned to the subpopulation where they were born. If neither of the preceding conditions applied, seals were assigned to the subpopulation where they underwent moult. Finally, if moult was not observed, seals were assigned to the subpopulation where they were seen closest to 15 May.

#### *Discovery curves*

The cumulative number of unique seals identified in a given subpopulation within a given year plotted against cumulative field effort is called the discovery curve.

Observers recorded when they began and ended daily surveys so that the number of person-hours of survey time expended was used to characterize effort for both systematic censuses and non-systematic surveys. To uniformly sample the accretion of new seals throughout a field season, the total number identified was tallied, as closely as possible, at 10 h intervals.

Our goal was to determine how informative the observed accumulation patterns were for revealing the true number of seals in the population. We expected that the number of new individuals would increase rapidly at the beginning of the season and, if field effort were sufficient, an asymptote would eventually be attained, representing total abundance. One objective was to develop criteria for determining when saturation sampling had occurred and all individuals in the population had been identified. Another aim was to determine whether we could extrapolate to reliably predict total abundance when the asymptote was not reached during a field season. The validity of such an approach requires a few simple assumptions.

1) Observers continuously attempt to identify new individuals throughout the field season;

2) There is no 'un-catchable' segment of the population, meaning that there are no seals that either never land or cannot be identified;

3) There are no additions to the population during the season that would cause true abundance to climb. This also means that the rate at which new individuals are discovered per unit effort should generally decline as the season progresses. We also assume that the number of seals that die during March to August prior to being identified is negligible.

The first assumption was met by confirming that, for all datasets analyzed, appropriate field protocols were in place such that observers regularly attempted to identify all seals present. Regarding the second assumption, all monk seals are believed to come ashore to give birth, moult, socialize, or rest. Thus, given sufficient field effort, all should eventually be available on shore to be identified either by tags, natural marks, or bleaching. Most monk seal births occur during spring and summer (Johanos *et al.* 1994), which contradicts the third assumption. Therefore, this analysis was restricted to animals older than pups. Pup production was assessed by documenting births that occurred during field seasons and tagging weaned pups present when teams arrived. Because field seasons occurred during the pupping season and pups typically remain near their birth site for approximately 2 months post-weaning (Henderson and Johanos 1988), pup production estimates are probably near complete.

To develop criteria for determining when, for practical purposes, total population enumeration had been achieved, we calculated the number of additional seals discovered following effort intervals of varying length when no new seals were identified. For each dataset, we determined the duration of these flat intervals with no new seals, then counted any new seals seen during the remainder of the field season. This indicates the likelihood that uncounted seals remain, given the amount of field effort expended with no new sightings. This approach is valid only if sufficient field effort is conducted following the start of a flat interval, so that yet-undiscovered seals would have a high likelihood of

being detected if present. We therefore considered only cases when at least 100 additional hours of effort were expended following the start of flat periods.

To explore abundance estimation using sighting accumulation data, we fitted a variety of asymptotic non-linear functions commonly found in the species accumulation (and species-area) literature (reviewed in Flather 1996, Tjørve 2003, Table 3.1<sup>8</sup>). This approach was evaluated using both simulated and field data. For simulations, we defined a hypothetical population consisting of 200 seals subdivided into as many as 20 groups, each group having a unique capture probability and comprising a specified proportion of the total population. At each simulated field effort time step, the status of each “un-captured” seal in the population was tested by comparing a number between 0 and 1 randomly drawn from a uniform distribution against the specified capture probability for the group to which the seal belonged. If the random number was greater than or equal to the operative capture probability, the seal was “captured”. With each capture, the cumulative number of seals detected at that effort step was incremented.

To test how the functions performed given different levels of field effort, curves were fitted to simulated detection of varying portions of the total population. First, to simulate field situations where the population is enumerated and effort continues with no new discoveries, curves were fitted to simulated datasets with all 200 seals captured plus 500 h additional effort after the last seal was identified. Next, to simulate incomplete sampling, we fitted curves to the same simulations truncated when 90% and 80% of the true population had been captured (that is, the effort steps at which the cumulative number of seals reached 180, and 160 seals).

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<sup>8</sup> We also explored some alternative function forms implemented in CurveExpert software (CurveExpert 1.38 by Daniel Hyams, [www.curveexpert.webhop.net](http://www.curveexpert.webhop.net), 1698 Chadwick Court, Hixson, TN 37343. Copyright © 1995-2003 Daniel Hyams.)

Table 3.1. Candidate asymptotic functions fitted to discovery curve data. Functions were drawn from those proposed for species accumulation and species-area analyses as reviewed in Flather (1996) and Tjørve (2003).

Model	Type	Function
Negative exponential	Convex	$y = a(1 - e^{-bx})$
Asymptotic regression	Convex	$y = a - bc^{-x}$
Rational function	Convex	$y = (a + bx)/(1 + cx)$
Monod	Convex	$y = a/(b + x)$
Weibull <sup>a</sup>	Sigmoid	$y = a(1 - e^{-bx^c})$
Weibull <sup>b</sup>	Sigmoid	$y = a(1 - e^{-b(x-c)^d})$
Weibull <sup>c</sup>	Sigmoid	$y = a - be^{-(cx^d)}$
Morgan-Mercer-Flodin <sup>a</sup>	Sigmoid	$y = ax^b/(c + x^b)$
Morgan-Mercer-Flodin <sup>c</sup>	Sigmoid	$y = (ab + cx^d)/(b + x^d)$
Cumulative beta-P distribution	Sigmoid	$y = a(1 - (1 + (x/c)^d)^{-b})$
Chapman-Richards	Sigmoid	$y = a(1 - e^{-bx})^c$
Lomolino	Sigmoid	$y = a/(1 + b^{\ln(c/x)})$
Gompertz	Sigmoid	$y = ae^{-e^{-(b - cx)}}$
Extreme value	Sigmoid	$y = a(1 - e^{-e^{-(b+cx)}})$
Logistic	Sigmoid	$y = a/(1 + be^{-cx})$

<sup>a</sup>Formula used by Tjørve (2003)

<sup>b</sup>Formula used by Flather (1996)

<sup>c</sup>Formula used in CurveExpert 1.38 by Daniel Hyams (1995-2003)

Candidate functions were then fitted to the resulting points (cumulative number of seals at effort intervals of 10 h) using the Levenberg-Marquardt algorithm (Levenberg 1944, Marquardt 1963), for non-linear least squares regression, as implemented in IMSL Fortran subroutines (Visual Numerics 1999). In a simulation context, the automation of non-linear curve fitting frequently presents difficulties associated with non-convergence or unreasonable results from local minima or other data anomalies. To minimize these problems, we began by fitting each function in Table 3.1 to the mean of 1000 simulated discovery curves under each capture probability scenario. Performance was assessed using the percent relative bias in the estimated asymptote ( $100 \times [\text{estimated abundance} - \text{true abundance}] / [\text{true abundance}]$ ). In this way, we screened the 15 functions to identify those that tended to provide the least biased estimates of abundance, and subsequently proceeded with automated fitting of the best performing functions to new sets of simulated discovery curves. In this latter process, we filtered out extreme outliers that would likely be rejected by a reasonable researcher dealing with real field data. Manual inspection of curve fits revealed that very high asymptotes typically reflected poor fits to the data with very high regression error terms. We conservatively stipulated that any asymptote exceeding twice the true population size (400 seals) should be rejected. The simulations were repeated until 1000 acceptable realizations were obtained for each scenario.

Four different capture probability scenarios were explored. In the simplest case, all individuals were assigned the same capture probability. We next considered a relatively extreme case of heterogeneity, whereby two capture probabilities differing by a factor of 10 were each operative for half the population. While this may be unrealistic, it demonstrates the influence of a high degree of heterogeneity. Moreover, one might

encounter an analogous situation where two groups of animals, one resident and the other far ranging, overlap in the same study area.

To more realistically explore capture heterogeneity observed in monk seals, we extracted distributions of the number of times individuals were identified during a single field season as a proxy for capture heterogeneity. Two representative distributions, one from a single island subpopulation and another from a multi-islet atoll, were selected. To convert these distributions of the number of occasions observed to capture probabilities for simulations, we simply rescaled the *y-axis*. In this way, we maintained the shape of the distributions while obtaining capture probability values that were convenient for simulations. In all simulations, capture probabilities were scaled such that the entire simulated population of 200 individuals would be identified after 1,000-3,000 h of effort (Figure. 3.2). Thus, in scenarios based on observed sighting frequencies, the capture probabilities do not estimate true values, rather they represent the relative range and frequencies observed.

Curves were likewise fitted to two real data sets (Laysan Island in 1997 and Lisianski Island in 1999), for which the total populations had almost certainly been identified (based on criteria developed here). As with the simulations, non-linear functions were fitted to the full data sets (all individuals identified), and to discovery curves truncated when 90% and 80% of the individuals had been identified.

## RESULTS

### *Discovery curves and total enumeration*

Patterns in discovery curves varied markedly among the six sites examined (Figure 3.3). At Laysan and Lisianski Islands, an asymptote was usually attained. While this was not the case at other sites, the curves always showed a decline in the rate of accumulation, suggesting that extrapolation to an asymptote might provide a useful abundance estimate.

The amount of field effort varied from less than 200 h to over 1,500 h per season, differing greatly among subpopulations. The single island subpopulations (Laysan and Lisianski) consistently had more effort than the multi-islet atolls, except at Midway where there was extensive effort in some years. These differences resulted from variability in both duration of field seasons and accessibility. For example, while all shorelines were accessible daily at single island subpopulations, inter-islet travel time and weather conditions that precluded boating sometimes limited the amount of effort that could be expended per day at multi-islet sites.

Because of the long field seasons at Laysan and Lisianski Islands, these sites provided most of the empirical data for determining when total enumeration was accomplished. Periods with no new sightings were too rare at Kure Atoll and Pearl and Hermes Reef to reveal patterns. At Laysan and Lisianski, an average of less than one additional seal was discovered following periods of at least 100 h with no new sightings (Figure 3.4). This finding was not simply an artifact of the requirement that there be a minimum 100 h of subsequent effort. This rule had little influence as it excluded relatively few cases. There were no flat periods of 100 h at French Frigate Shoals, but the pattern emerging from shorter periods suggests that this criterion might reasonably apply. At Midway, the observed pattern was similar, with the exception of two cases from 1999 where flat periods between 150 and 200 h duration were followed by the discovery of several new seals (circled points in Figure 3.4). This seems to have been an artifact of unequal sampling effort and lack of population closure. Seals from the adjacent subpopulations at Pearl and Hermes Reef and Kure Atoll frequently visit Midway Atoll (Harting 2002). In 1999, field effort was year round at Midway but lasted only about 1.5 mo at Kure Atoll and Pearl and Hermes Reef allowing animals moving between these sites a greater opportunity to be seen and counted as members of the Midway population.

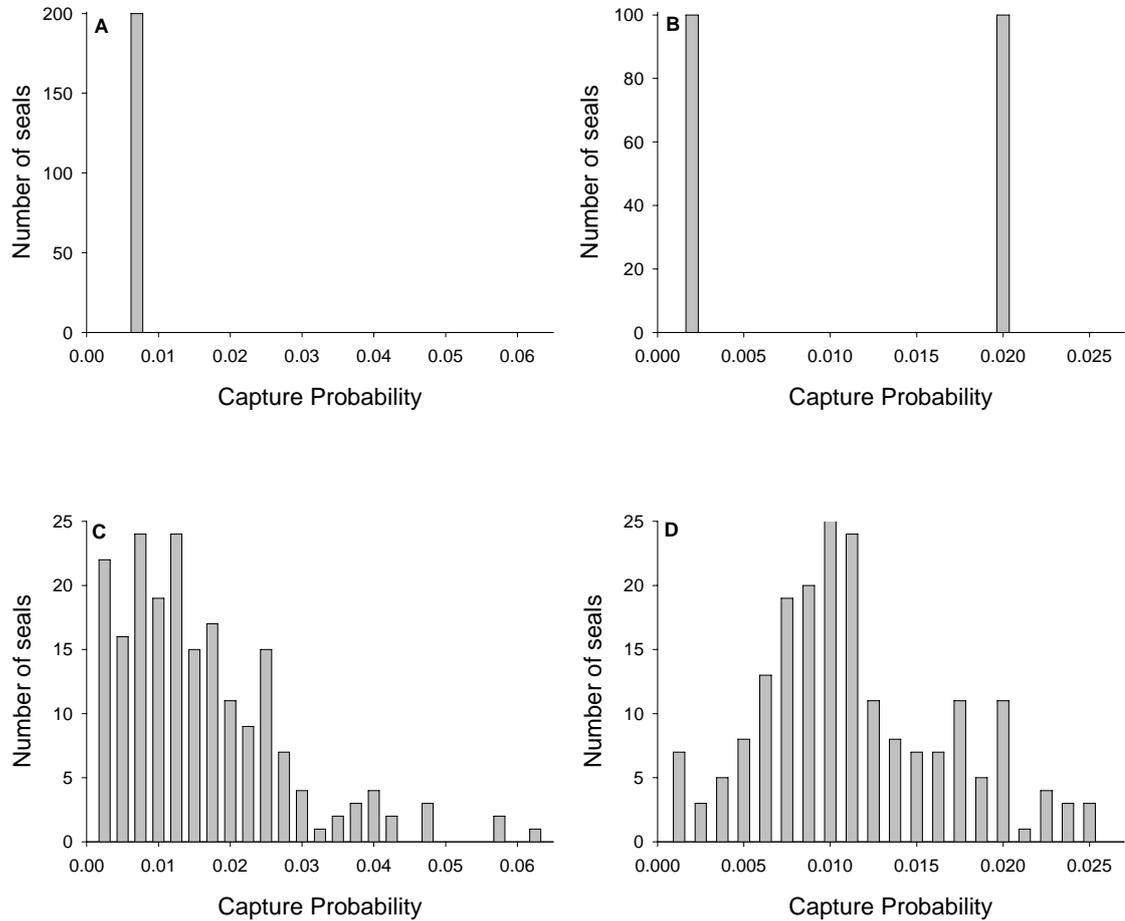


Figure 3.2. Distribution of capture probabilities operative for simulating discovery curve datasets for populations of 200 individuals under scenarios of A) Equal capture probabilities, B) high capture heterogeneity, and, reflecting the observed relative sighting frequencies of individuals at C) Pearl and Hermes Reef in 2002 and D) Lisianski I. in 2003. Capture probability units are per hour of effort.

The new seals observed at Midway after prolonged periods with no new sightings probably represent relatively recent migrants from the other atolls. Had field effort been as great at these other sites, those migrants would likely have already been counted as members of the other subpopulations.

Based on the preceding analysis, we conclude that a zero slope sustained for at least 100 h indicated that the population was very likely identified. Zero slopes sustained for somewhat less than 100 h suggest near total enumeration. Total enumeration was achieved in most years at Laysan Island, Lisianski Island and Midway Atoll. In contrast, the French Frigate Shoals, Pearl and Hermes Reef, and Kure Atoll populations were not fully enumerated.

To graphically represent whether a zero slope was achieved, and if so how long it was sustained, we plotted the slope of the line connecting each sequential point on the discovery curve from the beginning of the field season to the fixed point at the end of effort. The slopes obtained allowed us to place the accumulation curves into three informative categories. First, in many cases the slope never reached zero, indicating that new animals were still being discovered at the end of the field season and that the population was not totally enumerated (Fig. 3.5a). At the other extreme were cases in which a zero slope asymptote was attained and no new seals were observed even after hundreds of hours of additional effort, indicating that the population had been enumerated (Fig. 3.5b). Finally, there were intermediate cases where a zero slope was attained but not sustained for sufficient time to convincingly indicate total enumeration (Fig. 3.5c).

### *Simulations*

Bias in estimated abundance using asymptotes fitted to the means of 1000 simulated discovery curves varied greatly depending upon which function was used, the

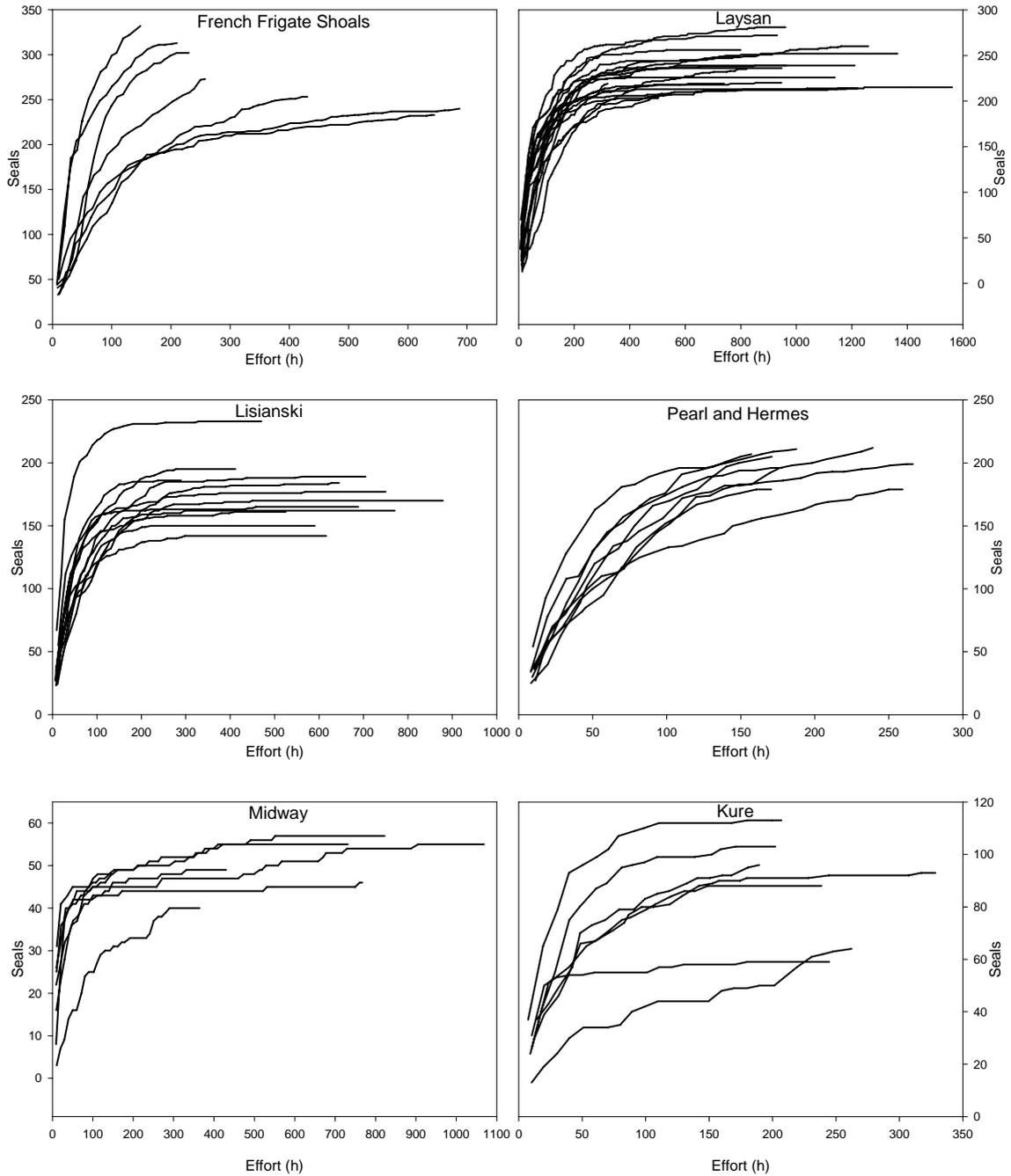


Figure 3.3. Discovery curves for several years at each of six Hawaiian monk seal populations. Cumulative total individuals (older than pups) identified is plotted against total hours of field effort. Years presented are those which were adequate for constructing discovery curves, including French Frigate Shoals and Midway (1997-2003), Pearl and Hermes Reef (1996-2003), Laysan (1983-1985, 1988-2003), Lisianski (1983, 1992-1993, 1995-2003), and Kure (1985, 1990, 1995, 1997-2003).

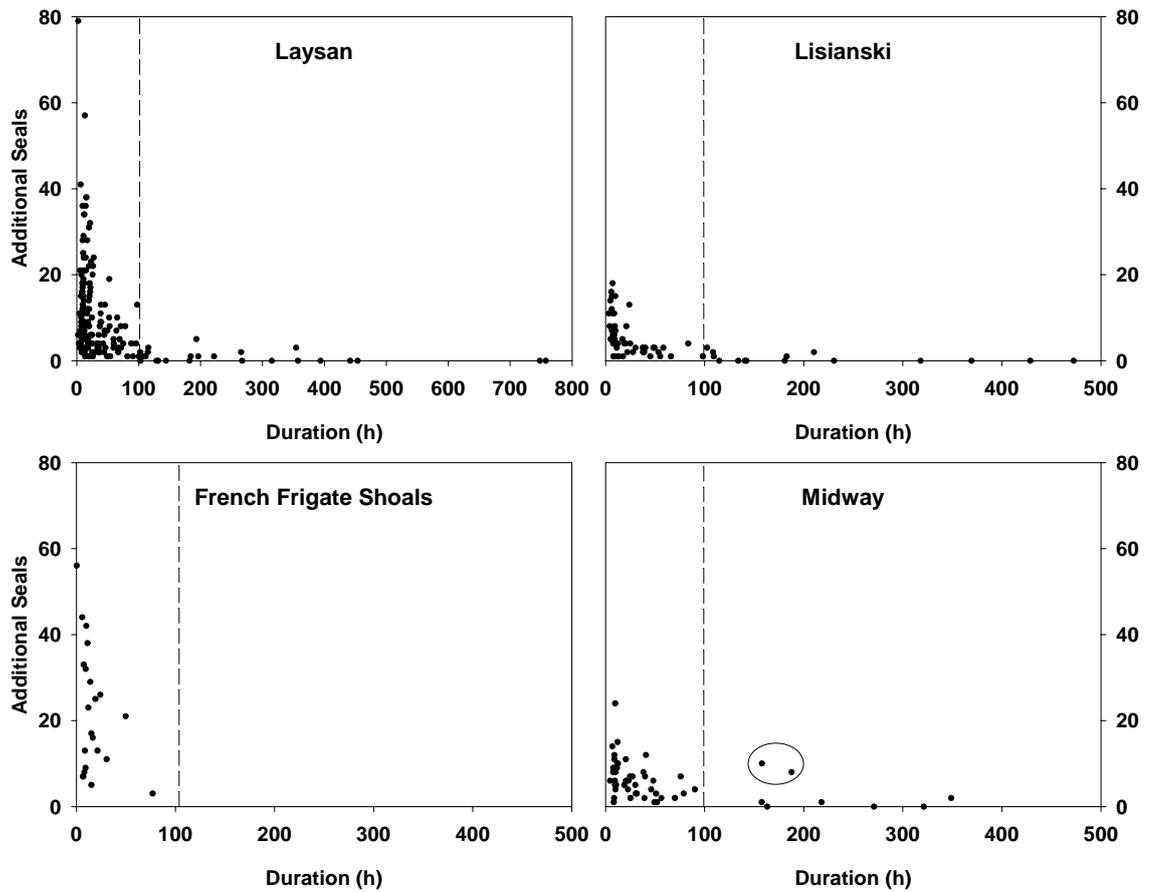


Figure 3.4. Number of additional new seals identified following varying duration intervals of field effort within which no new identifications were obtained. Few or no new seals were seen following such periods of at least 100 h (dashed vertical line) duration. The circled points on the Midway figure indicate two notable exceptions at this site in 1999, which are apparently artifacts of sampling effort and lack of population closure.

capture heterogeneity scenario and the proportion of the population that had been identified. The overall relative performance of the various functions was evaluated by averaging the absolute value of each function's biases for all scenarios. Based on this criterion, two distinct groups emerged, with four functions performing better than the rest. The average percent bias for the negative exponential, asymptotic regression, the Weibull (three formulae), and the Chapman-Richards was three times smaller than that of the remaining functions (5.9% versus 17.4%).

