

FORAGING ECOLOGY, POPULATION GENETICS AND RISK OF FISHERIES  
BYCATCH FOR THE LAYSAN ALBATROSS (*PHOEBASTRIA IMMUTABILIS*)

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

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY  
(ECOLOGY, EVOLUTION AND CONSERVATION BIOLOGY)

AUGUST 2009

By  
Lindsay C. Young

Dissertation Committee:

Sheila Conant, Chairperson  
Clifford Morden  
David B. Carlon  
Brian W. Bowen  
David C. Duffy

We certify that we have read this dissertation and that, in our opinion, it is satisfactory in scope and quality as a dissertation for the degree of Doctor of Philosophy in Zoology (Ecology, Evolution and Conservation Biology).

DISSERTATION COMMITTEE

---

Chairperson

---

---

---

---

---

Copyright 2009 Lindsay C. Young

All Rights Reserved

## DEDICATION

This dissertation is dedicated to my family- Howie, Patti, Courtney and Riley Young for their support of both my personal and professional endeavors. No matter which direction I set off in, they were always there to provide support in whatever way, shape or form.

And to my husband Eric who married me knowing this would end up being just as much his Ph.D. as mine and who has not only made me a better scientist, but a better person.

Thank you for all of your love.

## ACKNOWLEDGEMENTS

I am greatly indebted to many people that have not only made my Ph.D. into a project much more worthwhile than I had done this without their help, but who have made my time at the University of Hawaii truly some of the best years of my life. I would like to thank my advisor, Sheila Conant who decided after talking to me for an hour, primarily about dogs, that I should be admitted into the program and that was that. Never mind the fact that I had failed organic chemistry and had spent the last several years doing cancer research and not ornithology! I am extremely grateful that she took a chance on me and gave me the opportunity to completely switch fields and fall in love with biology all over again. She has provided endless support, both professionally and personally, and I am honoured to call her my friend and colleague.

I also would like to thank my committee members: David Duffy, David Carlon, Brian Bowen, and Cliff Morden who have truly been a pleasure to work with and have helped me to grow as a scientist. David Duffy convinced me that I should work on seabirds in the first place and help to cement my love for attaching small devices to birds to figure out where they go and I am grateful for the discussions that really jump-started my entire research project. All sequencing, genotyping and analysis were conducted in Dave Carlon's Laboratory at the University of Hawaii and I sincerely thank Dr. Carlon for the generous use of his lab.

This dissertation was a large project that involved numerous people all working together in the name of albatross conservation. I would like to thank the Hawaii Division of Forestry and Wildlife and the Natural Area Reserves System for permission to conduct the majority of the work at Ka'ena Point and for their ongoing management efforts to

provide a safe place for seabirds to nest on Oahu. I thank Betsy Gagne, Dave Smith and John Polhemus in particular for their enthusiasm, moral and logistical support of this project.

There has been a small army of volunteers that have accompanied me in the field to band birds over the years and I would like to thank Eric VanderWerf, Norine Yeung, Andrew McClung, Dawn Reding, Ken and Pam Hayes, Heather and Jaap Eijzenga, Sheldon Plentovich, Michael Boyle, Michelle Hester, David Hyrenbach, Chris and Naomi Swenson, and Alison Stimpert for accompanying me numerous time in the field as well as many others who came out to help me handle birds. I thank Beth Flint, Maura Naughton and Mark Romano for their lively discussions of albatross biology and for providing comparisons between the Northwestern and main Hawaiian Island colonies, and Diane Drigot and Marc Ono for sharing observations of Laysan albatross on the Marine Corp Base and Dillingham Airfield on Oahu. I would also like to thank Brenda Zaun in particular for sharing endless observations of Laysan albatross on Kauai and for assisting me in the field, on Kauai, Lehua and Oahu.