The distribution of estimated asymptotes revealed that these four functions performed quite well even with truncated datasets as long as capture probabilities were equal among animals. However, there was a slight tendency for positive bias and a large penalty in precision when less than 100% of the seals were identified (Fig. 3.6a). The functions also yielded low bias and high precision when fitted to complete datasets (100% identification) under all capture heterogeneity scenarios. However, when capture probabilities were unequal and all seals had not been identified (Fig. 3.6b-d), negatively biased and less precise estimates were usually obtained. An exception was that two of the Weibull functions yielded positive bias in the high heterogeneity scenario. In general, however, the magnitude of bias tended to increase with the degree of modeled heterogeneity and both bias and uncertainty decreased with the percentage of the population identified. The high heterogeneity scenario had the greatest bias, homogeneity resulted in no or low positive bias, while intermediate bias resulted from our scenarios based on observed variability in monk seal capture probabilities. Curves fitted to the field data sets (Fig. 3.6e,f) were essentially unbiased using all data available, relatively mild bias when truncated at 90%, and quite large bias at 80%. Unlike the typical pattern seen in the simulations, several functions produced large overestimates for the Laysan Island dataset truncated at 80% (Fig. 3.6f). In this case, 80% of the population was identified in

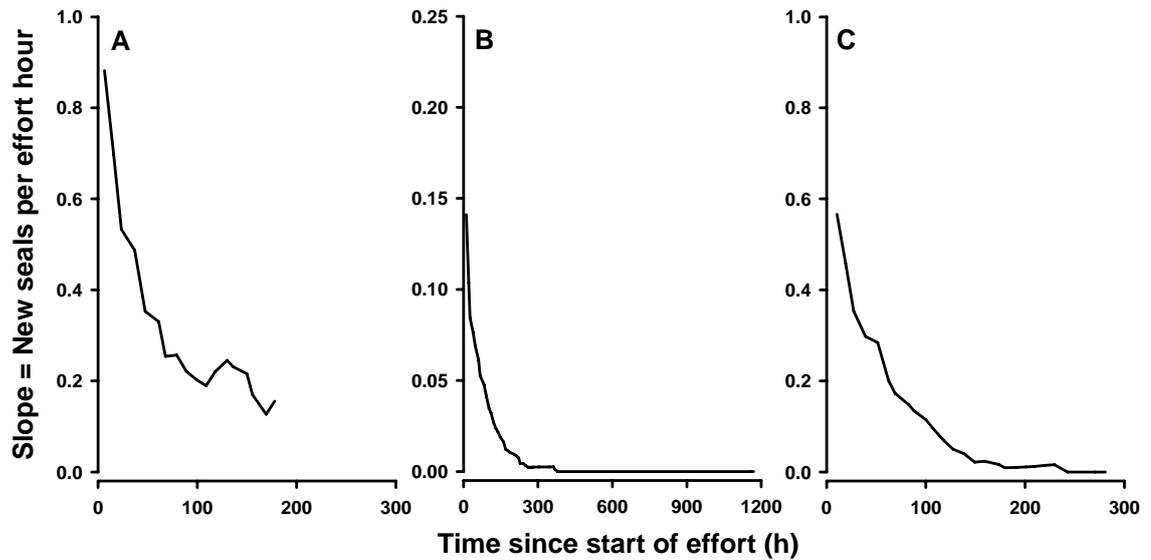


Figure 3.5. Three characteristic results showing the average slope of the line connecting each sequential point on the discovery curve from the beginning of the field season to the fixed point at the end of effort, plotted against the start point in the field season for each calculated slope (time since start of effort). A) zero slope not attained, indicating the population was not been completely enumerated (Pearl and Hermes Reef 2001), B) zero slope sustained for several hundred hours indicating total enumeration (Laysan 1996), C) intermediate result where zero slope was attained not long before field effort ceased, indicating at least near total enumeration (Lisianski 1993). Note that *y-axis* scales differ among the graphs.

less than 80 h of effort, so the functions (some with four parameters) were fitted to just seven data points, perhaps explaining the atypical bias.

## DISCUSSION

We found that discovery curves were useful for diagnosing when an entire population had been identified. The determination that all seals had been identified is based on an empirically derived criterion and involves no formal characterization of uncertainty. While this is less than ideal from a statistical perspective, we believe this approach is practically very reliable, given the wealth of data available on NWHI monk seal discovery curves. In our study it was fairly easy to distinguish between data sets where saturation sampling was attained and those where new seals continued to appear. We also found it useful to acknowledge an intermediate category of “nearly enumerated” populations, because while we could not say whether all seals had been counted, the negative bias was likely quite low.

If applications of this method to other species yield less clear distinctions, a more or less arbitrary decision can be made, weighing both one’s tolerance for underestimation and the reliability of alternative estimation methods. We prefer total enumeration when warranted, since we know that capture-recapture tend to be negatively biased for Hawaiian monk seals when compared with known minimum abundance (Chapter 2).

Simulations suggest that unless capture heterogeneity was negligible, an unlikely scenario in any real population, no non-linear function examined provided unbiased estimates of abundance by extrapolating incomplete discovery curves. Because the level of bias and uncertainty increased when less of the population had been identified, we

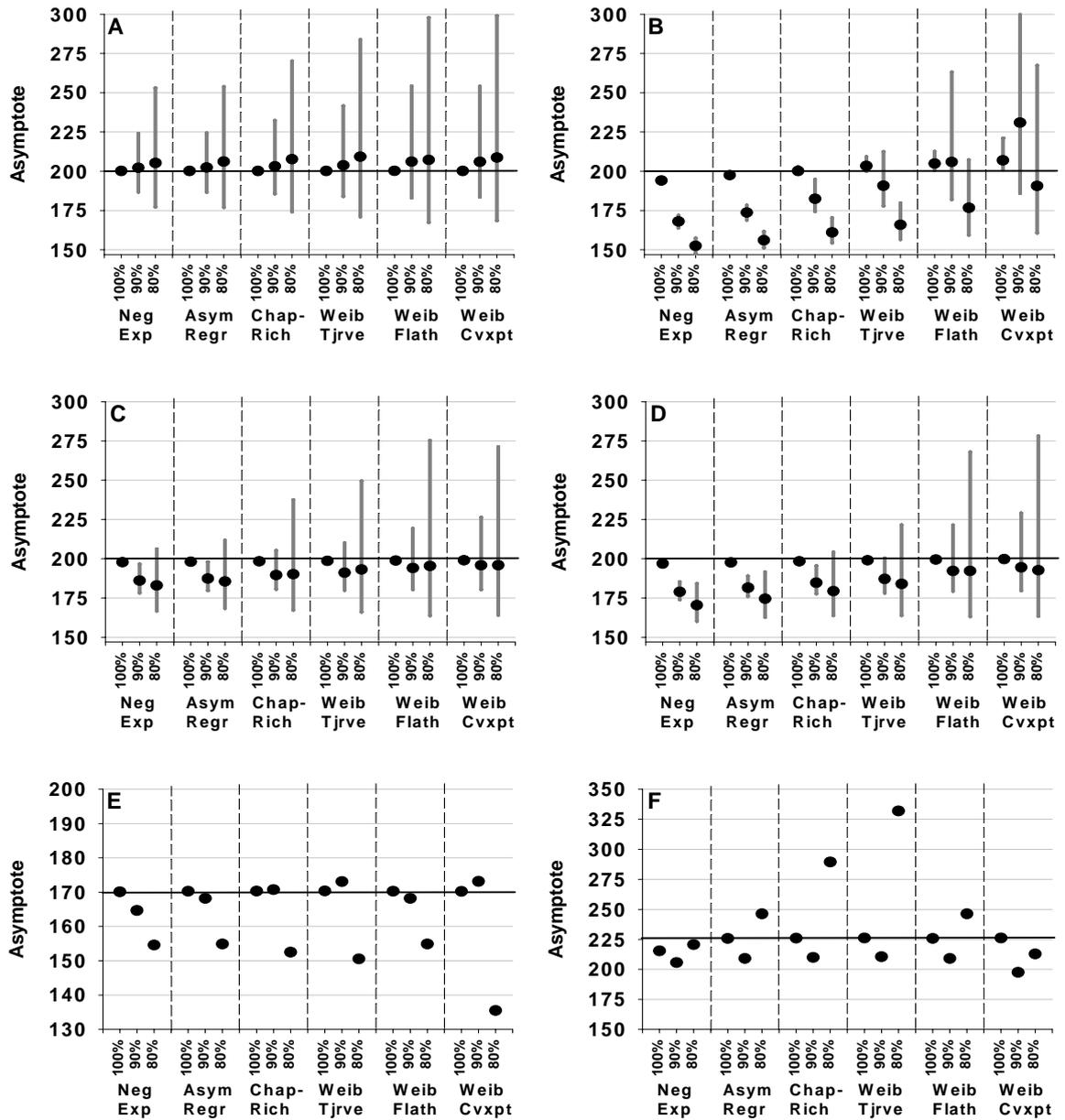


Figure 3.6. Estimated abundance using non-linear asymptotic functions fitted to four simulated and two field data sets. Results for the top performing functions (negative exponential, asymptotic regression, Chapman-Richards and three Weibull formulae) are depicted under simulated scenarios with A) equal capture probabilities, B) high capture heterogeneity, reflecting the observed relative sighting frequencies of individuals at C) Pearl and Hermes Reef in 2002, and D) Lisianski Island in 2003. Means are indicated with solid circles and bars span the range between 5<sup>th</sup> and 95<sup>th</sup> percentiles. Estimates from the same functions fitted to field data sets are shown for E) Laysan 1997 and F) Lisianski 1999 in which the entire populations were enumerated. Results are presented for full data sets and for truncations at 90% and 80% of individuals identified.

conclude that extrapolating discovery curves has little practical value for Hawaiian monk seal assessment.

An interesting parallel exists where researchers have evaluated species-area and species-accumulation curves to estimate species richness through extrapolation (Soberon and Llorente 1993, Colwell and Coddington 1994, Flather 1996, Tjørve 2003, Ugland *et al.* 2003). Flather (1996) and Soberon and Llorente (1993) evaluated the performance of various models using empirical data and found that estimates of species number varied widely among model types. Further, they found that statistical criteria (such as the coefficient of determination) did not reliably indicate the best model. A good fit to the data, therefore, does not guarantee a valid extrapolation. Soberon and Llorente (1993) stressed that models should be derived based on explicitly stated assumptions about the underlying processes that generate species accumulation curves. Likewise, Tjørve (2003) emphasized that species-area models should be based on underlying biology rather than statistics. Unfortunately, the depth of understanding required to ascertain the appropriate emergent function for any particular ecosystem or area is difficult or impossible to attain. In light of these problems, and particularly recognizing that species will have differing detection probabilities less than one, Cam *et al.* (2002) suggest using capture-recapture models with capture heterogeneity to estimate species richness.

Our analysis has yielded valuable information regarding allocation of effort and design of the monitoring program. Clearly better total abundance estimates could be obtained by allocating effort optimally. For example, field seasons could be shorter at Laysan, Lisianski, and Midway, without significantly compromising the identification of all individuals. It appears that a modest extension of the field seasons at Kure could yield saturation sampling. Finally, at French Frigate Shoals and especially at Pearl and Hermes Reef, significantly longer field seasons might be necessary to identify all individuals.

Analysis of discovery curves has great practical appeal, especially for relatively small, closed populations of marked individuals. With sufficient sampling, one can develop criteria, as we have, for determining whether the whole population has been enumerated. Moreover, discovery curves can assist in the design of monitoring programs, by indicating the amount of field effort required for saturation sampling. If total enumeration is not practical, then alternative study designs, for example, to optimize capture-recapture estimates, may be more appropriate.

#### ACKNOWLEDGEMENTS

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## **Chapter 4. Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal**

### ABSTRACT

Estimates of variability in pinniped survival rates are generally based on observations at single sites. Consequently, it is difficult to separate apparent from real survival rates and to determine whether observed rates represent the whole population. Here, we provide a comprehensive analysis of spatio-temporal variation in age-specific survival rates for endangered Hawaiian monk seals based on capture-recapture analyses of > 85% of the pups weaned in this population over the last 2 decades. Uniquely, these data have been collected from six subpopulations, encompassing all major breeding sites across its 1800-km long core range. Analyses of individual subpopulations revealed similar patterns in age-specific survival, characterized by relatively low survival rates from weaning to age 2 yrs, intermediate rates to age 4 yrs, and then relatively high “mature” survival rates until age 17 yrs, after which a senescent decline was observed. Juvenile, sub-adult, and adult survival rates all varied significantly over time. Trends in survival among subpopulations were coherent with their relative geographic positions, suggesting regional structuring and connectedness within the archipelago. Survival rates for different age classes tended to be positively correlated, suggesting that similar factors may influence the survival for seals of all ages.

### INTRODUCTION

Understanding variability in survival patterns is fundamental to life history theory, wildlife management, and conservation biology (Caughley 1966, Stearns 1976, Eberhardt 1985). In mammals, survival theoretically follows a pattern of relatively low juvenile

rates, improved survival in adulthood, followed by a senescent decline (Caughley 1966). However, field studies that confirm these patterns, especially in long-lived species, are rare. In particular, evidence for senescence in mammals (eg., Promislow 1991) has been criticized because it relies heavily on cross-sectional age-structure data and associated assumptions of stable age distribution and representative sampling (Gaillard *et al.* 1994). Long-term studies of marked individuals are required to better characterize variability in survival across time and space.

Pinnipeds are well-suited for individual-based longitudinal studies. They are long-lived, can be marked relatively easily, and aggregate at terrestrial sites to which they show high fidelity, thereby allowing survival to be estimated using capture-recapture analyses (Lebreton *et al.* 1992). However, previous studies of age-specific survival in pinnipeds have generally been based on longitudinal studies at isolated breeding colonies (*e.g.* Boyd *et al.* 1995, Cameron and Siniff 2004, Hindell 1991, Pistorius and Bester 2002, Testa and Siniff 1987), which represent just a small portion of the population. Inferences from these studies are constrained for three important reasons. First, it is frequently difficult to discriminate between mortality and emigration to alternative sites. Second, failure to detect senescence may result when the range of sampled ages does not encompass animals old enough to exhibit senescence. Third, these species often inhabit large geographical areas, and it is unclear to what extent findings from smaller scale studies represent larger scale patterns across the species range.

The Hawaiian monk seal (*Monachus schauinslandi*) presents a rare opportunity to characterize spatio-temporal variation in survival. Currently, the world population of only approximately 1300 Hawaiian monk seals is declining (Carretta *et al.* in press, Antonelis *et al.* 2006). Poor juvenile survival has been suggested as the primary proximate cause for this downward trend (Carretta *et al.* 2006, Craig and Ragen 1999). A better understanding

of recent trends in survival is therefore crucial to support current efforts to conserve this critically endangered species.

The monk seal's endangered status has meant that the species has been consistently monitored throughout nearly its entire range for over 20 years. Since the early 1980's, most individuals in the population have been marked in their birth year and re-sighted throughout their lives, overcoming concerns about whether the marked animals represent the species at large. Re-sighting surveys have been conducted within each of the six main sub-populations across the species' core range, the 1800-km-wide Northwestern Hawaiian Islands, such that migration has negligible potential to confound survival estimates. In this paper, we exploit this unique set of circumstances to characterize spatial and temporal variability in age- and sex-specific survival of this long-lived mammal throughout its principal range.

## METHODS

### *Data collection*

Monk seals occur throughout the lands and waters of the Hawaiian archipelago (Figure 4.1), although some 80–90% of them inhabit six main subpopulations that are scattered throughout the 1800-km span of the Northwestern Hawaiian Islands (NWHI), including French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll (Carretta *et al.* 2006; Stewart *et al.* 2006). A relatively small number of seals reside at Necker and Nihoa Islands (which have limited landing area for seals) and in the main Hawaiian Islands; only 2 of the more than 4200 individuals tagged in the NWHI since 1981 have been sighted in the main Hawaiian Islands (Chapter 6). This study was conducted at all six primary NWHI subpopulations, thereby

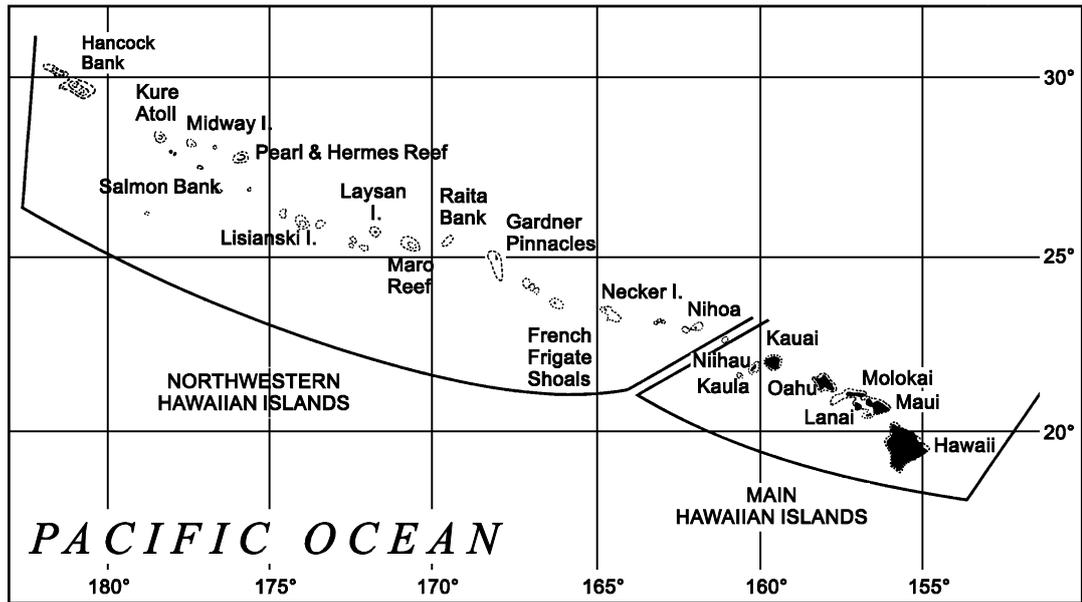


Figure 4.1. The Hawaiian Archipelago, indicating the primary Northwestern Hawaiian Islands subpopulations of monk seals at French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll and Kure Atoll.

encompassing nearly the entire species range and nearly all individuals born into the world population over 20 years.

Field studies typically ranging from 2 to 5 months duration per year were conducted in the NWHI. The six subpopulations are located either at relatively large single islands (Laysan—4.1 km<sup>2</sup>, Lisianski—1.5 km<sup>2</sup>) or atolls that are each made up of two to nine permanent islets and ephemeral sand spits. The total land area of these atolls ranges from 0.2 to 1 km<sup>2</sup> at French Frigate Shoals, Pearl and Hermes Reef, and Kure Atoll, up to 6.4 km<sup>2</sup> at Midway Atoll (Juvik and Juvik 1998). Subpopulation abundance has varied dramatically over the past 20 years and currently range from less than 100 to approximately 300 at the various sites (Chapter 2; Antonelis *et al.* 2006).

Female monk seals give birth to single pups and nurse them for 5 to 6 weeks during a protracted reproductive season, with most births occurring March to August (Johanos *et al.* 1994). In this study, pups were double-tagged on their rear flippers with unique plastic tags (and, since 1990, also marked with injected Passive Integrated Transponders—PIT tags (Wright *et al.* 1998) soon after weaning. Individual identities were maintained long term by periodic re-tagging of individuals to replace lost or broken flipper tags. Also, an extensive photographic (and, previously, hand-drawn) identification system documenting scars, pelage marks, and other distinct natural features was maintained annually so that they could still be identified if they were to lose all flipper and PIT tags, (Harting *et al.* 2004). Finally, temporary pelage bleach marks were applied to as many seals as possible to facilitate within-season and sometimes between-year re-sighting.

Regular surveys were conducted in each of the six sub-populations to re-sight individual seals. All land areas used by seals were searched, and seal identity, sex, size, class (pup, juvenile, subadult, and adult size) (Stone 1984), and location were recorded.

Data recorded in the field were entered into a computerized database and automated error checking routines that compared tag numbers, other identifiers, sex, and size class were used to further validate identifications. Only absolutely certain re-sightings were used in survival analyses. The duration of field seasons and intensity of surveys varied between sites and years, but they typically occurred during the main period of pupping and mating. Additional site-specific details of the field studies are provided in Chapter 2.

### *Analysis*

Individual sighting histories were constructed from annual tagging and re-sight data. Animals were first marked at weaning, thus allowing annual survival estimates to be generated from weaning onward. Animals observed at any time during a calendar year were considered to have survived the age transition from the previous to the current year.

Maximum likelihood estimates (MLE) of survival rates and capture probabilities were obtained using the “recaptures only” analysis implemented in Program MARK (White and Burnham 1999). This extended the basic Cormack-Jolly-Seber fully time-dependent model to evaluate age dependence, as well as the influence of categorical factors (*e.g.*, sex and subpopulation) (Lebreton *et al.* 1992). We fitted a variety of models, described below, which were ranked and evaluated using the small-sample Akaike’s information criterion (AICc, see Anderson *et al.* 2000).

Goodness of fit was evaluated by using estimates of the variance inflation factor ( $\hat{c}$ ), a measure of overdispersion. We used the median- $\hat{c}$  approach (Cooch and White 2005) to evaluate goodness of fit for models selected as best (based on AICc) for each subpopulation and the combined subpopulation analysis. Following Lebreton *et al.* (1992), we considered values of  $\hat{c}$  less than 3 as indicative that model structure provided an adequate fit to the data.

Assumptions underlying capture-recapture analysis of this dataset are discussed fully by Chapter 2, with respect to abundance estimation, and by Craig and Ragen (1999) in relation to Jolly-Seber estimates of juvenile survival. Here we assume that, once marked, individual identities are maintained throughout the study. Craig and Ragen (1999) estimated monk seal survival to age 2 yrs and found minimal tag loss occurred. As we evaluate survival to  $> 20$  yrs, the potential for tag loss to bias estimates is greater if tags were the only method used for identification. However, flipper tags were periodically replaced when worn or lost, and the use of PIT tags, additional temporary pelage bleach marks, and extensive photographic identification effort minimized the risk of mark loss.

Following Craig and Ragen (1999), heterogeneity in capture probability was reduced by collapsing all sighting effort within a field season to a single event (seen or not seen). Capture heterogeneity was further addressed by explicitly modeling differences in sightability among groups (classified by age, sex, subpopulation and year) so that constant capture probability need only be assumed within each group (Lebreton *et al.* 1992).

The following notations were used to describe models and parameters throughout this paper. Survival is denoted with  $\Phi$ , and capture probability is denoted with  $p$ . Subscripts denote age-specific survival rates; thus,  $\Phi_1$  is survival from weaning to age 1 yr,  $\Phi_2$  is survival from age 1 to age 2 yrs, etc.

The purpose of our analyses was to characterize lifetime survival patterns, including temporal and spatial variability. As a result, models were fitted to evaluate the influences of age, sex, year, and subpopulation. Likewise, these same variables might influence capture probabilities. However, a global model incorporating all these effects would be greatly over-parameterized. With over 20 age classes and re-sight years, 6 subpopulations and 2 sexes, the total number of parameters in this global model would

approach 5000. Clearly, some simplification was required, so a separate analysis was conducted at each location.

We anticipated that the duration of field seasons would have the largest impact on  $p$ . Thus, within each subpopulation-specific analysis, we fitted an age-dependent  $\Phi$  and time-dependent  $p$  model. We then reduced the number of  $ps$  by assigning a single parameter to years when estimated  $ps$  did not differ. Next, we explored whether age and sex significantly influenced  $p$ . Once the best fitting and most parsimonious model with respect to  $p$  was found, we turned to analyzing  $\Phi$ .

According to our *a priori* expectation, age-specific survival would start relatively low, rise to an asymptotically “mature” rate, and possibly exhibit senescence among older animals. However, we had no expectation of the ages at which these transitions would occur. We therefore examined age-specific estimates of  $\Phi$ , gradually combining consecutive ages (*i.e.*, constraining them to share the same parameters) and evaluating the support for the reduced models with AICc. After determining which age groups’  $\Phi$ ’s differed, we tested whether those age groups’ survival rates varied over time. If time dependence significantly improved models, we re-evaluated the support for age group break points with time dependence in the model. Finally, the effect of sex on survival was evaluated both as a simple additive factor (*i.e.*, a single adjustment for all ages and years) and as an interactive effect with time and age. In this way, we derived a best model for each subpopulation.

To evaluate spatial patterns in survival, we combined sighting histories from all six subpopulations. To minimize the potential for confounding location and time effects, we limited this analysis to years for which data were available at all sites (1984–2004). The exception was Midway Atoll, which was included even though only a few pups were born there until the mid 1990s. Significant differences in  $ps$  found in the subpopulation-

Table 4.1. Number of known-aged Hawaiian monk seals identified (marked or re-sighted) at six Northwestern Hawaiian Island subpopulations, 1981–2004.

Year	French Frigate	Laysan	Lisianski	Pearl and Hermes	Midway	Kure	Total Identified
1981	0	0	0	0	0	8	8
1982	0	0	13	0	0	11	24
1983	0	20	34	10	0	14	78
1984	85	46	44	19	0	19	213
1985	158	72	58	34	0	23	345
1986	246	88	75	47	0	22	478
1987	326	102	87	60	0	26	601
1988	398	135	61	73	1	32	700
1989	443	127	4	81	1	39	695
1990	400	100	85	38	1	44	668
1991	367	120	86	103	3	52	731
1992	342	141	103	110	4	61	761
1993	346	144	104	115	4	67	780
1994	305	155	40	10	3	65	578
1995	259	161	113	150	12	69	764
1996	249	176	114	150	13	80	782
1997	241	185	114	151	18	86	795
1998	248	212	117	177	25	95	874
1999	257	245	132	177	32	102	945
2000	255	253	136	188	40	102	974
2001	217	243	124	185	36	96	901
2002	218	241	128	169	35	93	884
2003	211	245	135	155	36	83	865
2004	220	248	147	165	39	91	910

specific models were duplicated in the combined analysis. For this analysis, we set identical age groupings among sites to avoid confounding age and subpopulation effects. We began by fitting distinct, time-dependent survival rates for each age group at each subpopulation, and then sequentially fitted models with multiple combinations of subpopulations to determine where differences between subpopulations occurred.

## RESULTS

Marking weaned monk seals and subsequent re-sighting efforts began at a few sites in the early 1980s and at all the primary subpopulations sites by 1984. Effort at Midway began later because few animals were sighted at the location in earlier years. A total of 3421 pups was marked, representing more than 85% of pups weaned during the study. The number of animals marked or re-sighted for each year is shown in Table 4.1. Intensity of effort varied considerably over time but became more consistent after the mid-1990s, with field seasons typically ranging from approximately 50 to 200 days depending on the site.

Values of  $\hat{c}$  ranged from 1.01 to 1.33 for the best subpopulation model and the combined subpopulation analysis, indicating only modest overdispersion and adequate model fit.

### *Individual subpopulations*

Capture probabilities ( $p$ ) were typically high at most sites, often approaching 1. Notable exceptions corresponded to years and locations where field effort was low (Figure 4.2). In a few cases, model fits were significantly improved by taking into account sex differences in capture probabilities. At French Frigate Shoals, males generally had lower capture probabilities than females, and females aged 1–7 yrs were

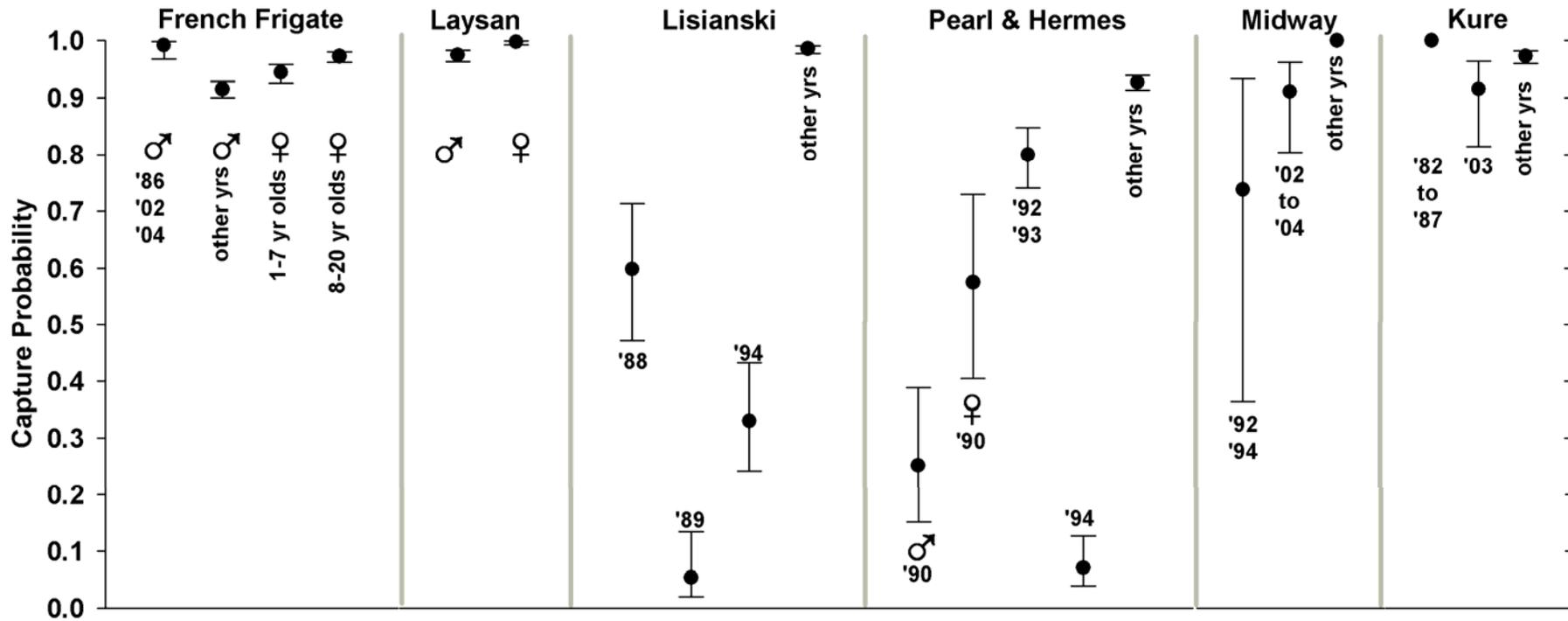


Figure 4.2. Estimated capture probabilities ( $p$ ) (with 95% confidence intervals) of Hawaiian monk seals at the six main subpopulations in the Northwestern Hawaiian Islands. Text and symbols indicate years and sexes to which distinct estimates apply.

less likely to be seen than older females. At Laysan Island, males also had a slightly lower capture probability, and this pattern was seen at Pearl and Hermes Reef in 1 year (1990).

Independent analyses of survival rates from the six subpopulations revealed remarkably similar patterns (Table 4.2, Figure 4.3). In particular, age-specific differences in survival were consistent among sites. In five of the six subpopulations, survival to 1 and 2 yrs was the same, but significantly lower than older animals. There was some variation in the next older, “sub-adult” group among subpopulations, but a “mature” rate was consistently achieved between the 4<sup>th</sup> and 6<sup>th</sup> year and maintained for many years. Finally, a senescent drop in survival was detected at four of the six sites, beginning in the 18<sup>th</sup> year at three sites, and just 1 year earlier at another. Senescence was not detectable at Lisianski nor Midway Atoll.

Similarly, some time variation in survival rates was detected at all sites except Midway Atoll (where the sample size was smallest). At Lisianski Island and Kure Atoll (with intermediate samples sizes), time variation was detected only in the younger age groups. However, at French Frigate Shoals, Laysan Island, and Pearl and Hermes Reef (largest sample sizes), significant variation in adult survival was evident (Figure 4.3).

Gender appeared to have little influence on survival. The exception was French Frigate Shoals, where females were found to have significantly higher survival rates than males and was most apparent among the 1–2 yr age group. However, including gender as an additive factor across all ages at this site was a significant improvement over a model with sex differences only in the youngest age group ( $\Delta AIC_c = 6.9$ ), and far better than a model with no gender effect ( $\Delta AIC_c = 13.3$ ). At most other subpopulations, models involving sex differences showed marginally worse fits than those with equal male and female survival  $\Delta AIC_c$  from 1.0 to 2.0). We selected the latter models for their parsimony and slightly better fits. Moreover, the models with sex differences indicated opposing

Table 4.2. Summary of separate subpopulation analyses of Hawaiian monk seal survival rates, indicating where significant differences in age-specific survival, temporal variability, and sex were found.

Supopulation	Years	Age groups (yr)	Time variation	Sex
French Frigate Shoals	1984–2004	1–2, 3–4, 5–17, 18–20 <sup>9</sup>	All but 18–20 yr	All ages <sup>10</sup>
Laysan Island	1983–2004	1–2, 3–4, 5–17, 18–21 <sup>9</sup>	All age groups	No
Lisianski Island	1982–2004	1–2, 3–4, 5–22	1–2 and 3–4 yr	No
Pearl and Hermes	1983–2004	1–2, 3–16, 17–21 <sup>9</sup>	All but 17–20 yr	No
Midway	1988–2004	1–2, 3–5, 6–16	No	No
Kure	1981–2004	1, 2, 3, 4–17, 18–23 <sup>9</sup>	Only 1 yr	No

<sup>9</sup> Oldest age group had reduced survival.

<sup>10</sup> Females had higher survival than males.

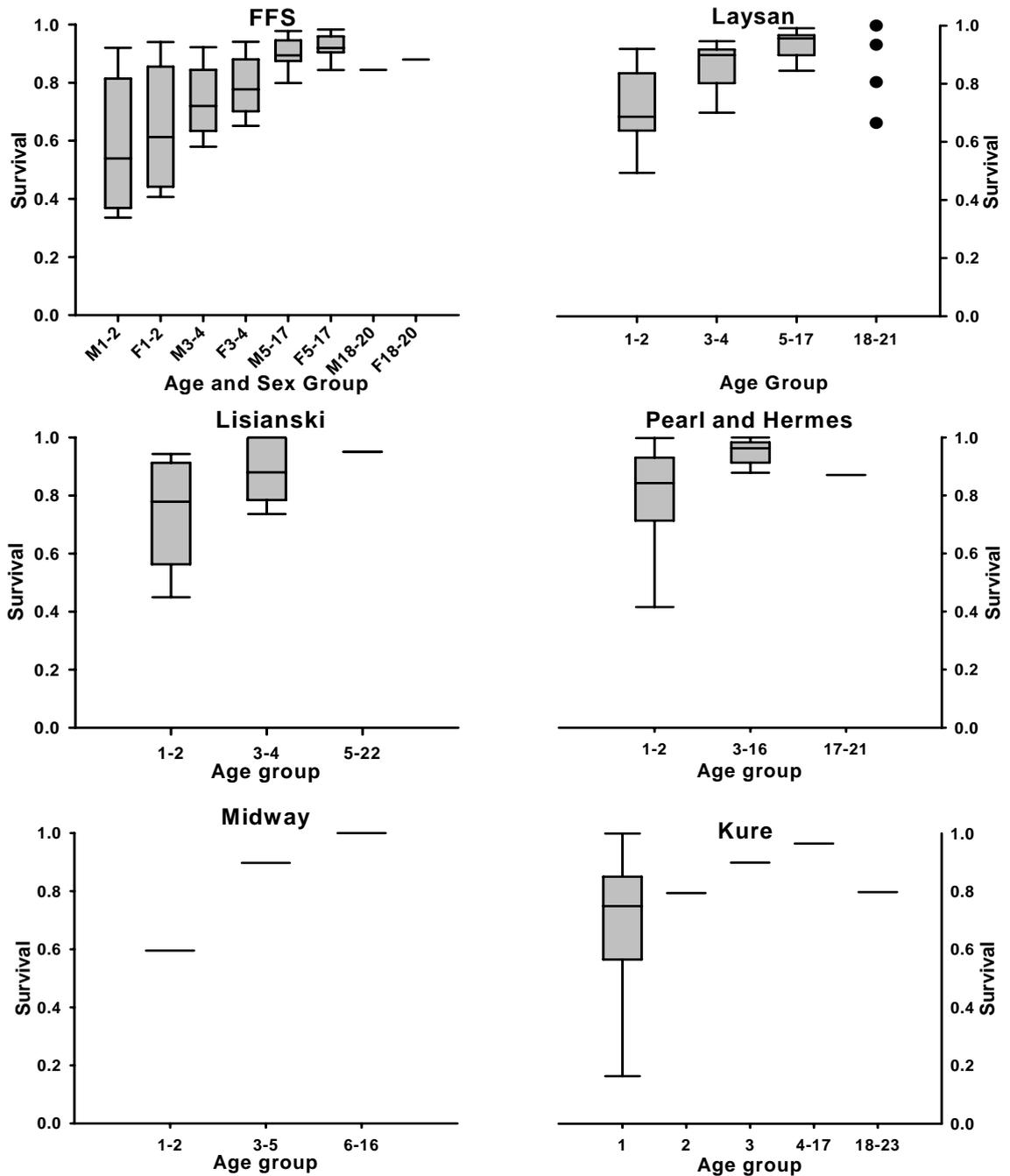


Figure 4.3. Results of separate subpopulation analyses of Hawaiian monk seal survival rates. Age groups found to have significantly different survival rates are plotted separately, showing an increase in survival with age until senescence is expressed. Sex differences in survival were found only at French Frigate Shoals. Box plots show the distribution of point estimates of survival rates over time. The lower boundary of the box indicates the 25<sup>th</sup> percentile, a line within the box marks the median, and the upper boundary of the box indicates the 75<sup>th</sup> percentile. Error bars indicate the 90<sup>th</sup> and 10<sup>th</sup> percentiles. Horizontal lines alone indicate single point estimates where time variation was not detected. At Laysan Island, significant temporal variation was detected in the 18–21 yr age group, and the four available estimates are shown in lieu of a box plot.

trends among sites— slightly higher male survival at Lisianski and Kure. At Pearl and Hermes Reef, there was no support for gender differences ( $\Delta AIC_c = 16.5$ , no sex difference *versus* additive sex effect).

### *Combined subpopulations*

In the analysis of all subpopulations combined, the best model had subpopulations that were grouped in a manner coherent with their geographic distribution (Figures 4.4 and 4.5). At one end of the Hawaiian chain, survival rates at French Frigate Shoals were decoupled from other sites for all except the oldest senescent age group. At the opposite end of the island chain, Pearl and Hermes, Midway, and Kure survival rates were indistinguishable from each other at all ages. Finally, at the central sites, most survival rates at Laysan and Lisianski Islands did not significantly differ from each other. The exception was the youngest animals' survival ( $\Phi_{1-2}$ ) at Lisianski, which was more similar to rates at Pearl and Hermes, Midway, and Kure. For the oldest age group ( $\Phi_{18-20}$ ), no detectable temporal or spatial variability was observed, but sample sizes were small. Within the subpopulation groups found to have similar survival rate trends (Figure 4.5), pair-wise correlations of estimated survival rates among age groups were positive in all cases, and statistically significant in 50% of cases (Table 4.3).

## DISCUSSION

Age-specific survival trends in Hawaiian monk seals accord well with the generalized pattern proposed by Caughley (1966). At most of the six subpopulations, the survival rate was lower for the first 2 years, then somewhat higher for 2 more years before reaching a “mature” level maintained until the 18<sup>th</sup> year of life. We expected that the survival rate from weaning to age 1 yr would be significantly lower than the

subsequent year, as weaned pups must learn to feed independently. Post-weaning survival rates may in fact be lowest, but this difference could be obscured because we pooled all sightings over several-months-long field seasons to reduce capture heterogeneity.

Consequently, a seal initially marked late one year and re-sighted early the next but which dies soon thereafter, will be credited with having survived the full first year, even though it may have died a few months earlier. As a result, the estimated survival rate for that year will be biased upward and the subsequent year's estimate will be biased downward. Few dead animals are observed during field seasons, making the magnitude of this error source difficult to assess. However, it will mostly affect juvenile survival estimates, as mortality is highest for young animals and they are therefore most likely to die after being observed within a field season than adults. This may blur the distinction between consecutive age-specific survival rates of juveniles.

### *Senescence*

The senescence we detected in Hawaiian monk seals is consistent with declining reproductive rates among older females reported by Harting *et al.* (in review). They found that the proportion of females giving birth began to decline between 15 and 18 yrs of age, slightly earlier than the decline in survival reported here.

Detection of senescence in marine mammals is the exception rather than the rule. Cameron and Siniff (2004) reported no evidence of senescence in Weddell seals, at least up to 17 yrs old. Pistorius and Bester (2002) analyzed survival rates in southern elephant seals at Marion Island and likewise found no increased mortality up to age 17 yrs. However, they suggested that the high adult mortality rates in this population may mean individuals did not live sufficiently long for senescence to occur. Boyd *et al.* (1995) did not detect a statistically significant drop in survival among Antarctic fur seals up to 18 yrs old, although point estimates of survival declined after 13 yrs of age. Here, small sample

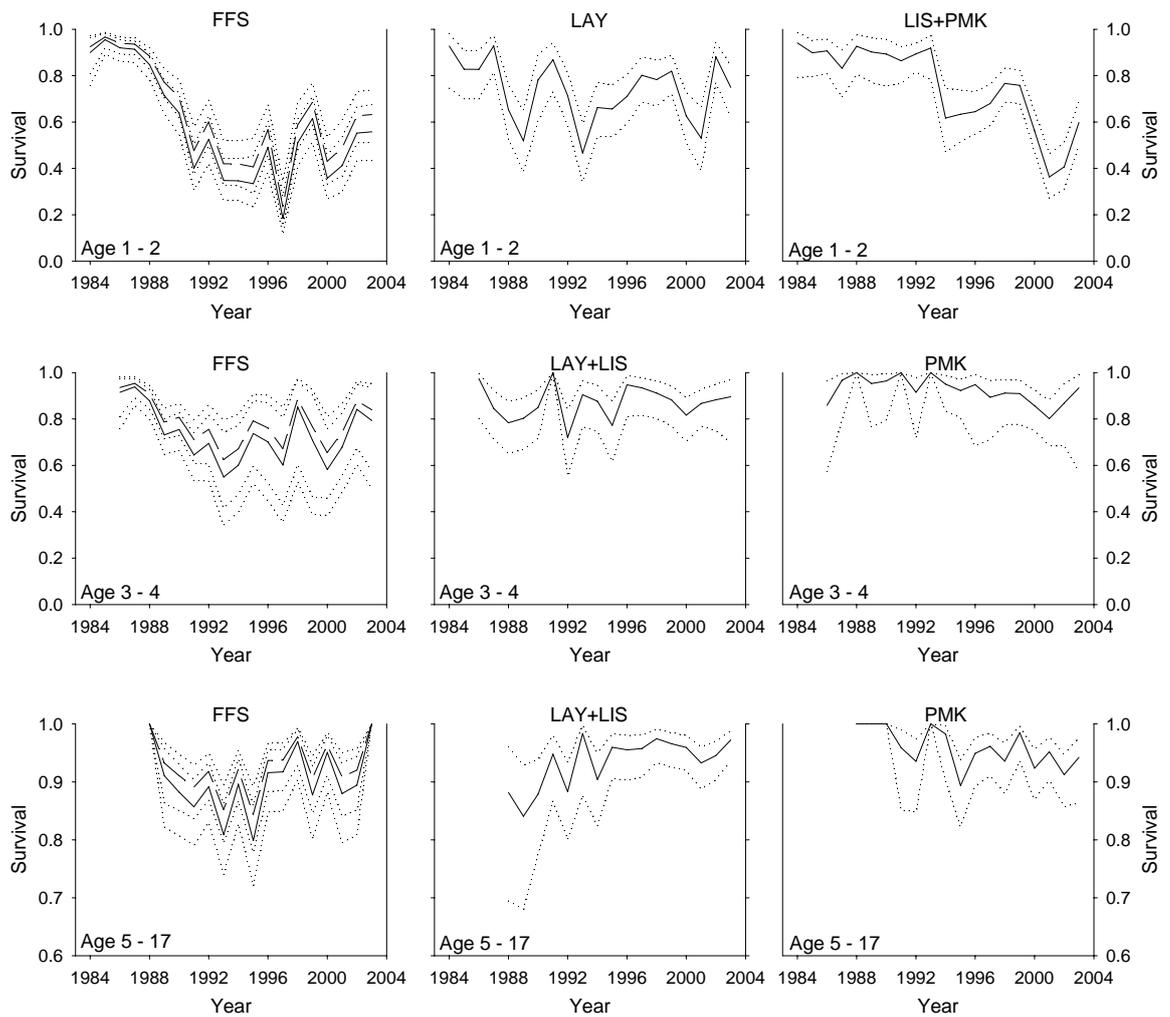


Figure 4.4. Spatial and temporal variation in estimated Hawaiian monk seal survival rates from combined analysis of six subpopulations. Solid lines (and dashed lines for French Frigate Shoals females) indicate survival estimates and dotted lines represent 95% confidence intervals. Survival to age 1–2 yrs is presented in the top row of graphs, age 3–4 yrs in the middle row, and age 5–17 yrs in the bottom row. Columns of graphs separate subpopulation groups that had significantly different survival rate trends over time. FFS = French Frigate Shoals, LAY = Laysan Island, LIS = Lisianski Island, PMK = Pearl and Hermes Reef, Midway Atoll, and Kure Atoll. Sex differences in survival were only detected at FFS. Note that the y-axis scale in the bottom row differs from the two rows above.

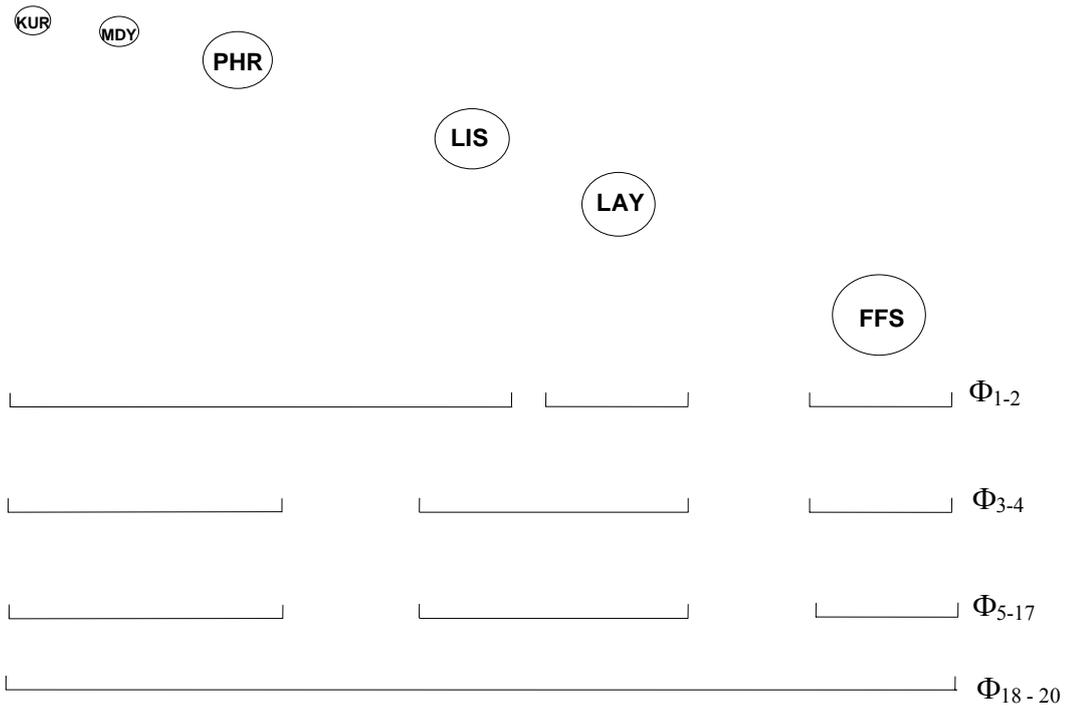


Figure 4.5. Spatial patterns in survival of Hawaiian monk seals at six Northwestern Hawaiian Islands subpopulations, 1984-2004. Brackets indicate subpopulation/age group combinations with indistinct survival rate temporal trends. Survival rate ( $\Phi$ ) subscripts indicate age groups. FFS = French Frigate Shoals, LAY = Laysan Island, LIS = Lisianski Island, PHR = Pearl and Hermes Reef, MDY = Midway Atoll, KUR = Kure Atoll.

sizes among older seals may have prevented a statistically significant effect. Beauplet *et al.* (2006) found both decreased survival and fecundity of subantarctic fur seals after 13 yrs of age.

#### *Sex differences in survival*

In mammals, females frequently have higher survival rates than males, and this pattern has been largely attributed to the costs of sexual selection for males in polygynous systems (Ralls *et al.* 1980, Clutton-Brock *et al.* 1985, Promislow 1992, but see Loison *et al.* 1999, Owen-Smith and Mason 2005). Some sex-specific survival rate estimates are available from longitudinal studies of marine mammals. Hindell (1991) found female southern elephant seals exhibited a higher survival rate in this highly dimorphic, polygynous species. The Weddell seal, another polygynous pinniped, also has a higher female survival rate (Cameron and Siniff 2002, Hastings *et al.* 2004). The polygynous grey seal has a higher, female first-year survival rate (Hall *et al.* 2001). Conversely, survival does not vary with gender in Florida manatees, a species whose females are slightly larger and whose levels of male-male competition are low (Langtimm *et al.* 1998).

It was difficult to anticipate whether Hawaiian monk seals might exhibit sex differences in survival. The mating system of monk seals is poorly understood, but they are not sexually dimorphic and it is likely to be a promiscuous species (Stirling 1983). Observed levels of male-male aggression are lower than seen in polygynous, territorial pinnipeds. Given the uncertainty about the role of male competition in the mating system, the finding that sex did not strongly influence survival in Hawaiian monk seals is not surprising. However, the fact that female-biased survival was detected at French Frigate

Table 4.3. Correlation of survival rates among age groups (1–2 yrs, 3–4 yrs, 5–17 yrs) within subpopulations with indistinct survival rate trends. Subpopulations are abbreviated as follows: FFS = French Frigate Shoals, LAY = Laysan Island, LIS = Lisianski Island, PMK = Pearl and Hermes Reef, Midway Atoll, and Kure Atoll. Correlation coefficients ( $r$ ) are shown and statistical significance is indicated.