For deployment of the geolocators on Kure Atoll, I am forever grateful to Cynthia Vanderlip and Karin Flynn who trusted my judgment and worked with me to remotely deploy (and then retrieve!) the tags when I was unable to make it to Kure Atoll. For analysis of the tracking data, and I extremely grateful for the time and effort Scott Shaffer took to help teach me how to use Matlab on short notice and who was instrumental in helping me to graduate on time. I am grateful for the assistance of Karen Fischer, Peter Williams, Tom Kong and Shannon Fitzgerald who were all very helpful in assisting me

in compiling fishing effort data and to Michelle Hester and Bill Henry who helped to standardize the collection of bolus data.

For assistance with the genetics component of this project I am indebted to Ken Hayes who not only convinced me that this would be a worthwhile addition to my dissertation, but who helped me through every step of the way from sample collection all the way through to data analysis. Catherine Lippe and Norine Yeung provided invaluable help in the lab and taught me how to do many of the techniques required to complete the work, and were patient during many troubleshooting sessions. I would not have been able to complete this component of the project without the three of you. For genetic samples I thank: Tomohiro Deguchi, Cynthia Vanderlip, Rachel Seabury-Sprague, Stefan Kropidowski, Angela Anders, Jason Baker, Jessica Lopez, Beth Flint, Brenda Zaun, Bill Henry, Scott Shaffer, Jeremy Bisson and Sharon Burke at the Burke Museum.

This research was funded by the Hawaii Conservation Alliance, the University of Hawaii Department of Zoology Jessie Kay Fellowship, and several Ecology, Evolution and Conservation Biology research awards as part of NSF grant DGE02-32016 to K.Y. Kaneshiro, the British Antarctic Survey, and the Hawaii Audubon society. The UH graduate student organization, the Pacific Seabird Group and the American Ornithologists Union were generous in providing funding so that I could attend professional meetings throughout my degree program. I thank the Hawaii Division of Land and Natural Resources, the U.S. Fish and Wildlife Service, the National Oceanic and Atmospheric Administration, the United States Geological Survey and the government of Japan for permission to collect samples and for access permits.

Finally, I would truly like to thank my friends and family who have made this such a great experience. The ‘SPAM’ lab at UH (both current and former) were a constant source of support, and amusement: Norine Yueng, Sheldon Plentovich, Andrew McClung, Laurie Strommer, Elaine Franklin, and ‘honorary spamlings’ Pat Aldrich, Erin Baumgartner, Marty Meyer, Kevin Hall and Ken Hayes. My long distance friends, Christina (McGuire) Ryder, Cylena Stern and Eline Lorenzen all ensured that I remained sane through all of this and I look forward to visiting all of you more often. Mahalo.



## ABSTRACT

The geographic and genetic dispersal patterns of marine predators that are not physically limited by dispersal have rarely been studied. Indeed, Laysan albatross (*Phoebastria immutabilis*) are highly vagile seabirds, foraging throughout the North Pacific Ocean but breeding on a limited number of oceanic islands. Despite mark-recapture data indicating natal philopatry, Laysan albatross re-colonized several anthropogenically extirpated breeding locations in the 1970's. During the same interval, a breeding site in the Northwestern Hawaiian Islands was lost to erosion indicating that the colonization events could have been due to displacement rather than dispersal. This study determined the status and genetic origin of new breeding populations of Laysan albatross, examined whether birds from Kure Atoll and Oahu ingest different plastic loads based on their at-sea foraging ranges through geolocation tracking, and determined the fisheries bycatch risk for each population. As of 2008, the Laysan albatross population on Oahu of 365 adults (47% active breeders) was increasing by 27% annually. Hatching (62%), fledging (78%) and overall reproductive success (48%) were comparable to other colonies. High rates of dispersal were documented between Oahu and Kauai. Supporting this observation, genetic analyses of newly-colonized sites showed colonizers from multiple source populations indicative of species wide dispersal, not displacement from disappearing habitat. Microsatellites found weak population structure, and mitochondrial control region sequences revealed moderate population structure. Tracking results revealed that foraging ranges of birds from Oahu and Kure did not overlap in the breeding season, but did overlap in the non-breeding season when they were not constrained to the nest. This difference in breeding season foraging led to chicks from

Kure Atoll being fed ten times the amount of plastic as chicks from Oahu. Overlaying fishing effort on tracking results indicated that Laysan albatross are at greatest risk for being caught as bycatch during the breeding season in international pelagic long-lining fisheries as opposed to U.S. based fleets. These results indicate that a predator that is not dispersal limited will still practice central place foraging while breeding to conserve energy and that natal philopatry in the absence of geographic barriers can still influence genetic population structure.

## TABLE OF CONTENTS

Dedication.....	iv
Acknowledgements.....	v
Abstract.....	ix
List of Tables.....	xii
List of Figures.....	xiii
Chapter 1: Introduction.....	1
The Laysan albatross as a Model Study Species.....	1
Population Biology in the Absence of Physical Barriers.....	2
Purpose and Content of Chapters.....	8
Chapter 2: Demography and Natural History of Laysan albatross on Oahu, Hawaii.....	11
Introduction.....	13
Methods.....	15
Results.....	18
Discussion.....	20
Chapter 3: Bringing Home the Trash: do Differences in Foraging Lead to Differences in Plastic Ingestion in Laysan albatross?.....	29
Introduction.....	32
Methods.....	34
Results.....	38
Discussion.....	41
Chapter 4: Colonization History and Population Genetics of Laysan albatross.....	53
Introduction.....	55

Methods.....	57
Results.....	62
Discussion.....	65
Chapter 5: Do differences in Foraging Lead to Differences in Risk of Fisheries Bycatch in Laysan albatross?.....	79
Introduction.....	81
Methods.....	83
Results.....	87
Discussion.....	90
Chapter 6: Summary.....	98
Foraging ecology of Laysan albatross.....	98
Population genetics of Laysan albatross.....	100
Significance of the Research and Conservation Implications.....	100
Future Research Opportunities.....	102
Appendix 1: Laysan albatross Haplotype Distribution List.....	105
Literature Cited.....	109

LIST OF TABLES

<u>Table</u>	<u>Page</u>
3.1. Overlap of the core utilization ranges of Oahu and Kure Laysan albatross with each other and marine debris broken down by breeding cycle.....	42
4.1. Characteristics of five microsatellite loci .....	72
4.2. Sequence and genotypic data summary by population.....	72
4.3. Pairwise $F_{ST}$ and $\Phi_{ST}$ values for microsatellites and mtDNA.....	73
4.4. Migration estimates from source populations.....	74
4.5. Mixed stock analysis summary.....	75
4.6. Regression of source population size and distance vs. proportional contribution to each new colony.....	75
5.1. Burke Museum accession number for bycatch samples obtained.....	95
5.2. Proportional contribution of source populations bycatch samples.....	95

## LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
2.1. Map of Laysan albatross breeding locations on Oahu.....	26
2.2. Graph of reproductive attempts of Laysan albatross on Oahu from 1992-2008....	27
2.3. Graph of reproductive success of Laysan albatross on Oahu from 2004-2008.....	28
3.1. Map of current systems and distribution of marine debris in the North Pacific...	45
3.2. Photograph of plastic ingestion by a dead Laysan albatross chick.....	46
3.3. Photograph of geolocator attachment methods.....	47
3.4. Box plots of mean oceanographic parameters for Kure vs. Oahu tracked Laysan albatross by breeding cycle.....	48
3.5. Map of utilization distribution kernels for Laysan albatross tracked on Oahu according to breeding cycle.....	49
3.6. Map of utilization distribution kernels for Laysan albatross tracked on Kure Atoll according to breeding cycle.....	50
3.7. Map of the overlap of utilization distribution kernels for Laysan albatross tracked on Oahu and Kure Atoll according to breeding cycle.....	51
3.8. Box plots of bolus content analysis for Laysan albatross from Oahu and Kure Atoll.....	52
4.1. Distribution map and genetic sample sizes obtained of genetic samples.....	76
4.2. Laysan albatross haplotype network.....	77
4.3. Graph of observed vs expected mismatch distribution for Laysan albatross.....	78
5.1. Map of Laysan albatross tracked on Oahu and overlap with fishing effort.....	96
5.2. Map of Laysan albatross tracked on Kure and overlap with fishing effort.....	96