	FFS 3–4	FFS 5–17	LAY + LIS 3–4	LAY + LIS 5–17	PMK 3–4	PMK 5–17
FFS 1–2	0.73 <sup>b</sup>	0.42				
FFS 3–4		0.47				
LAY 1–2			0.38	0.22		
LAY + LIS 3–4				0.55 <sup>a</sup>		
LIS + PMK 1–2					0.80 <sup>b</sup>	0.61 <sup>a</sup>
PMK 3–4						0.55 <sup>a</sup>

<sup>a</sup> $P < 0.05$ .

<sup>b</sup> $P < 0.01$ .

Shoals, and only there, is perplexing. Insufficient sample sizes did not prohibit detecting the trend elsewhere. In the individual subpopulation analyses at other locations, fitted survival rates were not consistently higher for females regardless of the lack of statistical significance. Further, analysis of all subpopulations combined bore the highest statistical power to detect sex differences had they existed but instead confirmed that female survival rates exceeded that of males only at French Frigate Shoals. The unique finding of sex differences in survival at French Frigates Shoals therefore remains unexplained.

*Temporal and spatial variance in survival*

Juvenile survival of monk seals has been highly variable over the past two decades (Figure 4.4). The rates generally declined after the late 1980s, leading to an overall decline in total abundance (Harting 2002, Craig and Ragen 1999, Ragen 1999). We found that adult and sub-adult monk seal survival rates also varied significantly over time. Though the magnitude of adult survival variability was much lower than for juveniles, the population growth rate is more sensitive to the former, such that adult survival has the potential to greatly influence population trends (Goodman 1981). Furthermore, the positive correlation of survival rates among age groups (Table 4.3) suggests that similar factors influence all age groups. This co-variation of survival among age groups will tend to amplify their influence on the population growth rate (Coulson *et al.* 2005).

Spatial patterns in monk seal survival suggest that the NWHI archipelago is not a homogenous habitat, but neither is each monk seal subpopulation subject to unique environmental influences. Rather, the survival prospects of seals at some subpopulations appear to be in synchrony, while others tend to be independent. The fact that these groups

are coherent with the spatial distribution of different breeding sites (Figure 4.5), suggests regional structuring and connectedness (see also Schmelzer 2000, Parrish 2004).

The spatial and temporal patterns we found in monk seals demonstrate two important points. First, sampling a single localized population of a widely distributed species may poorly represent the dynamics of the species at large, especially where habitat is heterogeneous. Conversely, broadly sampling throughout a species range can be a powerful tool for elucidating biogeographic structure.

Spatial links in survival rates among subpopulations presumably result from individuals at different sites experiencing similar conditions. This can occur either because environmental conditions span more than one site, or because animals from different sites move sufficiently that their ranges overlap. Seals were assigned to a subpopulation at birth and this assignment was not altered if they were subsequently seen at other locations. Overall, the probability of seals being seen away from their initial capture sites was low (< 10%), but these rates were higher among sites with similar survival trends (*e.g.*, Pearl and Hermes, Midway and Kure) than among sites with dissimilar trends (*e.g.*, Laysan and French Frigate Shoals)(Harting 2002). Stewart *et al.* (2006) also found that seals tracked from different subpopulations showed similar patterns in overlap of presumed foraging areas. Thus, spatial patterns in monk seal survival likely result from regional structuring of the ecosystem coupled with animal movements.

#### ACKNOWLEDGEMENTS

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**Chapter 5. Effect of variable oceanic productivity on the survival  
of an upper trophic predator, the Hawaiian monk seal,  
*Monachus schauinslandi***

ABSTRACT

The Hawaiian monk seal population is declining and low juvenile survival due to prey limitation is believed to be a primary cause. The Transition Zone Chlorophyll Front (TZCF) is a large-scale oceanographic feature separating the vertically stratified, low surface chlorophyll subtropical waters and the vertically mixed cool, high chlorophyll Transition Zone waters. The TZCF annually migrates over 1000 km in latitude, and its southern extent in winter varies. We hypothesize that when the front migrates southward, it brings colder, more productive waters into monk seal foraging habitat, thereby enhancing the prey base and consequently survival. We expect this effect will be strongest at seal populations situated furthest north and nearest the TZCF. To test this hypothesis, we explored relationships of the survival of more than 3000 monk seals during 1984–2004 to the southern-most latitude of the 18°C isotherm (a proxy for the TZCF). We found a statistically significant non-linear relationship between the winter position of the TZCF and survival of monk seals through 4 years of age at the most northerly atolls. When the front remained farther north, survival was poorer. The relationship was strongest following a 1- or 2-year lag, perhaps indicating the time required for enhanced productivity to influence the food web and improve the seals' prey base. No such relationship was found at subpopulations located farther south or among adult animals at any site. Variation in ocean productivity may mediate prey availability in monk seal foraging habitat and consequently influence juvenile survival in the northern portion of their range.

## INTRODUCTION

The Northwestern Hawaiian Islands (NWHI) is an oceanic island ecosystem composed of a chain of atolls, islands and seamounts extending 1800 km across the subtropical Pacific. This region is generally characterized by low oceanic productivity (Mann and Lazier 1991). The dynamics of productivity in the NWHI archipelago is poorly understood, but decadal-scale changes in productivity have been linked to variability in the mixed layer depth, which in turn is driven by the Aleutian Low Pressure System (Polovina *et al.* 1994, 1995). Schmelzer (2000) summarized a variety of oceanographic parameters, which, within the NWHI, indicated a gradient of higher-to-lower productivity from north to south.

The endangered Hawaiian monk seal, *Monachus schauinslandi*, has been the subject of long-term demographic research. The species is distributed throughout the NWHI and is concentrated in six main subpopulations spanning the width of the archipelago. While monk seals come on land to rest and rear their offspring, they forage on nearly every reef, bank, and submerged seamount within approximately 500 m of the surface in the NWHI (Stewart *et al.* 2006).

In Chapter 4 more than 20 years of individual monk seal sighting histories were evaluated and patterns in survival were characterized for the species. Considerable fluctuation was observed in survival rates, both temporally and spatially, though the causes of variable survival remain largely unknown. However, periods of low juvenile monk seal survival appear to be related to food limitation (Craig and Ragen 1999).

To better understand NWHI ecosystem dynamics and also aid in the conservation of the monk seal, it is imperative that the underlying drivers of variable vital rates in this imperiled species are discovered. Polovina *et al.* (1994, 1995) found that a regime shift in the late 1980s, marking a transition to a shallower mixed-layer depth and lower primary

productivity in the NWHI, was associated with decline in survival and productivity at higher trophic levels (lobsters, seabirds and monk seals) at one NWHI location, French Frigate Shoals. Antonelis *et al.* (2003) found that monk seal pup girth at weaning was greater in El Niño years than non-El Niño years, suggesting that short-term fluctuations in ocean conditions influence monk seals. Building on this foundation, in this paper we focus on the Transition Zone Chlorophyll Front (TZCF), a large-scale oceanographic feature separating the vertically stratified, low surface chlorophyll subtropical waters and the vertically mixed cool, high chlorophyll Transition Zone waters. The TZCF annually migrates over 1000 km in latitude and its southern extent in winter varies (Bograd *et al.* 2004). The frontal region is associated with surface convergence, thereby likely concentrating resources throughout the food chain. Polovina *et al.* (2000) showed that juvenile loggerhead turtles migrate along transition zone fronts and hypothesized that in doing so they maximize encounters with prey.

We hypothesized that the TZCF represents a possible mechanism for variable NWHI ecosystem productivity, and consequently, variable monk seal survival. We expected that in years when the front extends further south in winter, it bathes the NWHI in more productive waters, thereby increasing productivity throughout the food web and ultimately resulting in greater prey availability and survival of monk seals. Conversely, when the front remains further north, NWHI waters are relatively unproductive, ultimately resulting in lower juvenile survival. Three additional expectations follow if our central hypothesis is true. First, the effects of the TZCF variability should be most pronounced in the northerly portion of the archipelago most proximate to the front. Second, juvenile Hawaiian monk seals should be most affected by changes in productivity, as they are relatively inexperienced foragers, have limited diving capabilities relative to older animals (and thereby have fewer alternative strategies when

prey is scarce), and exhibit more variable survival rates (Chapter 4). Third, the relationship of changes in the latitude of the TZCF to seal survival should involve a time lag, allowing for the propagation of presumed fluctuations in primary productivity up through the food web to result in altered monk seal prey availability.

## METHODS

### *Monk seal survival*

Estimates of Hawaiian monk seal survival presented in Chapter 4 were used, and detailed field and analysis methods are described in that chapter. Briefly, since 1984, weaned pups were double-marked with unique plastic rear flipper tags in their year of birth. Subsequent resighting efforts occurred during typically 2- to 5- month-long field seasons through 2004 at each of the six main NWHI subpopulations. Tag and resight effort at one site, Midway Atoll, began in the late 1980s as there had been few or no births in previous years. Individual identities were maintained through a redundant system involving re-tagging, photographic and hand-drawn documentation of scars and other natural markings, and temporary bleach marks applied to the seals' fur (Harting *et al.* 2004).

Individual sighting histories were constructed from the tag and resighting records and maximum likelihood estimates (MLE) of survival rates and capture probabilities were obtained using the "recaptures only" analysis implemented in Program MARK (White and Burnham 1999). In this paper, first-year survival refers to survival from weaning to age 1 yr, second-year survival refers to survival from age 1 to 2 yrs, etc. Chapter 4 presents the following patterns in monk seal survival rates. Survival was lowest from weaning through the second year, then increased through the fourth year, and leveled off from age 5 to 17 yrs, before a senescent decline occurred. Significant time variance was

detected for all but the oldest (18–20 yr-old) age groups. Spatial patterns were also evident as French Frigate Shoals survival rates were different from other sites for all except the oldest senescent age group. Pearl and Hermes, Midway and Kure survival rates were indistinguishable from each other at all ages. Laysan and Lisianski Islands did not significantly differ from each other, with the exception that the youngest animals' (first- and second-year survival) at Lisianski was more similar to rates at Pearl and Hermes, Midway and Kure. Finally, at French Frigate Shoals only, females exhibited higher survival than males. For this study, we compared estimated survival rate time series for each of these groups with distinct survival rate trends to variability in the TZCF (Table 5.1).

#### *TZCF dynamics*

The northern atolls of the NWHI lie at the boundary between the subtropical gyre and the Transition Zone. This boundary is dynamic and in the winter is characterized by several fronts. The TZCF is a surface chlorophyll front, identified as the latitude corresponding to the surface chlorophyll level of  $0.2 \text{ mg m}^{-3}$  (Figure 5.1, Polovina *et al.* 2001). North of Hawaii the TZCF also corresponds very closely to the position of the  $18^\circ\text{C}$  sea surface temperature (SST) isotherm (Bograd *et al.* 2004). Since satellite-derived surface chlorophyll records became available only in late 1997, we used the  $18^\circ\text{C}$  SST proxy for the position of the TZCF to extend our time series of the latitude of the TZCF back to 1982. While the TZCF is very visible from satellite surface chlorophyll data, a second front south of the TZCF in the winter, termed the South Subtropical Front (SSTF), is located from the latitude of the  $20^\circ\text{C}$  SST isotherm (Seki *et al.* 2002). While the SSTF does not have a surface expression in chlorophyll, it represents a strong temperature front and an abrupt shoaling of the deep chlorophyll maximum from about 100 m on the south to about 50 m on the north (Seki *et al.* 2002).

Table 5.1. Twelve combinations of age/subpopulation/sex groups with distinct temporal trends in Hawaiian monk seal survival rates (from Chapter 4). Northwestern Hawaiian Islands subpopulations are abbreviated as follows: French Frigate Shoals (FFS), Laysan Island (LAY), Lisianski Island (LIS), Pearl and Hermes Reef (PHR), Midway Atoll (MDY), and Kure Atoll (KUR). Sex differences (F = females, M = males in survival were found only at FFS.

Age Group	Subpopulation / Sex Group			
1-2 yr	FFS F	FFS M	LAY	PHR+MDY+KUR+LIS
3-4 yr	FFS F	FFS M	LAY+LIS	PHR+MDY+KUR
5-17 yr	FFS F	FFS M	LAY+LIS	PHR+MDY+KUR

For 1997, chlorophyll *a* data collected by the Ocean Color and Temperature Scanner (OCTS) on the ADEOS satellite were used. From September 1997 to present, we used chlorophyll *a* data collected by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) instrument on board the Seastar spacecraft. These data are derived from the raw measured wavelength bands using the SeaWiFS algorithm (SeaWiFS L3 CHLO product). Both chlorophyll *a* products used in this study are a 9-km pixel resolution product on an equidistant cylindrical projection distributed as version 4.

Reynolds' optimally interpolated, sea surface temperature data were used to derive SST proxies for the TZCF and SSTF. This interpolated analysis incorporated data collected by Advanced Very High Resolution Radiometers (AVHRR) onboard NOAA polar orbiting satellites with in-situ data derived from both ship and buoys. Both these data sets are optimally interpolated (Reynolds and Smith 1994) onto a 1° x 1° grid monthly with an accuracy of  $\pm 0.5^{\circ}\text{C}$ . To construct the SST-based proxy indicators used in this study, the minimum latitudinal position of the 18°C and 20°C SST isotherms were calculated from each monthly dataset to construct a time series from 1984–2004.

#### *Statistical analysis*

We analyzed the support for a relationship between the 18°C SST isotherm's southernmost latitude and the survival rate time series representing all combinations of three age groups and four subpopulation/sex groups identified as distinct Chapter 4, Table 5.1). For each cell in Table 5.1, we fitted seven models: a null model (no predictor), three linear models (with the 18°C SST isotherm as a predictor lagged by 0, 1 and 2 years), and to allow for non-linearity in the relationship, three generalized additive models (GAMs) with two degrees of freedom, also lagged by 0, 1, and 2 years. Models were ranked and

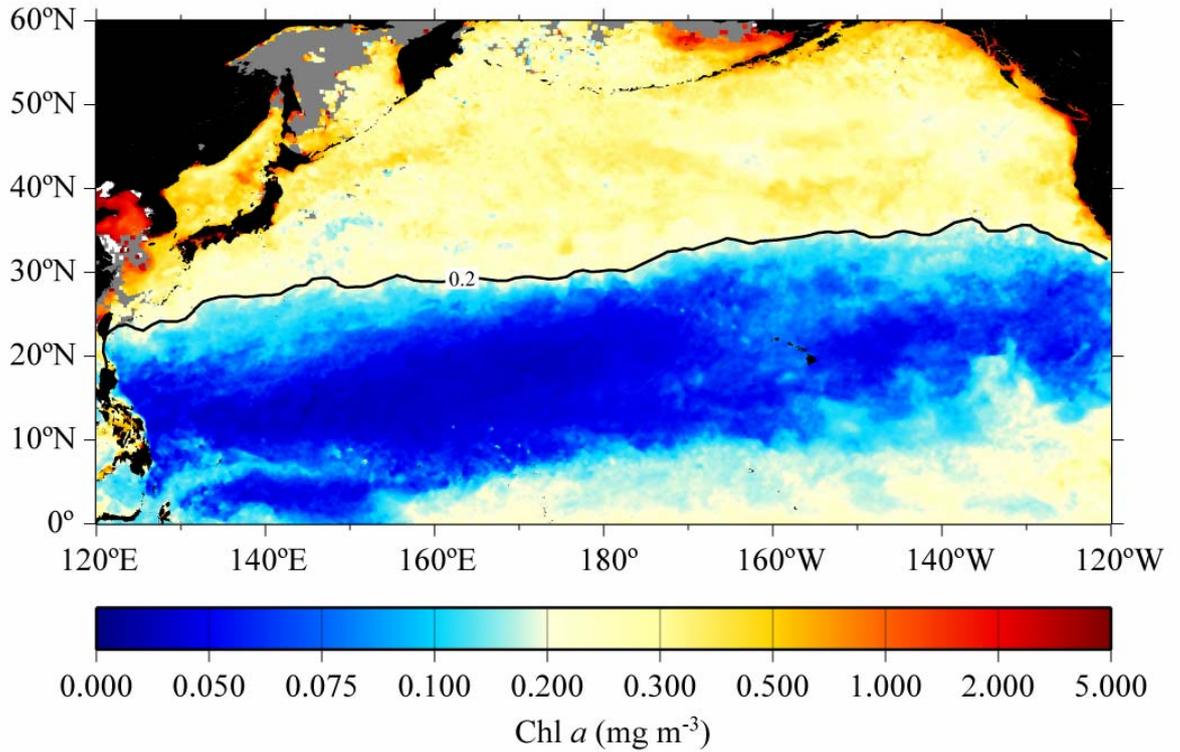


Figure 5.1. Surface chlorophyll estimates from SeaWiFS ocean color over the North Pacific for February 2000. The black line represents the 0.2  $\text{mg m}^{-3}$  chlorophyll surface contour indicating the Transition Zone Chlorophyll Front (TZCF).

their support evaluated using the small-sample Akaike's information criterion (AICc, see Anderson *et al.* 2000). Models were fitted using the statistical software program R.

## RESULTS

As noted previously (Bograd *et al.* 2004), there has been considerable variability in the wintertime southern extent of the TZCF (Figures 5.2, 5.3). In most years, the subsurface chlorophyll maximum, as indicated by the 20°C isotherm (Seki *et al.* 2002), intersected the latitudes where the three most northerly atolls are situated. The positions of the 18°C and 20°C SST isotherms were highly correlated ( $r^2 = 0.94$ ) such that they are essentially equivalent indicators of the same phenomenon. Consequently, using either time series as a predictor yielded nearly identical model results and, for brevity, only the results using the 18°C isotherm are presented here. A rather strong inverse relationship was found between first and second year survival of monk seals at the most northerly sites (Lisianski, Pearl and Hermes, Midway and Kure) and the southernmost latitude of the TZCF (Table 5.2) after a time lag. A GAM with a 2-year time lag (Figure 5.4a) had far more support than the null model ( $\Delta\text{AICc} = 8.6$ ). Linear fits with 1- and 2-year lags and a GAM with a 1-year lag had somewhat less support than the GAM with a 2-year lag. There was a similar relationship between third and fourth year survival at Pearl and Hermes, Midway and Kure and the southern reach of the TZCF ( $\Delta\text{AICc} = 6.2$  relative to the null model). In this case, a GAM with a 1-year lag fitted best, and a 2-year lag had somewhat less support (Table 5.2, Figure 5.4b).

Survival of adults (age 5-17 yrs) at the northernmost atolls was not statistically associated with the TZCF trend, nor was any such association found for survival of any age group at the other monk seal subpopulations. For all these remaining subpopulation/age groups, the null model was the best fit or had  $\Delta\text{AICc}$  values only

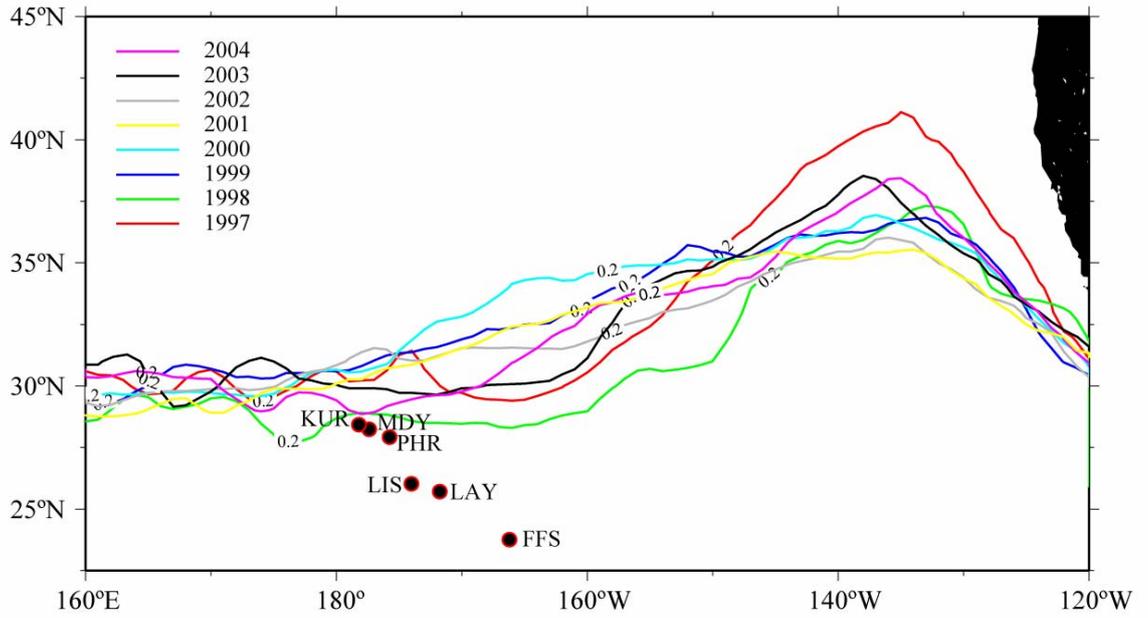


Figure 5.2. Annual variation in the January-February location of the  $0.2 \text{ mg m}^{-3}$  countour, 1997–2004.

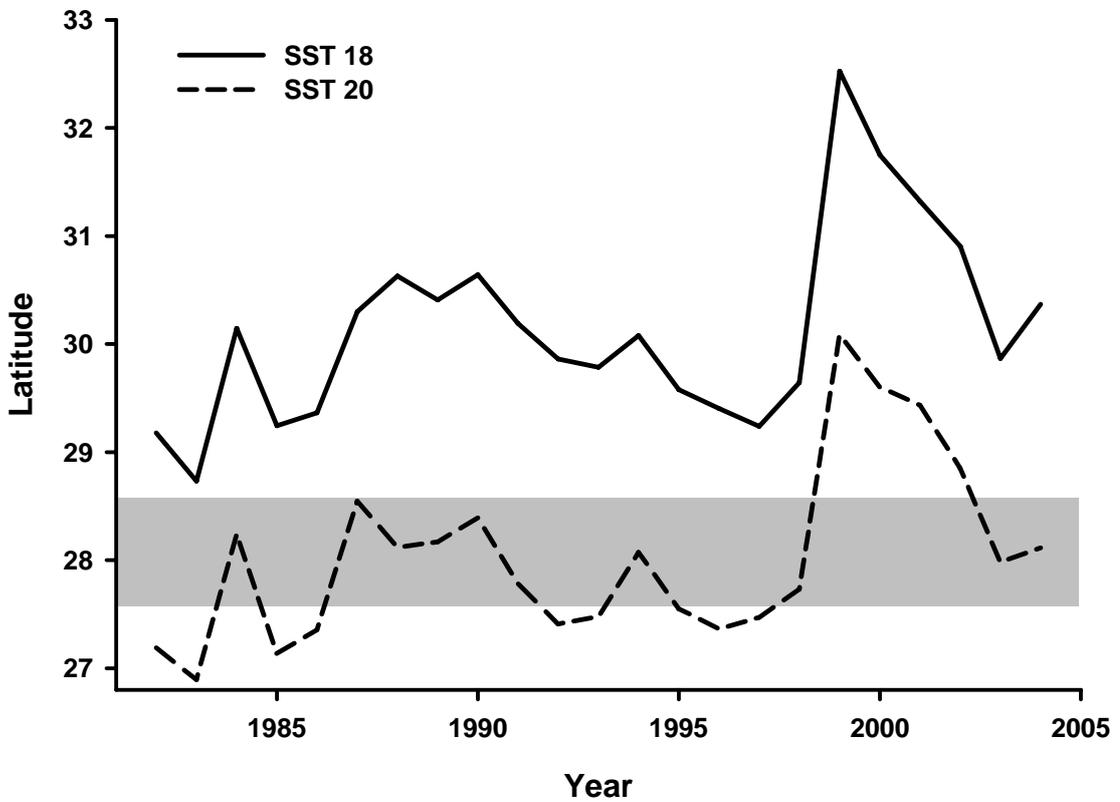


Figure 5.3. Temporal trend in the southernmost extent of the TZCF as indicated by the  $18^{\circ}\text{C}$  and  $20^{\circ}\text{C}$  SST isotherms. The shaded box indicates the latitudinal ranges of the three northernmost NWHI atolls, Pearl and Hermes, Midway, and Kure.

marginally larger ( $< 1.3$ ) than the lowest AICc value. To elucidate patterns in the relationship between the front's wintertime position and monk seal survival, we examined the simple linear correlation coefficients ( $r$ ) between the TZCF and survival time series for all subpopulation/age groups with 0, 1, and 2-year lags. Figure 5.5 reveals that most of the correlations were negative, and that the magnitude of the correlations tended to be greatest for the youngest ages (year 1 and 2), somewhat less for year 3 and 4, and lowest for the adults (age 5-17 yrs). There was also a tendency for correlations to strengthen moving from the southern to the northern portion of the archipelago (*i.e.*, from French Frigate Shoals through to Pearl and Hermes, Midway and Kure). Finally, at the northern subpopulations, the correlation of survival with the TZCF tended to strengthen after a 1- or 2-year time lag.

#### DISCUSSION

Our results accord remarkably well with our *a priori* expectations. The relationship between survival and the southern extent of the front was inverse as expected, statistical significance was detected only for young animals at the northern atolls most proximate to the front, and only after a time lag. Further, the pattern in correlations (Figure 5.5) was consistent with a graduated effect across latitude and seal age. One caveat that must be recognized is that the statistical support for the relationships depicted in Figure 5.4 are largely a result of 3 consecutive years (1999–2001), in which the TZCF remained further north than in all other years in our study, and which were followed by 3 years of unusually poor survival. This raises the possibility that the apparent relationship may not be cause and effect, rather an artifact of two auto-correlated time series. However, the fact that this relationship was only observed for young animals in the northern portion of the archipelago after a time lag, suggests that it is not spurious. Future monitoring of both monk seal survival and central North Pacific oceanography will likely clarify this issue.

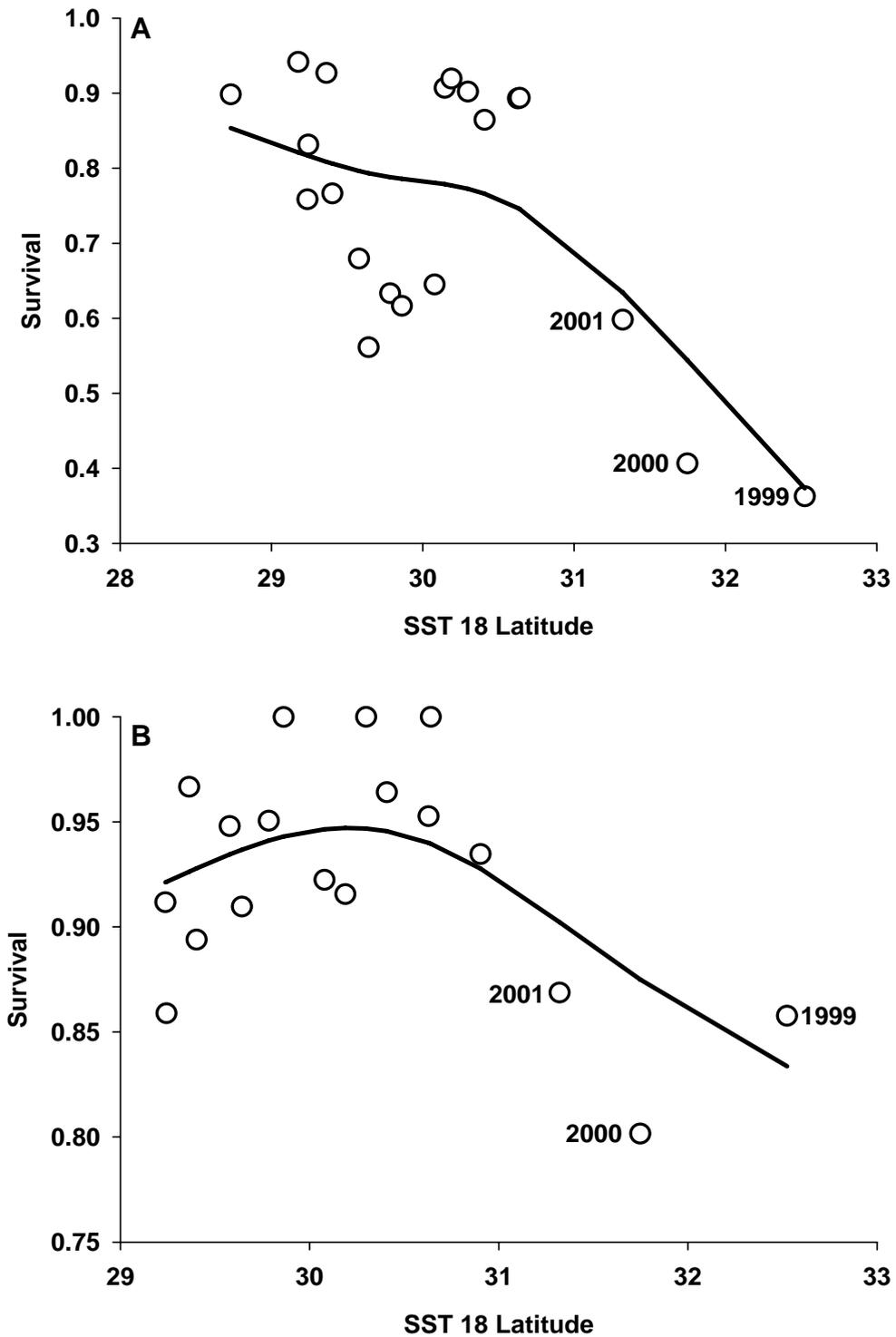


Figure 5.4. Relationship between the southernmost wintertime latitude of the Transition Zone Chlorophyll Front (TZCF, as indicated by the 18°C SST isotherm) and survival of Hawaiian monk seals lagged by A) 2 years for first and second year seals at Lisianski Island, Pearl and Hermes Reef, Midway Atoll and Kure Atoll, and B) 1 year for third and fourth year seals at Pearl and Hermes Reef, Midway Atoll and Kure Atoll. Solid lines represent generalized additive model (GAM) fits. Three consecutive years (1999–2001) when the front remained furthest north are identified.

Table 5.2. Modeling results indicating statistical support for relationships between the TZCF and monk seal survival the same year, and lagged by 1 or 2 years. Linear (LM) and Generalized Additive Models (GAM) are compared to each other and a null model (no predictor) using the difference in small sample Aikake's Information Criterion ( $\Delta AICc$ ). Models are presented in order with the most supported (lowest  $AICc$ ) first.

1 <sup>st</sup> and 2 <sup>nd</sup> year survival at Lisianski, Pearl and Hermes, Midway and Kure Atoll					
Model Type	Time lag (yr)	<i>N</i>	<i>df</i>	<i>AICc</i>	$\Delta AICc$
GAM	2	20	3	-17.67	
LM	2	20	2	-15.01	2.66
GAM	1	20	3	-14.64	3.04
LM	1	20	2	-14.24	3.44
Null	—	20	1	-9.10	8.57
LM	0	20	2	-8.57	9.10
GAM	0	20	3	-8.27	9.40

3 <sup>rd</sup> and 4 <sup>th</sup> year survival at Pearl and Hermes, Midway and Kure Atoll					
Model Type	Time lag (yr)	<i>N</i>	<i>df</i>	<i>AICc</i>	$\Delta AICc$
GAM	1	18	3	-56.44	
GAM	2	18	3	-53.71	2.73
GAM	0	18	3	-52.00	4.44
LM	2	18	2	-51.46	4.98
LM	1	18	2	-50.50	5.94
Null	—	18	1	-50.29	6.15
LM	0	18	2	-49.07	7.37

The mechanisms by which the dynamics of the TZCF influence monk seal survival are uncertain. Presumably, when the front moves further south, it raises primary productivity in the northern NWHI (Figure 5.3), which eventually propagates vertically through the food web to the level at which monk seals forage. Parrish *et al.* (2005) found that juvenile monk seals tend to forage on sand banks and generally take small (< 10 cm) cryptic, benthic prey. They proposed that conditions which affect the settlement of larval fishes on sand banks could be a link between oceanography and juvenile monk seal survival. This presents a testable hypothesis that the dynamics of the TZCF influence the abundance or growth of larval fishes on sand banks in the NWHI.

An analogous coupling of oceanographic variability and vital rates of an endangered marine mammal occurs in the northwestern Atlantic (Greene and Pershing 2004). Variability in the North Atlantic Oscillation (NAO) Index influences water temperatures in the Gulf of Maine and Scotian Shelf regions, which in turn drives the abundance of the copepod *Calanus*. This is the primary prey of the endangered North Atlantic right whale, and *Calanus* abundance influences the whales' reproductive rates. This system involves a 1–2 yr time lag between changes in oceanography and reproductive rates, similar to what we have observed in monk seals.

The 1–2 yr lapse between a northerly shift of the TZCF and reduced seal survival could prove opportune for monk seal conservation efforts. In the past, undersized young seals have been fattened up in captivity and released back into the wild at sites experiencing favorable conditions. Recent declines in monk seal survival, especially in the northern portion of the NWHI (Chapter 4), have generated renewed interest in rehabilitation and release programs. Monitoring excursions of the TZCF may serve as a valuable early warning signal of poor survival 1–2 yr hence, thereby allowing management interventions to be scheduled when they are most needed.

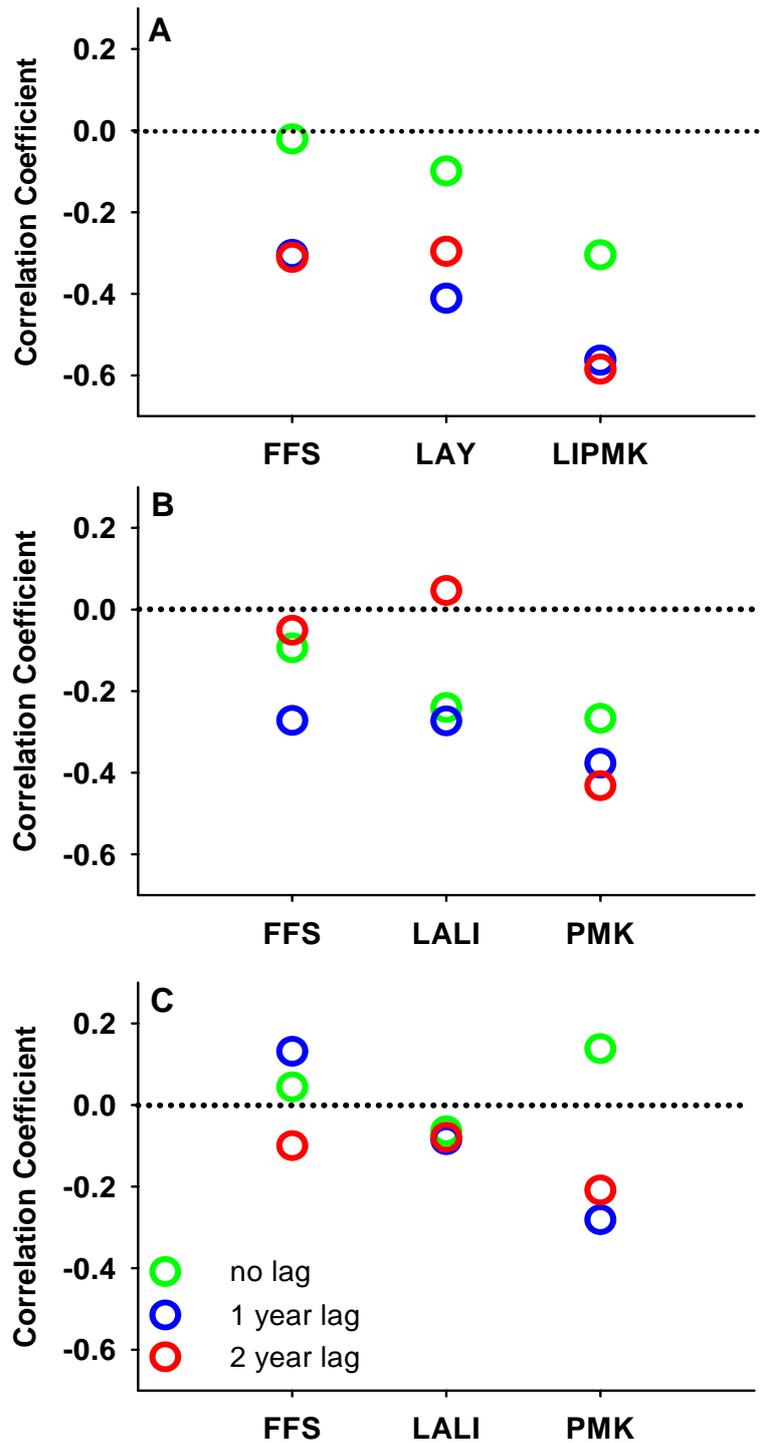


Figure 5.5. Simple linear correlation coefficients ( $r$ ) between the southernmost wintertime latitude of the Transition Zone Chlorophyll Front (TZCF, as indicated by the  $18^{\circ}$  C SST isotherm) and survival trends of A) first- and second-year seals, B) third- and fourth-year seals, and C) 5–17 yr old Hawaiian monk seals, lagged by 0–3 years. Three subpopulation groups for each panel are arrayed on the  $x$ -axis, and are abbreviated as follows: FFS = French Frigate Shoals, LALI = Laysan and Lisianski Islands, PMK = Pearl and Hermes Reef, Midway Atoll and Kure Atoll, LIPMK = Lisianski Islands grouped with PMK.

The drivers of variable productivity and consequent status of biological communities in the NWHI ecosystem remain largely unknown. Polovina *et al.* (1994, 1995) first provided evidence that decadal scale shifts in the North Pacific influence NWHI organisms at a whole range of trophic levels. Our analyses indicate that oceanographic variability on a shorter time scale also influences at least the northern NWHI. In fact, the dynamics described by Polovina *et al.* (1994, 1995) and those presented in this paper are essentially one and the same, differing only in the magnitude of change and time scales over which they occur.

#### ACKNOWLEDGEMENTS

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## Chapter 6. Abundance of the Hawaiian monk seal in the main Hawaiian Islands<sup>11</sup>

### ABSTRACT

Most of the extant *circa* 1400 Hawaiian monk seals *Monachus schauinslandi* live in the Northwestern Hawaiian Islands (NWHI). However, an increasing number of sightings and births have recently occurred in the main Hawaiian Islands (MHI), where no systematic surveys of monk seals were conducted prior to 2000. We estimate that there were at least 45 seals in the MHI in 2000 and at least 52 in 2001, based on aerial surveys of all MHI coastlines, supplemented by sightings of seals from the ground. Moreover, annual births in the MHI have evidently increased since the mid-1990s. Weaned pups in the MHI are longer and have greater girth than those in the NWHI, perhaps reflecting greater per-capita abundance of prey resources. We think that Hawaiian monk seals have recently re-colonized the MHI, which were very likely part of their historic range. Regardless, the MHI habitat appears to be favorable for continued increases of this endangered species.

### INTRODUCTION

Channell and Lomolino (2000) examined patterns in range contraction among 245 species and found that remnant populations had a significantly greater than expected tendency to occur in the periphery of their historic range. Moreover, 37% of species examined occurred exclusively in the periphery of their historic range, whereas only 2% remained solely in the core of their original range. This suggests that approaches to

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conserving endangered species should evaluate the potential for restoration in vacated areas of the historic range, in addition to preserving remnant populations *in situ*. This requires an assessment of whether unoccupied habitat remains suitable or has been altered to the extent that it may no longer sustain viable populations. The Hawaiian monk seal provides a valuable case study in the practical application of these considerations.

Virtually all of the extant *circa* 1400 Hawaiian monk seals inhabit the remote Northwestern Hawaiian Islands (NWHI) in six main subpopulations (Figure 6.1) (Ragen and Lavigne 1999, Carretta *et al.* 2002). Owing to substantial declines in abundance after the late 1950's, the species was listed as “endangered” under the U.S. Endangered Species Act in 1976, and subsequent efforts by the U.S. National Marine Fisheries Service (NMFS) to monitor and foster the species’ recovery have been focused in the NWHI. These efforts often involve discovering and, when possible, responding to natural and anthropogenic crises and threats to the species, such as human disturbance, fisheries interactions, entanglement in marine debris, intraspecific aggression, shark predation, starvation, and clustered mortality events (Gerrodette and Gilmartin 1990, Hiruki *et al.* 1993*a,b*, Starfield *et al.* 1995, Craig and Ragen 1999, Lavigne 1999, Ragen 1999, Donohue *et al.* 2001, Henderson 2001, Bertilsson-Friedman 2002; Carretta *et al.* 2002). Nevertheless, substantial challenges remain to ensure long-term persistence of this species.

The historic and current abundance of monk seals in the main Hawaiian Islands (MHI, Figure 6.1) is not well known. Rare sightings of monk seals in the MHI in the early 20<sup>th</sup> century were documented by Kenyon and Rice (1959). Beginning in the 1990s, an increasing number of monk seal births and sightings have been recorded in the MHI, but because these reports are not based on systematic surveys, evaluation of trends is equivocal. Similarly, little is known about the physical condition and reproductive

success of individuals which breed in the MHI, information which would provide insight regarding habitat quality and the potential for recovery. Here we report the results of studies conducted to document the abundance and physical condition of Hawaiian monk seals in the MHI.

## METHODS

### *Study site*

The main Hawaiian Islands (Figure 6.2) are a subset of the Hawaiian Archipelago. They include eight islands spanning 600 km: Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii. There are also three small uninhabited crescent-shaped volcanic islets: Kaula Rock, Lehua, and Molokini Crater, and several islets offshore of the various primary islands. The human population on the main eight islands ranges from none (Kahoolawe, a former U.S. military bombing range now under restoration), to 876,000 on the island of Oahu (U.S. Census Bureau 2001). The total coastline of the MHI is 1,506 km (Juvik and Juvik 1998).

### *Survey methods*

We conducted surveys of the MHI in 2000 from a Partenavia Observer (twin-engine, high-wing aircraft) with a plexiglass “bubble” nose to facilitate visibility. We searched all coastlines at altitudes ranging from 30-150 m and at an average speed of 145 km $\square$ hr<sup>-1</sup>. To improve detection of seals, we conducted surveys from slower-moving (60-110 km $\square$ hr<sup>-1</sup>) helicopters (Hughes 500) in 2001. All surveys were made in summer and autumn, after most births should have occurred (Johanos *et al.* 1994) and when weather was most favorable.

Each individual island survey was completed within 1 day, and to the degree possible, islands located near each other were surveyed the same day to minimize the

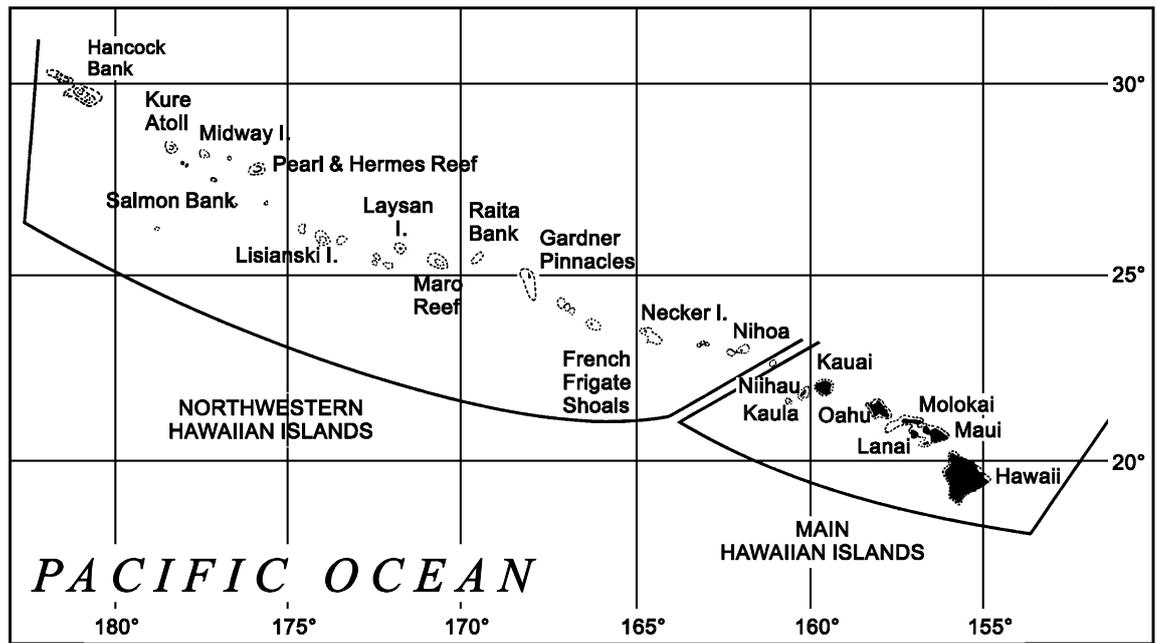


Figure 6.1. The Hawaiian Archipelago. The six main subpopulations where monk seals reside in the Northwestern Hawaiian Islands are Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island, and French Frigate Shoals. Some seals also occur at Necker and Niihau Islands.

potential for double counting seals that might have moved within or between islands. When possible, surveys were begun approximately mid-day following the protocol for ground census' of seals in the NWHI (Johanos and Baker 2001). When a seal was seen, we recorded time and location using a Global Positioning System (GPS) receiver, and took photographs when possible. We classified seals as nursing pups, weaned pups, juveniles (roughly 1-2 years old), sub-adults (roughly 3-4 years old) or adults (minimum of 5 years old), according to size and morphology (*cf.* Johanos and Baker 2001). In some cases, sex could also be determined if seals were lying with their ventral surface exposed, or by association with a nursing pup. Photographs were later examined to confirm field assessments of size and sex.

#### *MHI births and weaning condition*

Records of monk seal births in the MHI are typically reported by the public and cooperating agencies. NMFS biologists attempt to confirm all records of births, and weaned pups are double-tagged in the rear flippers with Temple Tags<sup>TM</sup>. At the time of tagging, axillary girth and standard dorsal length are measured (Craig and Ragen 1999). Because pups lose mass while they fast after weaning, statistical analysis of girth and length of pups born at the six main NWHI subpopulations was limited to measurements taken within 2 weeks of weaning. All MHI, Necker, and Nihoa Islands pup measurements were analyzed, even when weaning dates were imprecisely known, in order to use the few samples available. Girths of pups with unknown weaning dates are likely more negatively biased than those measured within 2 weeks post-weaning. Girths and lengths were analyzed using ANOVA with Student-Newman-Keuls tests for multiple comparisons among locations.

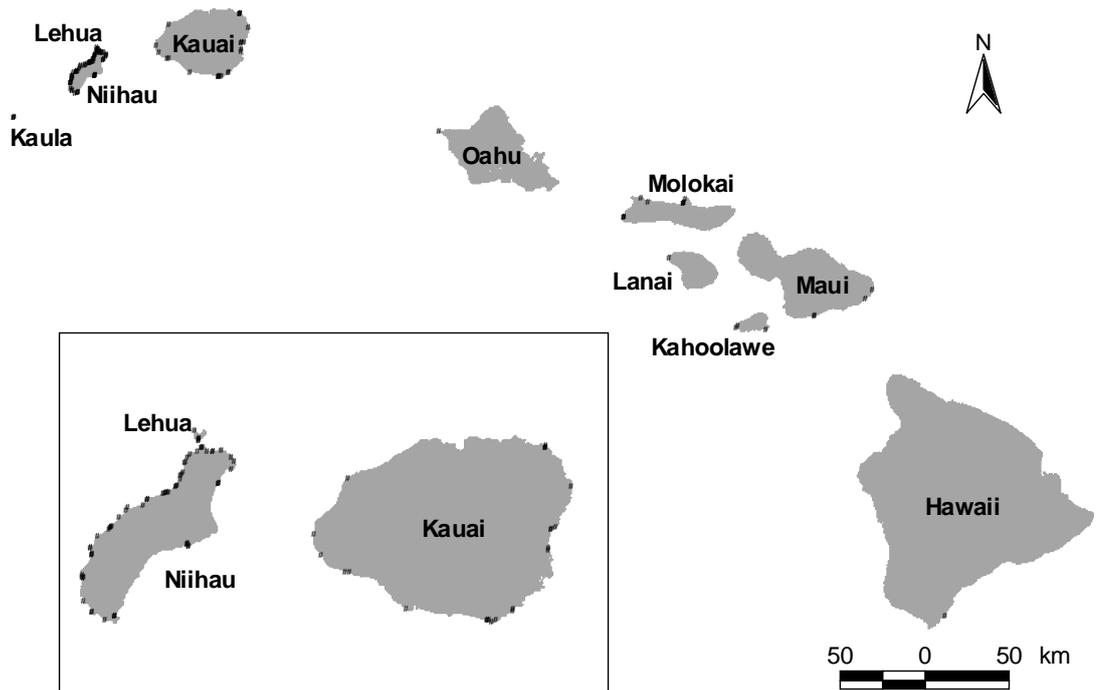


Figure 6.2. Location of Hawaiian monk seals observed during aerial surveys (and additional ground sightings) in the main Hawaiian Islands during 2000-2001. Insets of Kauai and Niihau (not to scale) are provided. Sightings of multiple seals near one another often appear as one dot.

## RESULTS

### *Minimum abundance*

In 2000, we surveyed the islands of Hawaii, Maui, Kahoolawe, Molikini Crater, Lanai, Molokai and Oahu once during 10-12 July 2000. Surveys of the remaining islands were delayed owing to military operations. Consequently, we surveyed Kauai, Niihau, Lehua, and Kaula Rock on 8 August. Because of the relatively large number of seals seen then, we conducted a second survey of those islands on 26 September 2000.

We counted a total of 45 seals in 2000. This was the sum of the maximum counts from each aerial survey, plus four additional seals counted from the ground, but not seen from the air (Table 6.1, Fig. 6.2).