## CHAPTER 1

### INTRODUCTION

#### THE LAYSAN ALBATROSS AS A MODEL STUDY SPECIES

Albatross (Diomedidae) are a family of seabirds belonging to the order Procellariiformes, which includes petrels, shearwaters, and other tube-nosed seabirds (Tickell 2000). Three sympatric species are found in the North Pacific: Laysan albatross (*Phoebastria immutabilis*), Black-footed albatross (*P. nigripes*) and Short-tailed albatross (*P. albatrus*; Tickell 2000). Of these, Laysan albatross are the most abundant and are the focus of this study.

Laysan albatross are long-lived, socially monogamous seabirds characterized by a delayed onset of reproduction and high juvenile and adult survival. They are annual breeders that raise one chick per year, and will not re-nest if the initial nest fails. Laysan albatross breed on remote islands in the subtropical North Pacific Ocean (Whittow 1993, Tickell 2000) with the vast majority of individuals (97%) nesting in the Northwest Hawaiian Islands (NWHI), and several small colonies in the Main Hawaiian Islands, Japan, and off of Baja Mexico (Tickell 2000).

Despite breeding on a limited number of oceanic islands, Laysan albatross have broad pelagic distributions spanning tropical, subtropical, and subarctic latitudes (8° to 59°N) in both the breeding and non-breeding seasons (Whittow 1993, Hyrenbach et al. 2002). Longitudinally they range from the west coast of North America (120° W) to Japan (140° E; Shuntov 1974, Whittow 1993, Hyrenbach et al. 2002). The oceanic environment is primarily heterogeneous, with productivity gradients existing at macro

scales (1000-3000 km), but patchy variation at meso-scales (1-100 km; Hyrenbach et al. 2002). Laysan albatross feed on a variety of fish, fish eggs, cephalopods, crustaceans and other invertebrates that are associated with upwelling and high primary productivity (Harrison 1990, Ballance et al. 1997, Blight and Burger 1997, Cherel and Klages 1998, Gould et al. 1998, Fernandez and Anderson 2000, Tickell 2000, Spear et al. 2001)

Little empirical data has been gathered on the pelagic distribution and foraging patterns of the Laysan albatross or the extent of interactions and dispersal patterns between birds from different breeding colonies (Weimerskirch and Wilson 2000, Gould and Hobbs 1993). As a result, a unique opportunity exists to document the physical and genetic dispersal patterns of a marine predator that is not limited by dispersal and to determine how this information can be used to formulate science-based conservation priorities.

## POPULATION BIOLOGY IN THE ABSENCE OF PHYSICAL BARRIERS

When searching for prey, an organism is expected to maximize energetic gain, while minimizing energy expenditure. To accomplish this, organisms should increase the probability of detecting food patches by altering their movement path relative to the availability of prey (Schoener 1979, Stephens and Krebs 1986). Unlike terrestrial environments, where physical barriers and geography often put constraints on movement, most oceanic environments are essentially unobstructed from the perspective of an albatross. As a result, the movements of marine organisms that are not dispersal limited can directly reflect their assessment of resource variation.



In the case of pelagic seabirds that nest on remote oceanic islands (Schreiber and Burger 2001), one would predict that breeding populations on distant islands should maximize energetic gain by exploiting resources closest to their breeding colony when they are nesting. This central-place foraging during the breeding season could potentially lead to local diet differences between colonies. When pelagic birds are not breeding, and therefore not constrained to the nest, the foraging patterns of birds from different colonies separated by thousands of kilometers could overlap and instead reflect the actual resource variation throughout their range (Weimerskirch et al. 1993, Shaffer et al. 2003, Pinaud and Weimerskirch 2007). Despite opportunities to test this hypothesis, few studies have addressed whether dispersive marine organisms that are not dispersal limited attempt maximize energetic gain, while minimizing energy expenditure (e.g. Weimerskirch et al. 1993, Shaffer et al. 2003, Pinaud and Weimerskirch 2007).