In 2001, we made one survey of Hawaii, Maui, Kahoolawe, Molikini Crater, Lanai, Molokai and Oahu from helicopters during 27-30 August. We surveyed Kauai, Niihau and Lehua Rock on 1 October 2001. Kaula Rock was not surveyed in 2001 because it was too far from fueling facilities. We counted 47 seals during the aerial surveys and 5 others were reported by ground observers, for a total of 52 seals (Table 6.1, Fig. 6.2). Immature animals (pups, juveniles, and subadults) accounted for 49% of the seals seen in 2000 and 56% of those seen in 2001.

### *Births*

The first recorded birth in the MHI occurred on Kauai in 1962 (Table 6.2), when a pup was found abandoned on the beach. The pup was turned over to the State Fish and Game Department, and presumably died soon thereafter. The next MHI birth was reported in 1988. Since 1996, births have been recorded every year and with increasing frequency on various islands, including seven pups we observed while surveying Niihau in 2000 and 2001.

Table 6.1. Number of Hawaiian monk seals counted during aerial surveys of the main Hawaiian Islands in 2000 and 2001<sup>12</sup>.

Island	2000 (1 <sup>st</sup> survey)	2000 (2 <sup>nd</sup> survey)	2001
Kaula Rock	3	0	-
Niihau	5	29	29
Lehua	2	0	3
Kauai	7	7(2)	5(2)
Oahu	0	-	1
Molokai	3(2)	-	3(2)
Lanai	0	-	1
Maui	1	-	3
Kahoolawe	1	-	2
Hawaii	0	-	0(1)
Minimum Abundance	24	45 <sup>13</sup>	52

<sup>12</sup> Numbers in parentheses indicates seals which were seen by observers on the ground that were not seen from the air.

<sup>13</sup> Total of second survey tally at Kaula, Niihau, Lehua, and Kauai plus the tally of single survey of all other islands.

*Weaning condition*

The axillary girth of weaned pups in the MHI averaged 121.7 cm ( $sd = 9.6$ ,  $N = 23$ ) compared to 104.7 cm ( $sd = 10.6$ ,  $N = 2003$ ) in the NWHI. Standard length of pups in the MHI averaged 140.3 cm ( $sd = 5.9$ ,  $N = 23$ ) compared to 126.0 cm ( $sd = 7.7$ ,  $N = 1910$ ) in the NWHI. At Necker, Nihoa, and the MHI we could not confirm if the measurements of nine pups were taken within 2 weeks of weaning. These size differences of MHI versus NWHI pups were highly statistically significant. Both girths and lengths of MHI pups were significantly greater when compared to those at French Frigate Shoals, Laysan Island, Lisianski Island, Pearl and Hermes Reef, Midway Atoll, and Kure Atoll ( $p < 0.001$ ) and the few pups measured at Necker and Nihoa Islands ( $p < 0.025$ ). Nearly all (20 of 23) pups measured in the MHI were born during 1996-2001. When data from NWHI pups were constrained to those same years, the means changed little and MHI girths and lengths remained significantly greater.

## DISCUSSION

Our counts of 45 seals in 2000 and 52 seals in 2001 (Table 6.1) are minimum estimates of the number of Hawaiian monk seals in the MHI, as some seals were undoubtedly at sea and thus not counted (*cf.* Ries *et al.* 1990, Thompson and Harwood 1990; Huber *et al.* 2001). In the NWHI, it has been estimated that two to three seals exist for every one counted during beach censuses (NMFS unpublished data). However, such multipliers are likely a function of terrestrial habitat characteristics, proportion of time spent foraging (which likely is determined in part by proximity and abundance of prey), and time spent in social activities and sleeping in the water (Parrish *et al.* 2000). These factors, especially habitat characteristics, may differ greatly between the NWHI and MHI, such that to assume NWHI correction factors apply in the MHI would be imprudent. In

Table 6.2. Known number of monk seal births in the main Hawaiian Islands.

Year	Niihau	Kauai	Oahu	Molokai	Maui	Kahoolawe	Hawaii	Total
1962	0	1	0	0	0	0	0	1
1988	0	1	0	0	0	0	0	1
1991	1	1	1	0	0	0	0	3
1992	0	1	0	0	0	0	0	1
1996	0	0	1	1	0	0	0	2
1997	0	0	1	1	1	0	0	3
1998	0	0	2	1	1	0	0	4
1999	0	1	0	1	1	0	0	3
2000	2	4	0	1	0	0	0	7
2001	5	3	0	2	0	1	1	12

addition to seals missed in the water, the probability of detecting seals on land during aerial surveys is less than 100%. The altitude, speed and turbulence of the aircraft, and regulations limiting flight distances from people and structures, all conspire to reduce sighting probability.

The location of MHI monk seals (Figure 6.2) suggests that two interacting factors may influence their distribution. The number of seals tends to decrease moving along the archipelago from the northwest to the southeast, and fewer seals occur where human presence is greater. Consequently, most seals were seen at Niihau at the northwestern end of the MHI, where only 230 people live (Juvik and Juvik 1998). The second highest counts were on Kauai (human population 58,000) just east of Niihau. Moving to the southeast, just one seal was seen on densely populated Oahu (population 876,000). However, seals were more regularly sighted on the next island to the southeast, Molokai (population 6,700), the remote areas of Maui (population 91,000), uninhabited Kahoolawe, and sparsely populated Lanai (population 3,200). Notably, the island furthest to the southeast, Hawaii (population 149,000), comprises 30% of the tidal shoreline of the MHI (Juvik and Juvik 1998), yet only one seal was found there during this study.

The documented number of births in the MHI is a minimum estimate, especially for Niihau. Most mothers selected remote areas for parturition, reducing the probability they are discovered. While most monk seals were seen on Niihau during aerial surveys, births on that island have not been reported by local residents. They have been documented only by research biologists on 3 occasions over 11 years.

The size of phocid pups at weaning is the result of both pre- and post-partum maternal investment, which in part reflects prey availability (Kovacs and Lavigne 1986, Fowler and Siniff 1992, Burton *et al.* 1997, Vergani *et al.* 2001). We think that the difference in body condition of monk seal pups weaned in the MHI compared to the

NWHI (Figure 6.3) may reflect better foraging conditions in the MHI. This contrasts with general findings of better conditions in the central portion of a species' range compared to the periphery (*e.g.*, Brown 1984). Moreover, substantial evidence indicates that some components of marine ecosystems around the MHI have been impoverished by sport and commercial fishing. For example, Friedlander and DeMartini (2002) estimated that the biomass of shallow water reef fishes was 260% greater in the NWHI than in the MHI, owing to fishing pressure.

We suggest three factors that may explain the differences in body condition of pups in the MHI compared to the NWHI. First, because the monk seal population in the MHI appears to be small, the per capita availability of prey may be relatively high, even if absolute prey abundance is lower than in the NWHI, where up to several hundred seals reside and forage at single atolls.

Second, absolute densities of preferred monk seal prey may not differ between the MHI and the NWHI as much as the comparison of total shallow water reef fish biomass in Friedlander and DeMartini (2002) would indicate. When apex predators (*i.e.*, sharks and jacks upon which monk seals do not prey) are excluded, the difference in the remaining components of shallow water reef fish biomass drop from 260% to 70% greater in the NWHI compared to the MHI (calculated from Friedlander and DeMartini, 2002, Table 6.1). Available information on the foraging habitat preferences of Hawaiian monk seals in the NWHI indicates that seals forage on the sea floor on the outer slopes of atolls and on terraces and submerged sea mounts with modal depths of 50-80 m and deeper (Abernathy 1999, Parrish *et al.* 2000, 2002, B. Stewart pers. comm.). No comparisons of prey abundance at those depths in the NWHI and MHI are available. Common prey items of NWHI seals include eels, wrasses, and many other benthic species which are not prized by sport and commercial fishermen (Goodman-Lowe 1998, Parrish

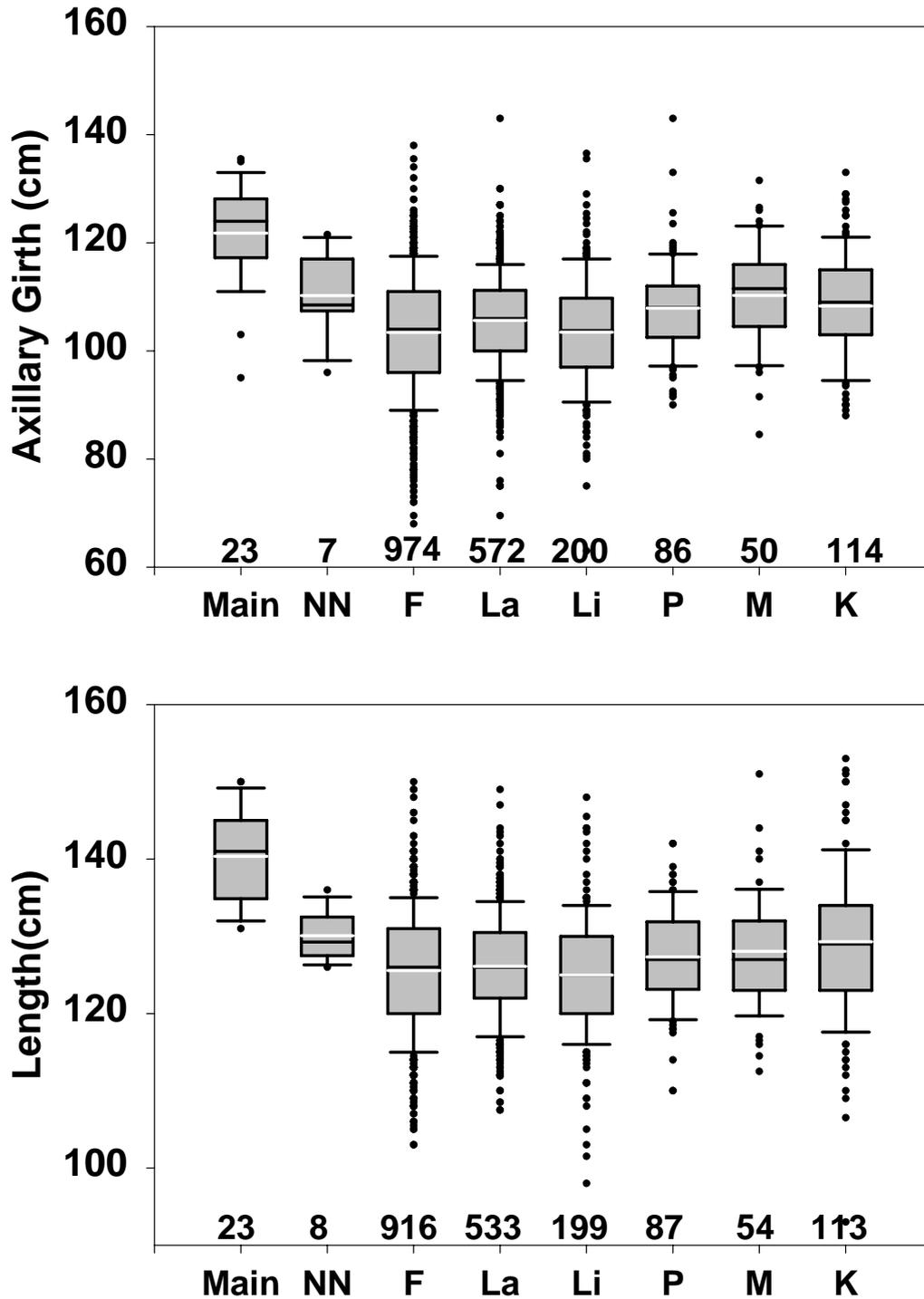


Figure 6.3. Box plots of weaned monk seal girth and length distributions by birth location. White bars indicate mean; black bars show medians. Boxes encompass 25th-75th percentiles; extended bars are 10th and 90th percentiles. Points indicate remaining outlying measurements. Numbers of pups measured in all years are shown below each plot. Main = main Hawaiian Islands, NN = Necker and Nihoa Islands combined, F = French Frigate Shoals, La = Laysan Island, Li = Lisianski Island, P = Pearl and Hermes Reef, M = Midway Atoll, K = Kure Atoll.

*et al.* 2000). Thus, the potential for competition between foraging monk seals and fisherman may be lower than it might seem at first glance. However, hookings of monk seals on recreational and perhaps commercial fishing hooks in the MHI indicate that some degree of overlap occurs. There have been 16 such hookings recorded, 11 since 1996 (NMFS unpublished data).

A third factor that may influence prey availability for monk seals in the MHI is a difference in the structure of the marine community relative to the NWHI. In the NWHI, apex predators such as large sharks and jacks are abundant (Friedlander and DeMartini 2002). The diets of these predators overlap with that of monk seals (Kenyon and Rice 1959, De Crosta *et al.* 1984, Sudekum *et al.* 1991, Wetherbee *et al.* 1996, 1997, Goodman-Lowe 1998; Meyer *et al.* 2001) and direct competition for prey items has been observed on video collected with seal-mounted cameras in the NWHI (F. Parrish pers. comm.). These interactions involve sharks and jacks associating with foraging seals, including kleptoparasitism. In contrast, large predators are rare in the MHI as large sharks and jacks have been heavily fished, the latter being a very popular trophy and food fish (Friedlander and DeMartini 2002). Thus, low interspecific competition with other top predators may enhance the foraging success of monk seals in the MHI. Further, Parrish and Boland (2004) suggest that high densities of apex fish predators can constrain the movements of reef fishes to habitat with predator refugia, thus effectively reducing reef fish productivity and density.

The history of monk seals in the MHI is indefinite. Kenyon and Rice (1959) reviewed seven MHI sightings accumulated from 1928-1956, and a long-time Niihau resident has reported that seals became common on Niihau after 1970 (interview with J. Baker). We think it likely that monk seals came to the MHI from the NWHI before tagging was consistently done, though it is also possible that some seals persisted in the

MHI prior to this hypothesized dispersal. The distribution of seals (Figure 6.2) and the fact that while most seals in the NWHI have been tagged since the mid-1980's, only two are known to have voluntarily moved to the MHI, suggests that seals may currently be spreading to other parts of the MHI from Niihau.

In addition to seals naturally occurring in the MHI, 21 adult males were translocated from the NWHI to the MHI in 1994 in order to correct a male-biased sex ratio at Laysan Island, where male aggression was reducing female survival (Hiruki *et al.* 1993*a,b*, Starfield *et al.* 1995). The translocated animals were all tagged, and account for only a small portion of sightings in the MHI.

Before Polynesians arrived approximately 1500-1600 years ago (Bellwood 1978), monk seals likely occurred throughout the MHI. The Hawaiian monk seal is thought to be an evolutionarily primitive species, having originated either elsewhere in the Pacific Basin or made its way to the Hawaiian Islands from the North Atlantic via the Central American Seaway, perhaps 15 million years ago (Repenning and Ray 1977; Repenning *et al.* 1979, Berta and Sumich 1999). The Hawaiian Archipelago is formed of volcanos which emerged from an oceanic hot spot in the central Pacific. The volcanos erode as they move to the northwest on the Pacific Plate at about  $9 \text{ cm}\cdot\text{yr}^{-1}$ , eventually evolving from large islands (such as the current MHI) to coral atolls and seamounts such as the NWHI (Juvik and Juvik 1998). The ages of various dated Hawaiian volcanos range from the island of Hawaii, less than one-half million years (mya) old, to Midway Atoll aged 27.7 mya (Juvik and Juvik 1998). Thus, when monk seals likely arrived in Hawaii, the current MHI and some of the more recent NWHI did not yet exist, while the older NWHI would have been larger and located further to the southeast than they are now. Monk seals would likely have colonized and eventually spread throughout the entire archipelago. In geologic time, they also would have necessarily abandoned atolls that subsided and

naturally colonized newly formed islands of the dynamically changing Hawaiian Archipelago.

Extinction of species following human colonization is well documented in the Pacific Islands and elsewhere (Olson and James 1982; Martin and Klein 1984, Martin *et al.* 1985, Anderson 1989, Stuart 1991, Caughley and Gunn 1996, Holdaway and Jacomb 2000, Burney *et al.* 2001, Grayson 2001, Duncan *et al.* 2002). After Polynesians arrived, monk seals may have been extirpated from the MHI and constrained to the NWHI, where, other than at Necker and Nihoa Islands, there is no evidence of Polynesian presence (Rauzon 2001). The NWHI, now the species' primary range, may represent formerly peripheral habitat. Caughley and Gunn (1996) note that "remnant populations of an endangered species often end up not in the habitat most favorable to it but in the habitat least favorable to its agent of decline." While there is no archaeological evidence of monk seals in the MHI, the seals occupy ephemeral shoreline habitats, making preservation of hard parts unlikely<sup>14</sup>.

Current abundance of monk seals in the MHI is low, but may be increasing, and the excellent condition of weaned pups indicates potential for further population growth. This poses both opportunities and challenges for the conservation of this species. The addition of another viable component to the monk seal metapopulation may enhance the species' long-term persistence. Public exposure to wild monk seals provides excellent opportunities for education and development of a conservation ethic. However, seals in the MHI are exposed to many threats. Monk seals have proven vulnerable to harassment by humans and their domesticated animals (Ragen 1999), and the human population in the MHI is approximately 1.2 million (U.S. Census Bureau 2001) compared to less than

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<sup>14</sup> Subsequent to this chapter being published, an overlooked study was discovered which documented monk seal remains on the island of Hawaii in the period 1400-1760 AD (Rosendahl 1994).

100 in the NWHI. Other threats in the MHI include hooking by fishermen, collision with vessels, and oil spills. Finally, there is potential for disease transfer to MHI monk seals from domesticated animals. If this occurs, and disease is subsequently transmitted to the NWHI population, the results could be devastating (Heide-Joergensen *et al.* 1992, Thompson *et al.* 1993, Forcada *et al.* 1999).

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**Chapter 7. Potential effects of sea-level rise on the terrestrial  
habitats of endangered and endemic megafauna  
in the northwestern Hawaiian Islands<sup>15</sup>**

ABSTRACT

Climate models predict that global average sea level may rise considerably this century, potentially affecting species that rely on coastal habitat. The Northwestern Hawaiian Islands (NWHI) have high conservation value due to their concentration of endemic, endangered and threatened species, and large numbers of nesting seabirds. Most of these islands are low-lying and therefore potentially vulnerable to increases in global average sea level. We explored the potential for habitat loss in the NWHI by creating topographic models of several islands and evaluating the potential effects of sea-level rise by 2100 under a range of basic passive flooding scenarios. Projected terrestrial habitat loss varied greatly among the islands examined: 3 to 65% under a median scenario (48-cm rise), and 5 to 75% under the maximum scenario (88-cm rise). Spring tides would probably periodically inundate all land below 89 cm (median scenario) and 129 cm (maximum scenario) in elevation. Sea level is expected to continue increasing after 2100, which would have greater impact on atolls such as French Frigate Shoals and Pearl and Hermes Reef, where virtually all land is less than 2 m above sea level. Higher elevation islands such as Lisianski, Laysan, Necker, and Nihoa may provide longer-term refuges for species. The effects of habitat loss on NWHI biota are difficult to predict, but may be greatest for endangered Hawaiian monk seals, threatened Hawaiian green sea turtles, and

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the endangered Laysan finch at Pearl and Hermes Reef. This study marks the first effort to detail the topography and evaluate sea level rise effects on NWHI species.

## INTRODUCTION

Climate change is an important conservation concern for marine ecosystems (McLean and Tsyban 2001). Predicting the effects of climate change on marine ecosystems is problematic, although some trends have been observed and the direction of future changes, such as global average temperature and sea-level rise, can be anticipated (Houghton *et al.* 2001). Sea level rose approximately 15 cm during the 20th Century (Ruddiman 2001). Further increases in sea level are anticipated due to several factors including thermal expansion of the warming oceans along with melting of glaciers and ice caps (Church *et al.* 2001). The difficulty in predicting the biological effects of climate change arises in part from uncertainties about how physical changes will be manifest in diverse environments as well as how individual species and communities might respond. Short-term and decadal-scale climate variation has been associated with distinct changes in marine ecosystems (Trillmich and Ono 1991, Polovina *et al.* 1994, Springer 1998, McGowan *et al.* 1999, Stirling 1999). Various responses among individual species or populations have been observed and attributed to recent climate change or variability, including changes in range, abundance, density, phenology and migration patterns (Hughes 2000, Walther *et al.* 2002).

In this study, we portray the potential effects of sea-level rise in the Northwestern Hawaiian Islands (NWHI), a remote archipelago consisting largely of low-lying oceanic islands and atolls. Endemic to these islands are four land birds, three terrestrial snails, 12 plants and over 60 species of terrestrial arthropods (Conant *et al.* 1984). For these species

living out their entire lives on land, the NWHI terrestrial habitat represents their only tether to persistence.

The NWHI are also important for large marine vertebrates including sea birds, green sea turtles (*Chelonia mydas*) and Hawaiian monk seals (*Monachus schauinslandi*), all of which feed at sea but require terrestrial habitat with few or no predators to either nest (turtles and seabirds) or raise offspring (seabirds and seals). The Hawaiian monk seal, listed as endangered under the U.S. Endangered Species Act, is one of the rarest marine mammals in the world, with a declining population of only approximately 1300 individuals - primarily in six NWHI subpopulations (Ragen and Lavigne 1999, Chapter 6, Carretta *et al.* 2006, Antonelis *et al.* 2006). Female seals tend to give birth on sandy beaches adjacent to shallow waters, which offer neonates access to the sea while providing some degree of protection from both large waves and the approach of predatory sharks (Westlake and Gilmartin 1990). Hawaiian green sea turtles, listed as a threatened stock under the Endangered Species Act, range over the entire Hawaiian archipelago, but over 90% of breeding females nest at one NWHI atoll, French Frigate Shoals, where their number has been increasing for the past 30 yr (Balazs and Chaloupka 2004). The NWHI are also habitat for some 14 million seabirds of 18 species (Harrison 1990). Nesting of Laysan (*Phoebastria immutabilis*) and black-footed albatross (*P. nigripes*) occurs almost entirely in the NWHI (Harrison 1990), and these species have been listed as vulnerable and endangered, respectively, by the IUCN<sup>16</sup>. The sooty, or Tristram's, storm petrel (*Oceanodroma tristrami*), has been listed as "near threatened"<sup>16</sup> and its most populous remaining breeding sites are in the NWHI (Harrison 1990). A significant proportion of the world population of Bonin petrels (*Pterodroma hypoleuca*) also breeds in the NWHI

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<sup>16</sup> IUCN Red List of Threatened Species ([www.iucnredlist.org](http://www.iucnredlist.org))

(Fefer *et al.* 1984, Harrison 1990). The remaining seabird species' nesting habitats are relatively widespread.

The NWHI's unique biota, high conservation value, and physical nature (primarily low-lying islands), make them distinctly vulnerable to the effects of climate change, especially sea-level rise. In this study, we develop predictions of sea-level rise effects on several sites in the NWHI and discuss their potential impact on selected species.

## METHODS

### *Sea-level rise scenarios*

We used predictions of sea level rise by 2100, that year being the endpoint used in the latest Intergovernmental Panel on Climate Change (IPCC) evaluation of a number of model scenarios, which yielded a central value of a 48 cm rise by 2100 (Church *et al.* 2001). The uncertainty of predictions increases over time, but the expectation is that sea level will continue to rise beyond 2100 (Church *et al.* 2001). Recent evidence suggests that sea level may rise more rapidly than previous models have predicted, due to an accelerated rate of ice loss from the Greenland Ice Sheet (Rignot and Kanagaratnam 2006).

We evaluated the effect of sea-level rise on certain land areas of the NWHI under passive flooding scenarios, whereby we simply estimated the area that would be lost if islands maintained their current topography and the sea were to rise by various amounts. We ran six scenarios, the low (9 cm), median (48 cm) and high (88 cm) values from Church *et al.* (2001), each evaluated at mean low water (MLW) and at spring tide. A mean spring tide value of 41 cm above MLW was estimated with WTides Software<sup>17</sup> at the Laysan Island tide station, which is situated near the center of the NWHI archipelago.

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<sup>17</sup> [www.wtides.com](http://www.wtides.com)

### *NWHI geography*

The NWHI (Figure 7.1) comprise an 1800-km chain of small islands and coral atolls built over the remnants of volcanoes formed between 7 and more than 27 million yr ago (Juvik and Juvik 1998). Nihoa and Necker Islands are volcanic remnants rising steeply 275 m and 84 m from the ocean. These islands, as well as La Perouse and Gardner Pinnacles, two smaller rocky islands, are not considered in this analysis. The remaining NWHI are either relatively large, low-lying islands (Laysan and Lisianski) or coral atolls consisting of a barrier reef enclosing lagoons dotted with two to ten permanent islets. French Frigate Shoals (FFS) contains nine islets (plus La Perouse). Pearl and Hermes Reef (PHR) has seven persistent islets and some tiny ephemeral sand spits which are only intermittently emergent. Midway and Kure Atolls contain three and two permanent islands, respectively. The total land area of the NWHI is reported to be 800 ha (Juvik and Juvik 1998).