The at-sea foraging patterns of the highly mobile Laysan albatross have been well documented (Whittow 1993, Fernandez et al. 2001, Hyrenbach et al. 2002, Shaffer et al. 2005). There are marked changes throughout their annual reproductive cycle. During incubation and chick guard stages they practice ‘central-place foraging’, but later, when they are not constrained to the nest, they forage throughout the North Pacific (Orians and Pearson 1979, Whittow 1993, Fernandez et al. 2001, Hyrenbach et al. 2002, Shaffer et al. 2005). However, it is unknown whether all breeding colonies exploit the same resources, or habitats, year round, that are well within their dispersal potential, or if colonies utilize locally available resources since previous studies have focused on a single breeding colony. The variable diet and flexible foraging strategy of this species (utilizing both scavenging and live capture; Harrison 1990, Whittow 1993) indicate that it is somewhat

of a generalist. As a result, birds in distant colonies should exploit resources closest to the colony during the breeding period, even though they are capable of travelling to virtually any foraging ground in the North Pacific.

Unlike terrestrial environments, where physical barriers and geography can put constraints on movement, most oceanic environment are unobstructed and open from the perspective of an albatross. As a result, the movements of foraging albatross can potentially reflect their assessment of spatial variation of important resources, and optimal foraging theory may be a useful predictor of inter-annual and colony differences in foraging habits of *P.immutabilis*.

Satellite telemetry data in conjunction with satellite-derived SST and chlorophyll concentrations indicate that albatross dispersion during the breeding season is influenced by large-scale, predictable water mass distributions, while foraging activity is associated with meso-scale factors such as frontal boundaries and bathymetric features (Hyrenbach et al. 2002). No single study has yet incorporated year-round dispersion and foraging activities with sample sizes larger than twenty animals (Fernandez et al. 2001, Hyrenbach and Dotson 2001, Hyrenbach et al. 2002). As a result, information gaps exist in our knowledge of the species, due in part to the relatively short field life and high cost of satellite tracking devices leading to small sample sizes.

In most taxa, dispersal capability and geographic isolation are often used to form *a priori* hypotheses concerning genetic diversity and variation between and within populations (Bohonak 1999). However, seabirds are not typically limited by dispersal, as demonstrated through numerous studies on their wing morphology, mark-recapture data, and satellite telemetry ( Fisher 1976, Austin et al. 1994, Bried and Jouventin 2002,

Schjorring 2001, 2002). For example, satellite telemetry and geolocation studies in other albatross species have documented lengthy (even circumpolar) foraging trips, but very little gene flow between populations (Jouventin and Weimerskirch 1990, Weimerskirch et al. 1993, Weimerskirch et al. 1994a, Abbott and Double 2003a & b, Burg and Croxall 2004, Walsh and Edwards 2005).

Despite their high dispersal potential, studies of banded populations of albatrosses have shown them to be extremely philopatric and often they return not only to their natal island, but to within 30m of their natal nest (Fisher 1976, Weimerskirch et al. 1985, Prince et al. 1994, Sagar et al. 1998, Tickell 2000). This has led to predictions of restricted gene flow which has been confirmed for several species (Abbott and Double 2003 a & b, Burg and Croxall 2004, Alderman et al. 2005, Walsh and Edwards 2005). Causes of genetic structure in a population can be influenced by a number of factors: geological processes that act as isolating mechanisms, selection or drift, limited dispersal and high natal philopatry. Despite these processes, if a certain number of 'effective migrants' disperse, genetic structure may be obscured by migration since gene flow is defined as the number of migrants per generation (Abbott and Double 2003 a & b). In the classic model of population genetics, and ultimately allopatric speciation, defined structure will be observed in geographically isolated populations unless organisms are capable of overcoming the dispersal barrier. In the case of albatrosses, which are not limited by dispersal, other mechanisms exist that can theoretically reduce the homogenizing effects gene flow. Natal philopatry is typically used to predict whether or not genetic structure will exist between seabird populations (Bohonak 1999). As stated earlier, Laysan albatross have extremely high natal philopatry and not only return to their

birth island, but typically to within 30m of their natal nest, despite their high dispersal potential. Examining the population structure of an animal not limited by dispersal or geography can potential directly reflect the level of natal philopatry required to produce population structure.

Studying how the dispersal and behavior patterns of a long-lived marine predator interact with longline fisheries may provide insights into how to better mitigate fisheries bycatch. The longline fisheries in the North Pacific have had a negative impact on numerous marine organisms (Brothers 1991, Dalziell and De Poorter 1993, Cherel et al. 1995, Brothers et al. 1999, Cousins et al. 2000, Belda and Sanchez 2001, Gilman 2002, Butchart et al. 2004). In the case of albatrosses, studies estimate that up to 1% of all albatrosses worldwide are killed annually in longline fisheries (Brothers et al. 1999), and longline fishing is now considered to be the single greatest threat to albatross species worldwide (Furness 2003, IUCN 2007).

Albatross are attracted to fishing vessels because they provide an obvious, easy source of food. In longline fisheries, mortality occurs when seabirds get caught while trying to take bait off hooks being set. Once hooked, the birds are dragged underwater where they drown (Gilman 2002). Longline vessels in particular have high incidental takes of albatross due to the choice of bait (clupeid fish species often eaten naturally as prey), the setting mechanism which allows the birds to take the bait off the surface of the water before it sinks (Anderson and McArdle 2002, Gilman et al. 2003) and the fishing locations which often corresponds to productive foraging areas.

Albatross populations are particularly vulnerable to the impacts of longline mortality due to the birds late reproductive maturity (5-9 years), high adult survivorship,

great longevity (over 50 years), and low reproductive output (one chick every one to two years) (Gilman 2002). Thus, once the sexually mature animals are removed from a population, it can take decades for the breeding stock to provide replacements.

Based on bycatch estimates it is highly likely that there is a significant amount of interaction occurring between Laysan albatross and fishing vessels. Preliminary data from stable isotope analysis of Laysan albatross diets indicates that birds killed as bycatch are feeding at a different trophic position than birds that die of natural causes in breeding colonies (Bisson 2007). This suggests that albatross mortality caused by longlining is not a result of a single encounter, but a result of a foraging strategy of scavenging from fishing vessels.

Many seabirds practice central place foraging, which is particularly pronounced during their breeding season. As a result, if fishing effort is not uniformly distributed (i.e. is greater closer to one breeding colony vs another), there is a greater probability of one colony experiencing higher bycatch rates relative to neighboring colonies. Areas where commercially valuable fish species congregate exhibit both spatial and temporal heterogeneity (Cherel et al. 2000, Spear et al. 2003), as a result fishing effort changes depending on the vessels' country of origin, the time of year, and the availability of fish (Tuck et al. 2001, Kiyota 2002, Tuck et al. 2003, Moreno et al. 2006). Similarly, the foraging ranges and resources exploited by albatross change according to prey availability and foraging intervals while provisioning for chicks. Since both the locations of fishing effort and the foraging areas of albatross in different breeding colonies vary over time, it is likely that different populations experience differing levels of mortality.

Pinpointing when and where populations are most at risk of being caught as bycatch will allow identification of which fisheries could benefit from increased mitigation measures

## PURPOSE AND CONTENT OF CHAPTERS

This dissertation examines the ecological and genetic dispersal patterns of Laysan albatross, and how this information can be used to form population-based conservation priorities to reduce fisheries bycatch. Chapter 2 documents the chronology, locations and sizes of Laysan albatross colonies on the island of Oahu and presents new, as well as revised, life history information on the species. Previous studies on Laysan albatross natural history have used plot designs in larger colonies, and as a result birds that have left the study plot are not accounted for which has resulted in biases in the estimation of several demographic parameters. Chapter 2 calculates several demographic parameters, such as reproductive rates, mate switching and age-specific dispersal for this population in a species wide context. The goal of this chapter is to update the known natural history of the species to provide baseline data that can be used in future comparisons with other studies and other species, and to update the known breeding locations for this species.