### *Spatial analysis*

We were unable to find elevation data for the NWHI other than references for the high points of individual islands. To characterize impacts of sea-level rise, we collected elevation data from three locations, including Lisianski Island, PHR and FFS. At these sites, some areas could not be surveyed due to logistical constraints or were avoided to prevent undue disturbance or harm to wildlife. At PHR, we surveyed the five largest islets (Southeast, Seal-Kittery, Grass, North and Little North). Bird and Sand Islands are tiny, low sand spits, which contribute negligibly to the total land area at PHR. At FFS, four of the five large islands were surveyed (East, Gin, Little Gin and Trig). Tern Island is the largest island (approx. 17 ha) at FFS, is mostly enclosed by a sea-wall, and has not yet been surveyed. Shark Island is a small permanent island omitted from the study, as were

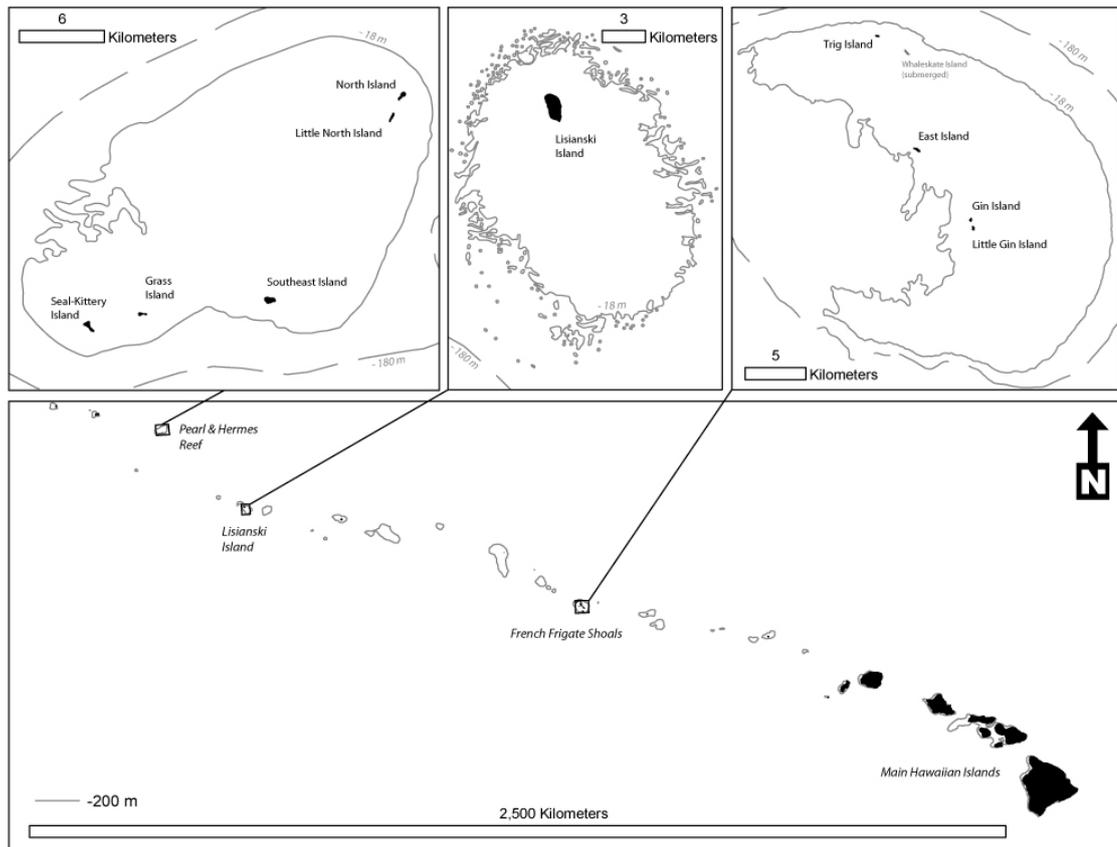


Figure 7.1. The Hawaiian Archipelago. Insets show where spatial modeling and projections of sea level rise effects were conducted.

Whale-Skate, Round, Mullet and Disappearing Islands - small, low sand spits occasionally or frequently awash at high tide.

The surveyed islands all have similar topography, characterized by beaches sloping upward from the waterline at various inclines to a berm, landward of which, the islands are essentially flat. There is little vertical relief and the moderate variations in elevation that do exist are very gradual. Therefore, the topography of the islands can be well-characterized by surveying the waterline and the elevation of the berm. Individual islands were surveyed by 2 people simultaneously walking the berm line and waterline carrying Wide Area Augmentation System (WAAS) global positioning system (GPS) receivers (GPS 76, Garmin, Olathe, KS, USA), which recorded tracks of each individual's path. Elevation was measured using an electronic digital theodolite (DT500A, Sokkia, Olathe, KS, USA) accurate to 5 seconds (or less than 1 cm in our application) at intervals ranging from 30 to 150 m, and GPS waypoints were recorded at each elevation site. The highest points of islands were measured, with the exception of Lisianski Island. Areas inland of the berm were not systematically surveyed to avoid damaging seabird nests. This was especially true at Lisianski Island, the interior of which is riddled with burrows. Thus, our modeled topography of island interiors is likely to be less precise. However, because the islands have little relief beyond the berm, it is unlikely that this omission has significantly influenced our results.

GPS tracks of island perimeters and theodolite stations were imported into ArcGIS 9.0 (ESRI, Redlands CA), after which clean lines representing the mean low water (MLW) level and the berm above shoreline were traced, geo-referenced and mapped with the Zone 3 (N) Universal Transverse Mercator (UTM) projection, using the World Geodetic System (WGS) 1984 datum. Theodolite station heights at PHR and Lisianski Island were referenced to MLW estimates for the Laysan Island tide station

using WTides Software. Theodolite station heights at FFS were referenced to MLW estimates for a local tide station using the same software.

To model the topography of each surveyed island, we created between 50 and 100 equidistant points along its MLW line with a height value of 0 m (see Figure 7.2b). These values, along with island heights measured at theodolite stations, were combined to produce a triangular irregular network (TIN) of island elevations. The TIN is a commonly used method for creating three-dimensional surfaces from point data. It is especially appropriate for our application, as it allows one to vary intensity of sampling according to the complexity of the relief (*e.g.*, beach slope and berm versus flat island interiors, Burrough and McDonnell 1998). To increase the smoothness of the TIN surface, we added interpolated elevation points between most of the measured theodolite stations along the berm (Figure 7.2b). There was little variation in elevation along the berm, such that these interpolated points could introduce only negligible error. Each TIN was reviewed and compared with theodolite survey notes. A small number of large discrepancies were noted (especially in island interiors where sampling had been sparse), in which the modeled surface exhibited peaks or dips below sea level that clearly do not exist. These were remedied by augmenting the TIN with additional points calculated by linear interpolation mid-way between measured theodolite stations along the berm and across the island. As above, these introduced data points provided mean height values for the space between theodolite stations, producing a more realistic model of the island. Each TIN was then rasterized to produce a floating point elevation grid of each island, with a horizontal resolution of between 3 and 8 m, depending on the size of the island and the number of theodolite stations available.

The 3-dimensional surface areas of each island, according to the above described sea-level change scenarios were then calculated using the Surface Volume tool in the 3D

Analyst Toolbox in ArcGIS 9.0. The raster elevation grid of each island was also reclassified into an integer grid comprised of 10 cm elevation bins using the Spatial Analyst Toolbox of ArcGIS 9.0. The resulting data on grid cell counts were plotted to illustrate the proportion of each island above MLW level at 10 cm elevation intervals.

## RESULTS

The projected effects of sea-level rise on surface area varied considerably among the islands examined and depending upon the sea-level rise scenario (Table 7.1). Lisianski Island is projected to be the least affected of the islands surveyed, losing only 5% of its area even under the maximum rise scenario. In contrast, the islets at FFS and PHR are projected to lose between 15 and 65% of their area under the median sea-level rise scenario. High tides have a large influence on the available habitat on various islands, even at present, compared to MLW (Table 7.1). On average, habitat loss was greater when current island areas were compared to future projected areas, both at spring tide. Under the maximum rise scenario, PHR islands would lose 51 and 69% at MLW and spring tide, respectively, while the group of islands analyzed at FFS would be reduced by 40 and 57% (MLW and spring tide, respectively). Under the latter scenario, Gin and Trig Islands at FFS all but disappear. Figure 7.2 illustrates the range of projected habitat loss for these scenarios at Lisianski Island, Southeast Island (PHR), and Trig and East Islands (FFS).

The integer grid elevation data provide a more complete picture of the distribution of area (Figure 7.3) of surveyed islands. Because sea-level rise is expected to continue after 2100, these cumulative elevation plots also depict the proportion of habitat expected to remain after increases in sea level beyond our basic scenarios. Lisianski Island may provide a longer-term refuge for NWHI species. Even after a 2-m rise in sea level, over

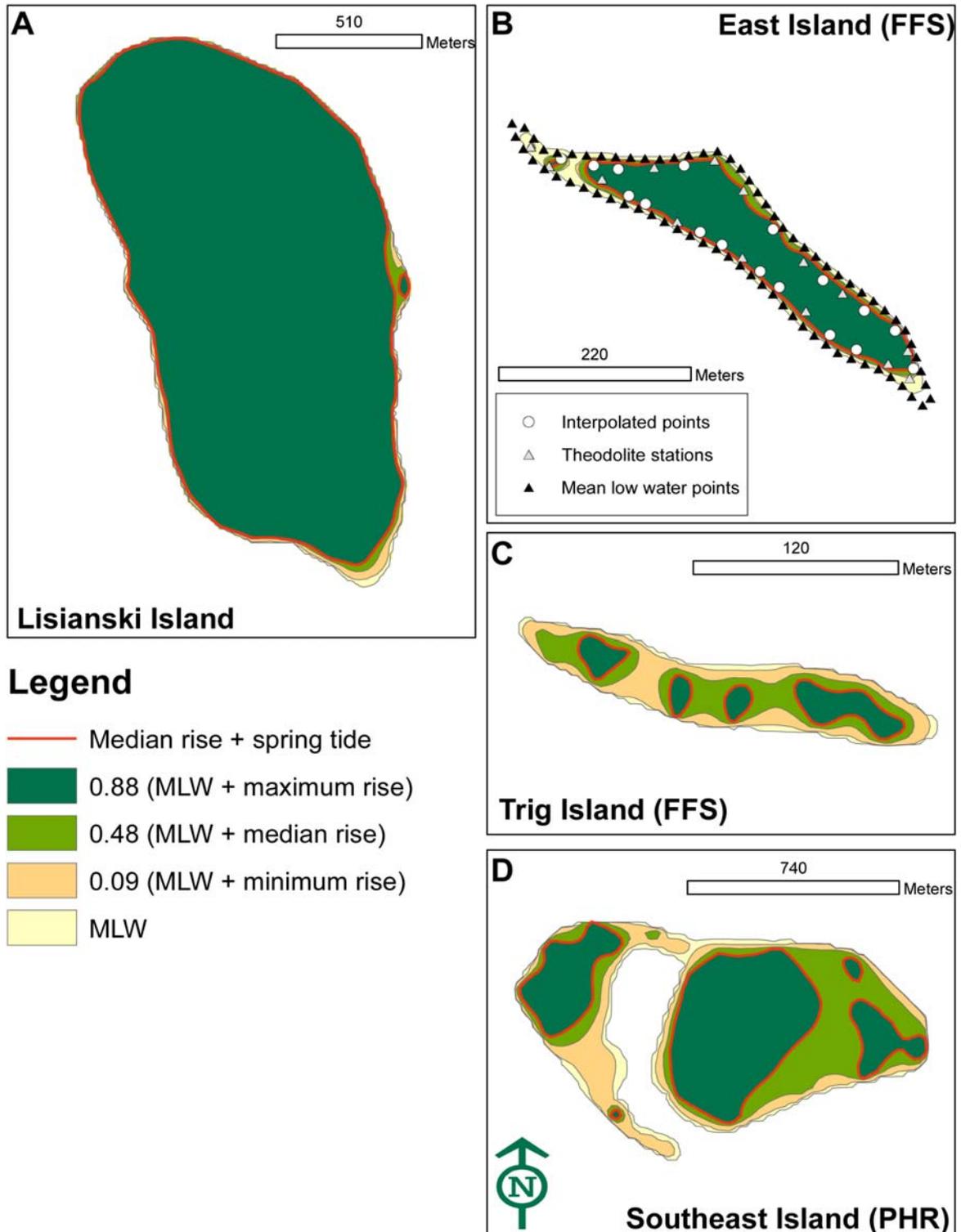


Figure 7.2. Current and projected maps of 4 Northwestern Hawaiian Islands at mean low water (MLW) with minimum (9 cm), median (48 cm) and maximum (88 cm) predicted sea-level rise. The median scenario at spring tide is also shown. A) Lisianski Island; B) East Island, French Frigate Shoals, showing the measured and interpolated points along the waterline and berm used to create the Triangular Irregular Network (TIN); C) Trig Island, French Frigate Shoals; D) Southeast Island, Pearl and Hermes Reef.

80% of the land area would be expected to remain (notwithstanding any potential effects of erosion from, for example, wave action). However, the island would rapidly become submerged rapidly as sea level rises above 2.4 m. The land areas we measured at FFS and PHR would disappear with a 2-m rise. These plots also indicate the islets within an atoll that likely would disappear first. Of those islets measured at FFS, East Island should persist the longest, whereas North Island would be the last remnant at PHR.

The cumulative elevation data also can be used to estimate the proportional rate at which land will disappear. For example, if sea level were to rise in a linear fashion, the shape of the curves in Figure 7.3 would reflect the proportional rate of change in land area at each respective island. Most sea-level models predict a relatively linear rise until some point in the middle of the 21st Century, after which the rate accelerates (Church *et al.* 2001). By assuming a particular pattern of sea-level rise and applying it to the cumulative elevation data presented here, one could estimate the pattern in habitat loss for islands over time. This may be useful for modeling the viability of island populations where land area can be used as an index of carrying capacity.

## DISCUSSION

A growing number of studies have related either short-term events such as El Niño or longer-term climate trends to changes in a wide range of biota, including pinnipeds, seabirds and sea turtles whose life history requirements span the marine and terrestrial (Trillmich and Ono 1991, Hughes 2000, Walther *et al.* 2002). In pinnipeds, El Niño has had dramatic negative impacts, including high mortality and decreased reproductive success, as well as possible beneficial effects in at least one case (Trillmich and Ono 1991, Antonelis *et al.* 2003). These impacts are largely related to changes in ocean

Table 7.1. Current and projected 3-dimensional surface areas (in ha) of selected Northwestern Hawaiian Islands under a range of sea level rise predictions (Church *et al.* 2001) at mean low water (MLW) and at spring tide. Proportional losses of area, shown in parentheses, reference projected MLW area to current MLW area and projected area at spring tide to current area at spring tide. Pearl and Hermes Reef total includes nearly all the permanent islands, with the exception of very small islets, which were not surveyed. French Frigate Shoals total does not include Tern Island, the largest islet at FFS, which was not surveyed. Four other very small islets were also omitted. Min: minimum; med: median; max: maximum.

<i>Place</i>	<i>Current</i>		<i>min. rise (9 cm)</i>		<i>med. rise (48 cm)</i>		<i>max. rise (88 cm)</i>	
	<i>MLW</i>	<i>Spring</i>	<i>MLW</i>	<i>Spring</i>	<i>MLW</i>	<i>Spring</i>	<i>MLW</i>	<i>Spring</i>
Lisianski	152.5	149.0	151.4 (0.01)	148.4 (0.00)	148.4 (0.03)	145.4 (0.02)	145.4 (0.05)	141.41 (0.05)
<i>Pearl and Hermes Reef</i>								
Southeast	17.08	13.47	15.88 (0.07)	12.97 (0.04)	13.02 (0.24)	8.41 (0.38)	8.41 (0.51)	2.86 (0.79)
Grass	4.00	2.95	3.67 (0.08)	2.74 (0.07)	2.76 (0.31)	1.95 (0.34)	1.95 (0.51)	1.35 (0.54)
Seal-Kittery	13.11	10.07	12.16 (0.07)	9.46 (0.06)	9.53 (0.27)	5.86 (0.42)	5.86 (0.55)	1.29 (0.87)
North	8.17	6.69	7.70 (0.06)	6.41 (0.04)	6.44 (0.21)	5.47 (0.18)	5.47 (0.33)	5.00 (0.25)
Little North	2.77	1.13	2.15 (0.22)	0.95 (0.16)	0.97 (0.65)	0.46 (0.59)	0.46 (0.83)	0.12 (0.90)
PHR-Total	45.13	34.30	41.56 (0.08)	32.53 (0.05)	32.73 (0.27)	22.16 (0.35)	22.16 (0.51)	10.62 (0.69)
<i>French Frigate Shoals</i>								
Trig	0.79	0.54	0.74 (0.07)	0.48 (0.12)	0.49 (0.39)	0.20 (0.63)	0.20 (0.75)	0.01 (0.99)
East	3.29	2.89	3.19 (0.03)	2.80 (0.03)	2.81 (0.15)	2.43 (0.16)	2.43 (0.26)	1.95 (0.33)
Gin	1.38	1.06	1.30 (0.06)	0.98 (0.07)	0.99 (0.28)	0.58 (0.45)	0.58 (0.58)	0.04 (0.96)
Little Gin	1.78	1.53	1.72 (0.03)	1.45 (0.05)	1.46 (0.18)	1.10 (0.28)	1.10 (0.38)	0.58 (0.62)
FFS-Total	7.24	6.02	6.95 (0.04)	5.71 (0.05)	5.74 (0.21)	4.32 (0.28)	4.32 (0.40)	2.58 (0.57)

productivity and prey resource distribution or density. Additionally, changes in the thickness, extent, and seasonality of sea ice may have severe repercussions for ice-breeding seals and walrus (*Odobenus rosmarus*) (Kelly 2001, Stirling and Smith 2004, Johnston *et al.* 2005). Likewise, a trend toward earlier ice breakup has altered the access of polar bears (*Ursus maritimus*) to ice-associated pinnipeds in Hudson Bay, leading to reduced condition and natality in the bears (Stirling *et al.* 1999, 2004).

Seabirds also have undergone changes in abundance and range shifts in response to climate change, typically believed to be mediated by altered abundance and availability of their marine prey (*e.g.*, Veit *et al.* 1997, Thompson and Ollason 2001, Hyrenbach and Veit 2003, Weimerskirch *et al.* 2003). Some Antarctic seabirds may be affected by variation in ice cover, which can determine the proximity of critical food resources to nesting colonies (Croxall *et al.* 2002). Related to the present study, Olson and Hearty (2003) conclude that sea-level rise during the Pleistocene era likely led to the extinction of a short-tailed albatross (*Phoebastria albatrus*) colony in the Atlantic Ocean.

Climate change entails a variety of potential effects on marine turtles, all of which exhibit temperature-dependent sex determination in the nest environment, with more females being produced at higher temperatures (Mrosovsky and Provancha 1989, Davenport 1997). Sea turtle phenology may alter in response to climate variability; for example, changes in the timing of nesting in loggerhead turtles have been correlated to increased sea-surface temperature (Weishampel *et al.* 2004). Using methods and scenarios similar to those presented in this paper, Fish *et al.* (2005) predicted up to 32% loss of Caribbean sea turtle nesting habitat with 0.5 m sea-level rise.

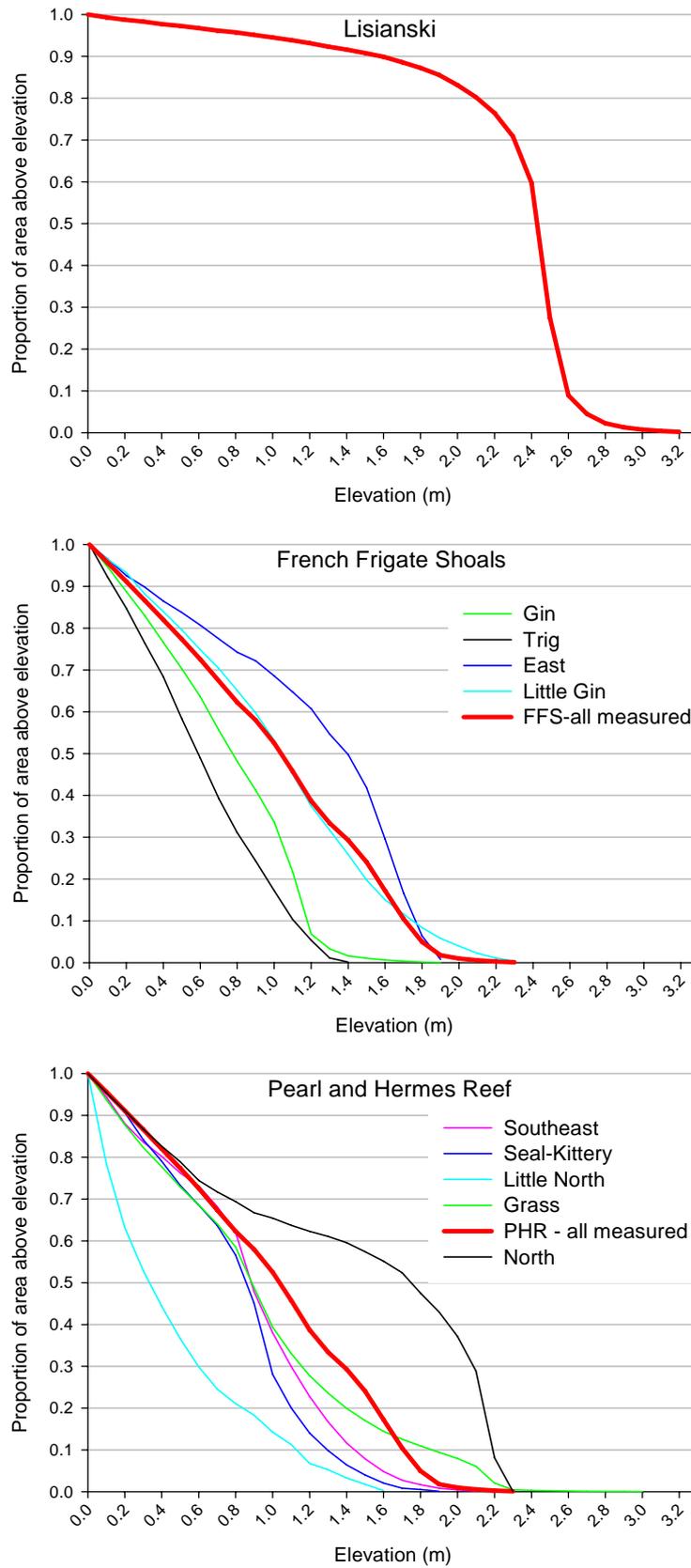


Figure 7.3. Cumulative elevation of selected Northwestern Hawaiian Islands. Curves indicate the proportion of island areas, which are above the elevation (m) indicated on the x-axis.

*Potential effects on some NWHI species*

Here, we evaluate how sea level rise might impact a number of species that are either already known to be vulnerable due to low abundance, or for which the NWHI represents terrestrial habitat that is vital for the species' persistence.

Monk seals, which require islands for resting, moulting, and, most importantly, parturition and nursing, might experience more crowding and competition for suitable landing sites when islands shrink. How this might translate into demographic effects is difficult to judge, as the amount of terrestrial habitat available has not been documented as a density-dependent factor in the demography of this species. However, recent observed changes in both habitat and population trends at FFS may provide some insight.

In 1963, Whaleskate Island at FFS was a 6.8 ha vegetated island (Amerson 1971). It was then the second largest island used by monk seals at FFS and from 1985 to 1996 an average of 35% of the atoll's pups were born there. For unknown reasons, FFS islands have eroded considerably since the early 1960's. In the late 1990's Whaleskate largely disappeared (Antonelis *et al.* 2006). Following this, Trig Island became the most common birth site, and pup survival fell dramatically in large part due to nearshore predation on pups by Galapagos sharks (*Carcharhinus galapagensis*), a species previously not known to take monk seals (Antonelis *et al.* 2006). It has been suggested, though not confirmed, that the crowding of females and pups onto Trig Island has facilitated shark predation. Our scenarios project that Trig Island may shrink an additional 7 to 75% from its currently already reduced size (Table 7.1, Figure 7.2). This reduction in habitat of an endangered and declining species can only be expected to exacerbate an already lamentable situation.

Because the vast majority of Hawaiian green sea turtles nest at FFS, habitat change at this atoll is most likely to influence this recovering population. Most of the

turtles at FFS nest at East Island (Balazs 1976), which may be fortunate since the island is projected to lose a smaller percentage of its area than the others analyzed. When evaluating the influence of sea level on turtle nests it is appropriate to consider the spring tide projections. These occur on full and new moons, and given the Hawaiian green turtle's average 66-day incubation period (Niethammer *et al.* 1997), nests located below spring tide level would be subject to periodic inundation and relatively high failure rates (Whitmore and Dutton 1985). Whaleskate was once a primary nesting site at FFS (Balazs 1976) but the island has since subsided. Trig, Gin and Little Gin stand to lose large portions of their area at spring tide under the median scenario (Table 7.1), indicating that East Island may become even more important for nesting sea turtles. Reductions in nesting habitat coupled with the fact that the population is growing (Balazs and Chaloupka 2004) suggests that nest density could rise considerably at East Island, perhaps to a level where intra-specific nest destruction becomes a density-dependent limitation on population growth (Bustard and Tognetti 1969, Girondot *et al.* 2002).

The largest population of the Laysan finch (*Telespiza cantans*), an endangered Hawaiian honeycreeper, occurs on Laysan Island. While we have not included Laysan Island in our study, it is larger and likely at least as high as Lisianski Island, which we project to lose up to only 5% of its area by 2100. If projections for Laysan prove consistent, the finch's primary habitat is probably fairly safe at least until sea level increases considerably over what has been projected for this century. However, in 1967, the U.S. Fish and Wildlife Service translocated 108 finches to Southeast Island at PHR, in order to establish a second population as a buffer against extinction. Approximately 400 finches have since resided on Southeast Island and smaller populations were established at Grass, Seal-Kittery, and North Islands, also at PHR (Tarr *et al.* 1998, McClung 2005). Since 1998, the populations on Seal-Kittery and North Islands have gone extinct

(McClung 2005). The primary population at Southeast Island has fluctuated greatly, ranging from 30 to over 1900 individuals (Tarr *et al.* 1998, McClung 2005). Considerable habitat for these already small populations would be lost under our median scenario (Figure 7.2, Table 7.1), which could greatly increase extinction risk (McClung 2005). Establishing another population of finches at a location less vulnerable to sea-level rise, such as Lisianski Island, may be warranted.

The other endemic NWHI land birds may see little or no impacts from sea-level rise in the foreseeable future. The Nihoa millerbird (*Acrocephalus familiaris kingi*) and Nihoa finch (*Telespiza ultima*) both reside on the high island of Nihoa. The Laysan duck (*Anas laysanensis*) lives in and around a hyper-saline lake in the interior of Laysan Island, which, as mentioned above, may persist largely intact well into the next century.

Impacts of sea-level rise on seabirds are more difficult to evaluate. The various species inhabiting these islands use diverse terrestrial habitats for nesting, including on or below vegetation, cliffs, burrows and open ground, including beaches. Certainly, some of these habitats will be reduced with sea-level rise. Seabirds nest on the cliffs and summit ridges of the steep volcanic remnants, Necker and Nihoa Islands. Because of their elevation and topography, sea-level rise should have negligible direct effects on seabirds using these islands. Lisianski Island, and most likely Laysan Island, will likely suffer relatively marginal losses, at least by 2100, and these are key nesting sites for species such as Laysan albatross, black-footed albatross, and Bonin petrels (Fefer *et al.* 1984). However, the magnitude of sea-level rise beyond 2100 will determine how much of these islands persist in the long term. Midway Atoll is another very important seabird nesting location; a spatial analysis of its islands' elevations has not yet been conducted.

*Caveats and uncertainties*

Our analysis indicates that sea-level rise may result in significant loss of terrestrial habitat for species in the NWHI. Corals should be able to sustain sufficiently rapid vertical growth in order to keep up with estimated rates of sea-level rise (Mackenzie 2003). To the extent that live coral reefs buffer islets within the lagoons, this might mean the land areas would continue to enjoy whatever current protection they have from ocean swells. However, changes in ocean chemistry associated with increases in dissolved CO<sub>2</sub> could slow coral growth (Mackenzie 2003). Additionally, if coral ‘bleaching’ events, such as that observed in the NWHI in 2002, become more common with rising ocean temperatures, this too could impact reef growth rates (Aeby *et al.* 2003).

Our projected scenarios treat the islands’ current configurations as static, though some, especially the smaller islets, are more likely to be dynamic. Therefore, the projections should be viewed as the currently best available demonstration of the potential effects of sea level rise. Furthermore, the passive flooding scenarios we present here do not take into account ancillary factors that could substantially influence the future of the NWHI. These include erosive recession of the shoreline causing land loss, long-shore drift redistribution of sediments (resulting in both gains and losses of land area), net permanent loss of sand volume offshore, and onshore sand deposition by overwash during high wave activity. A rise in the groundwater table during sea-level rise could also displace seabird burrows. If coral growth does match sea level rise, this could result in increased sand accretion, thereby mitigating losses. Island substrates may also influence vulnerability to erosion (Dickinson 1999). Shoreline response to increased sea level can be estimated using relatively simple (*e.g.*, Bruun’s Rule) or more complicated models (Gornitz *et al.* 2002). However, the lack of available information about ocean current dynamics, sand transport, and shoreline structure in the NWHI renders such methods

inapplicable at the present time. We simply conclude that the impact of factors other than simply passive flooding as a result of increased sea level could lead to greater or lesser loss of habitat than presented here.

*Past sea-level change and future challenges to NWHI biota*

NWHI species have persisted through vastly greater changes in terrestrial habitat than are predicted for the coming century, associated both with the formation of volcanic high islands (and their inexorable subsidence as they drifted to the northwest), and with global changes in sea level, including an approximately 125 m rise following the last glacial maximum (Fleming *et al.* 1998). One imagines that species survived either by virtue of being widespread throughout the islands or by colonizing newer islands before older ones disappeared. More recently, *i.e.* ca. 3500 years ago, sea level in Hawaii had reached a maximum height of 2 m above current levels (Grossman and Fletcher 1998), and this highstand is thought to have ended after approximately 2000 years ago, possibly decreasing as much as 0.5 m below the present sea level in the course of the past millennia. (C. Fletcher, pers. comm.). During this middle to late Holocene sea-level highstand, the land area of the NWHI may have been even smaller than today.

The current situation presents some new challenges for species seeking suitable habitat in the ‘high islands’ of the Hawaiian Archipelago, many of which have been transformed by human colonization and occupied by introduced predators such as mongoose, rats, cats and dogs. Between this occupation of main Hawaiian Islands refugia and sea-level rise in the NWHI, anthropogenic effects will squeeze species from both ends of the archipelago. The challenge for conservation is to either mitigate habitat loss on one end, and/or facilitate persistence on the other.

Our analysis represents a first step towards anticipating the effects of sea-level rise on the NWHI, and much remains to be done in order to more fully understand and

respond to this threat. For instance, we have not obtained elevation data for several important land areas in the NWHI (Laysan Island, Midway Atoll, Kure Atoll and parts of FFS). Also, it would be useful to obtain higher resolution elevation data, especially for the larger islands. This could be accomplished using Light Detection and Ranging (LIDAR) remote sensing technology. Coupling precise island topography with locally-based models of hydrodynamics and sediment transport would greatly improve predictions of sea level rise effects.

One possible mitigation measure to counter the effects of sea level rise in the NWHI may be beach nourishment, whereby sand is strategically deposited onto beaches. This has been proposed as a practical alternative for mainland countries in contrast to most Pacific Island nations where sand may be a scarce resource (Leatherman 1996). However, the islets in the NWHI are quite small relative to the size of beach nourishment projects typically undertaken in areas of human habitation, so that local sand resources might prove sufficient. The engineering and science of beach nourishment has been well-developed and successfully applied in many areas (*e.g.*, Hanson *et al.* 2002). Proper planning requires a great deal of site-specific data input into quantitative models (Capobianco *et al.* 2002). Special considerations are required for restoring beaches to be used by marine turtles for nesting habitat (Crain *et al.* 1995, Rumbold *et al.* 2001). Thus, while any undertaking of this sort in the NWHI would require a great deal of research and careful planning, beach nourishment could be a long-term practical measure for protecting terrestrial habitat in the region.

The potential loss of terrestrial habitat in store for the NWHI highlights the necessity of considering anticipated sea-level rise in resource management planning. These changes are likely to occur on a time scale commensurate with the planning horizon for endangered species recovery plans (Hoekstra *et al.* 2002), though sea level

rise effects typically plays little or no role in such plans. A great deal of effort and funds have been directed toward protection and preservation of the NWHI, but the focus has largely been on direct human impacts (*i.e.* disturbance, hunting, fishing, introduced species). The effectiveness of these measures could be substantially diminished if large portions of these essentially off-limits islands simply slip into the sea. Successful long-term protection of the NWHI requires more rigorous and thorough evaluation of current island elevations, regular monitoring for change, and mitigation planning.

#### ACKNOWLEDGEMENTS

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## Chapter 8. General Discussion

The preceding chapters synthesize over twenty years of Hawaiian monk seal population monitoring data to evaluate abundance estimation methods, elucidate patterns in survival and, with the addition of novel data, reveal some emerging issues related to habitat. In this chapter, I discuss how this work has helped shape future monk seal monitoring protocols, and relate the results to the broader context of population biology. Additionally, these studies have naturally led to further questions about monk seal population biology, ecology and conservation. Therefore, I also discuss plans for future inter-disciplinary research, which will endeavor to link monk seal demography with relevant data in such areas as foraging ecology, oceanography and coastal geology.

Capture-recapture methodology is a very active area of research and new analysis techniques are steadily being developed. Since the publication of Chapter 2 in 2004, several new capture-recapture methods papers have appeared in the literature (Durban and Elston 2005, Durban *et al.* 2005, Lukacs and Burnham 2005, O'Brien *et al.* 2005, Walther and Moore 2005, Whitehead and Wimmer 2005, Yang and Chao 2005, Yip *et al.* 2005, Bonner and Schwarz 2006, Coggins *et al.* 2006, Royle 2006). This is encouraging in that more flexible models are becoming available, especially to deal with capture heterogeneity. Chapter 2 is unusual in that it represents a relatively rare study where capture-recapture abundance estimation methods have been tested using data from a free-ranging population with robust independent estimates of abundance (Chapter 3). Compared to the number of new capture-recapture methods recently published, there are few cases where the performance of various models are evaluated using data from populations with known abundance (Efford *et al.* 2005, Conn *et al.* 2006). The results in Chapter 2 suggest that even methods designed to account for complications such as capture heterogeneity may still yield biased results when applied to real field data.

Chapter 3 represents the only case I know of in which the reliability of extrapolating non-linear functions fitted to discovery curves to estimate abundance has been evaluated using data simulated under varying underlying capture probability scenarios. The conclusion that capture heterogeneity, which tends to be the rule in wild populations, leads to biased results when extrapolating these curves is somewhat disappointing. In contrast, the derivation of a criterion for determining when saturation sampling has occurred may prove a useful model for researchers studying relatively small, localized populations, including nesting marine turtles and cetaceans.

Chapters 2 and 3 together have provided the foundation for a new composite approach for estimating abundance trends in Hawaiian monk seals, supplanting the beach count index. For each subpopulation where examination of discovery curves indicates that complete enumeration was achieved, the total count is used. In other subpopulations, estimates (with standard errors) are generated using Program CAPTURE. These estimates of animals older than pups are then summed along with the total pups counted for a total abundance estimate. This approach was used for the first time in the draft 2006 Stock Assessment Report for Hawaiian monk seals, a document required by the US Marine Mammal Protection Act for determining species' status and potential allowable levels of anthropogenic mortality. This has revealed an average  $3.8\% \text{ yr}^{-1}$  rate of decline in abundance in the NWHI from 1998-2004 (Figure 8.1).

The insights gained through the analyses presented in Chapters 2 and 3 have led to changes in the allocation of monk seal field research effort and data collection protocols. For example, the standard field season has consisted of 4-5 months at two sites (Laysan and Lisianski Islands), less (1.5-2 months) effort at Pearl and Hermes Reef and Kure Atoll, and some intermediate amount of effort at the remaining sites (French Frigate Shoals and Midway Atoll). This arrangement had evolved for a variety of reasons

involving logistics, infrastructure differences at the sites, and specific past conservation issues. However, evaluation of discovery curves clearly showed that in terms of identifying individual seals, Laysan and Lisianski Islands have been greatly over-sampled, while other sites, notably Pearl and Hermes, Kure Atoll and French Frigate Shoals have been under-sampled. Starting in 2007, effort will be distributed more evenly – approximately 3 months per site. It is anticipated that this will achieve better estimates of abundance, age-sex structures and survival at the sites with increased effort, without significantly compromising the data gleaned at the locations where effort will be reduced. Even so, total enumeration will probably not be achieved at French Frigate Shoals and Pearl and Hermes Reef. However, emphasis on increasing the number of full atoll censuses conducted should reduce the uncertainty in capture-recapture estimates at these sites. Finally, by allocating effort in this new way, considerably less labor will be required, thereby saving funds for other research and conservation efforts.

The analyses in Chapter 4 confirm the pattern in age-specific survival of long-lived mammals proposed by Caughley (1966). Most notably, monk seals exhibit senescence, but only after age 17 yr. It is relatively rare to detect senescence in long-lived species, perhaps for the very reason it may only be expressed at such advanced ages, by which time marked known-aged animals are so few that survival rate estimates are imprecise. Other outcomes of Chapter 4 were the detection of time variance in the survival of adult seals, and the tendency for temporal trends among age groups to be correlated. This suggests that all age groups may respond to at least one common underlying factor affecting survival (perhaps prey availability) on similar time scales. Owen Smith *et al.* (2005) and Owen-Smith and Mason (2005) found that adult and juvenile survival in South African ungulates were subject to differing environmental

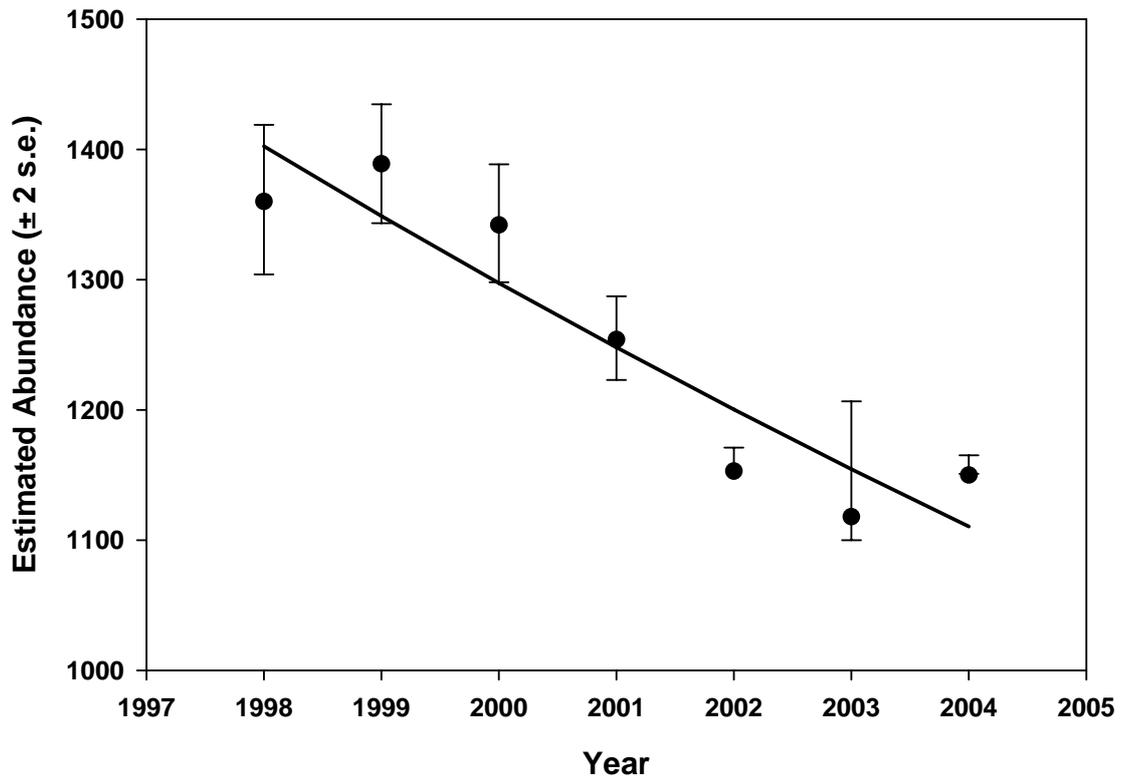


Figure 8.1. Trend in abundance of monk seals at the six main Northwestern Hawaiian Islands subpopulations, based on a combination of total enumeration and capture–recapture estimates. Error bars indicate  $\pm 2$  s.e. (from variances of capture–recapture estimates). Fitted log-linear regression line is shown. Figure reprinted from the draft 2006 Hawaiian monk seal Stock Assessment Report.

factors, and declining adult survival was the primary cause of declines in abundance of some populations.

Regarding monk seal conservation, key findings of Chapter 4 are that survival is not sex-biased (with the unexplained exception of French Frigate Shoals), senescence occurs, survival trends suggest regional structuring of the NWHI environment, adult survival varies significantly over time and survival of juveniles, sub-adults and adults tend to be positively correlated. The implications of these findings may be best explored through the monk seal stochastic simulation model (Harting 2002). To date, model runs have assumed equal survival among the sexes. Projections using the higher female rates observed at French Frigate Shoals, a population that has been in decline since the late 1980s, should indicate at least a somewhat less dire prognosis for this subpopulation. Moreover, the implications of regional structuring and correlation of survival over time among ages can be explored by comparing model outcomes where survival rates are drawn from independent distributions from each of the six subpopulations to outcomes where survival rates are drawn from the smaller number of distinct age and subpopulation groups depicted in Figure 4.5. This can be taken a step further by forcing those rates to be positively correlated to the degree observed (Table 4.3).

The observed relationship between oceanic productivity and monk seal survival (Chapter 5) represents the first apparent link between an environmental signal and highly variable juvenile survival rates. This relationship will be monitored into the future to determine whether it holds up in the longer-term. It also suggests a number of other research projects that should be pursued in the near future. First, we have hypothesized that variable primary productivity mediated by the dynamics of the Transition Zone Chlorophyll Front (TZCF) results in variable prey availability for juvenile monk seals, however we have no measure of prey availability. Through the use of seal mounted video

recorders, Parrish *et al.* (2005) identified the types of habitat and, to some degree, prey used by juveniles seals, while Stewart *et al.* (2006) documented submerged features used by young seals. New research is planned in 2007 to sample prey at selected known foraging sites and develop trend indices for monk seal prey abundance. If these data can be collected for a number of years with contrasting oceanographic conditions, it should provide considerable insight into the mechanisms linking seal survival to environmental variability.

Detecting this environmental driver of monk seal survival at the western end of the NWHI clearly represents progress, but it also begs the question - what drives the highly variable rates observed at other locations? Fairly dramatic fluctuations in juvenile survival have occurred at Laysan Island and low survival of juveniles has been chronic at French Frigate Shoals (Figure 4.4). At these sites, the position of the TZCF was only weakly correlated, if at all, with survival (Figure 5.5). Perhaps some yet undetected oceanographic features impinge upon the productivity of these areas, and future research will explore such relationships using remotely sensed oceanographic data linked with ongoing monk seal demographic monitoring. The geographic scale at which we observe relative synchrony in monk seal survival rates (Figure 4.5), suggests the likely scale at which these putative oceanographic processes may operate.

The number of monk seals that were observed in the main Hawaiian Islands (MHI) during the 2000-2001 aerial surveys garnered a great deal of attention from the monk seal research, conservation and management community. While there had been a general impression that more seals were about than had been in previous memory, a minimum count of 52 individuals in the MHI was the first tangible measure. That, coupled with the knowledge that 52 was likely far below the true population size and that negative interactions of seals with people, dogs, and fishing gear in the MHI was

becoming more common, led to changes in research and management emphasis and prioritization. This is apparent from a variety of indicators. In 2002, the US Marine Mammal Commission<sup>18</sup> held a stakeholders' workshop on the island of Kauai to discuss issues surrounding the apparently growing number of seals on MHI beaches and waters. The 1981 Hawaiian Monk Seal Recovery Plan<sup>19</sup>, mentioned only that seals are infrequently seen in MHI waters, and no recovery actions were recommended in the MHI (Gilmartin 1981). This was not an oversight, rather an indication of how rarely seals were seen in the MHI at that time. In 2006, the Recovery Plan is being revised and the document will devote a good deal of attention to the challenges and potential for recovery in the MHI. It will contain recommendations to conduct research, mitigate threats and conduct extensive public education to foster coexistence with seals.

From the research perspective, some significant initial steps have been taken since the aerial surveys to better understand the MHI seal population. Non-systematic sighting records provided by the public and partner institutions are being computerized and will be incorporated into a Geographic Information System (GIS). This will be a useful tool for managers to readily determine whether seals have been documented using a given area when assessing potential impacts, for example, of coastal development projects proposed in the MHI. Further, increased effort has been made to tag seals and a photographic identification database is being compiled to distinguish untagged animals. This effort will soon provide an improved minimum population estimate and allow for assessment of inter-island movement and survival estimates. In 2003, epidemiological sampling and

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<sup>18</sup> The Marine Mammal Commission is a US federal government agency created by the US Marine Mammal Protection Act and charged with oversight of marine mammal conservation policies and programs being carried out by federal regulatory agencies ([www.mmc.gov](http://www.mmc.gov)).

<sup>19</sup> Recovery Plans are mandated for species listed under the US Endangered Species Act.

satellite tracking projects were begun in order to identify at sea habitat use, foraging patterns, and disease exposure.

The above steps are an auspicious beginning to what should develop as a comprehensive MHI monk seal research program on a par with that currently in place in the NWHI. The MHI represent the only habitat where seals numbers appear to be increasing. That, coupled with the fact that their numbers are still low and, judging by the condition of weaned pups, food limitation is not in evidence, suggests that the MHI could become a key element in the long-term persistence of the species.

How many seals the MHI might potentially hold is a critical issue for long-term conservation planning and priorities. It should be possible to determine some plausible and informative boundary values on potential abundance in the MHI. Future research will focus on this question by comparing the relative amounts of available marine and terrestrial habitats in the NWHI and MHI (*cf.*, Lairdre *et al.* 2001, 2002). Available terrestrial habitat can readily be assessed by analysis of existing coastline maps. Much has already been done to document the geographic range and types of habitats monk seals use in the NWHI (Parrish *et al.* 2000, 2002, 2005, Stewart *et al.* 2006), and, as mentioned above, similar studies have begun in the MHI. Moreover, considerable detailed benthic habitat data are available throughout the Hawaiian archipelago and an ambitious program to expand this database is underway (Hawaii Mapping Research Group, [www.soest.hawaii.edu/hmrg](http://www.soest.hawaii.edu/hmrg)). By documenting available habitat of the type (depth, substrate type) used by foraging seals (and similarly, the amount of available terrestrial resting habitat) in the NWHI and MHI, respectively, one can estimate the relative amounts of habitat in the two regions. This value can then be used to scale current and past estimates of seal abundance in the NWHI to estimate lower and upper bounds for potential MHI carrying capacity.

Just as the research in Chapter 6 generated interest in the potential opportunity for monk seal expansion in the MHI, Chapter 7 will hopefully focus more attention on a potentially serious threat to the existing core monk seal habitat in the NWHI. The analysis of potential impacts of sea level rise on monk seal (and other species') terrestrial habitat should raise some alarm, but it is only a first, incomplete step. High priority next steps include generating high resolution maps of all the low-lying NWHI, gathering data on sub-atoll scale hydrodynamics and substrate characterization so that improved projections of sea level rise impacts can be generated and well-informed restoration and mitigation of losses (*e.g.*, through beach nourishment) can be devised. This calls for a multi-disciplinary approach involving oceanographers, coastal geologists and engineers, as well as biologists. Additionally, the initial efforts to document habitat losses to date (Antonelis *et al.* 2006) should be expanded to include analysis of all available information on NWHI island area. This could involve analysis of historical records and photographs.

The analyses presented in the foregoing chapters have provided insights into Hawaiian monk seal assessment methods, population biology and ecology. Some of the findings should be relevant for other long-lived mammals as well. Hopefully, the primary value of this research will prove to be a strengthening of the scientific foundation upon which conservation strategies for the imperiled monk seal will be built. There is little doubt that additional enlightening research on the species (some of it previewed in this chapter) will be conducted in the future. What is less certain is that conservation measures will be as successful. Since Hawaiian monk seal monitoring began in the late 1950's, overall abundance trends have either been in decline or, at best, held steady. Currently, the numbers are falling once again, and have reached the lowest levels ever recorded. Our great challenge is to find ways to halt this trend and reverse it. The winning measures that will achieve this result, however, are by no means clear, despite all our knowledge of the

species. Meanwhile, the monk seal's status is sufficiently dire that inaction is not a viable approach. Therefore, it is critical not only that ambitious conservation measures are undertaken on behalf of the monk seal, but that these are crafted in a rigorous experimental fashion, so that their efficacy can be scientifically evaluated.



Figure 8.2 Hawaiian monk seal weaners at Pearl and Hermes Reef. Photo: Chad Yoshinaga.

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