Chapter 3 continues the investigation of physical dispersal by comparing the at-sea foraging patterns of Laysan albatross from Oahu and Kure Atoll through the use of geolocation data loggers. The goal of this chapter is to test whether Laysan albatross exhibit some of the characteristics of optimal foraging theory by practicing central place foraging during their breeding season, and if this translates into differences in plastic ingestion. Few studies have tested whether animals that are not limited by dispersal or geographic barriers alter their foraging patterns to minimize energetic expenditures and

how this translates into differences in their diet. The issue of plastic ingestion in Laysan albatross is significant, and this is the first study to combine diet and tracking data in an attempt to pinpoint where this species is at greatest risk for ingesting marine debris.

Chapter 4 addresses the question of genetic dispersal and the role of natal philopatry in producing genetic structure of Laysan albatross populations in the Northwestern Hawaiian Islands, and by determining the genetic origin(s) of new colonization events across the Pacific. This is the first study to present the complete population genetic results for this species and is one of the few studies to utilize a mixed stock analysis to infer colonization patterns. The results from this chapter are discussed in a conservation framework to prioritize colony conservation measures based on genetic diversity.

Chapter 5 utilizes the at-sea tracking and genetic data and correlates them with fishing effort to determine the bycatch risk for each population and to pinpoint specific times, locations or fisheries which could benefit from increased mitigation measures. Bycatch is one of, if not the greatest, source of mortality for many seabird species, so by determining when and where birds are most likely to be caught, we can attempt to mitigate the effects of commercial fishing. This is one of the first studies to incorporate both genetic and spatial data in an attempt to provide a more complete picture of the bycatch risk for Laysan albatross.

Finally, Chapter 6 summarizes the major findings of this study, makes some overall conclusions and provides future research suggestions based on outstanding questions. Perhaps more importantly though, Chapter 6 also discusses the conservation value of this work and how resource managers charged with the protection of albatross,

as well as other seabirds species, can use this information to make scientifically informed decisions. Despite being an already intensively studied animal, the Laysan albatross provides a wealth of opportunities to study ecological, behavioral, evolutionary and conservation topics that have relevance across taxa.



## CHAPTER 2

### DEMOGRAPHY AND NATURAL HISTORY OF LAYSAN ALBATROSS ON OAHU, HAWAII

As accepted by the Wilson Journal of Ornithology, April 14<sup>th</sup>, 2009:

LINDSAY C. YOUNG,<sup>1,2,7</sup> ERIC A. VANDERWERF,<sup>2</sup> DAVID G. SMITH,<sup>3</sup> JOHN  
POLHEMUS,<sup>3,6</sup> NAOMI SWENSON,<sup>4</sup> CHRIS SWENSON,<sup>4</sup> BRENT R.  
LIESEMEYER,<sup>5</sup> BETSY H. GAGNE,<sup>5</sup> AND SHEILA CONANT<sup>1</sup>

<sup>1</sup> Ecology, Evolution and Conservation Biology Program, Department of Zoology,  
University of Hawaii, Honolulu, HI 96822, USA.

<sup>2</sup> Pacific Rim Conservation, 3038 Oahu Avenue, Honolulu, HI 96822, USA.

<sup>3</sup> Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife,  
2135 Makiki Heights Drive, Honolulu, HI 96822, USA.

<sup>4</sup> U.S. Fish and Wildlife Service, Pacific Islands Coastal Program, 300 Ala Moana  
Boulevard, Room 3-122, Honolulu, HI 96850, USA.

<sup>5</sup> Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife,  
Natural Area Reserves System, 1151 Punchbowl Street, Honolulu, HI 96813, USA.

<sup>6</sup> Current address: JT Productions, P. O. Box 437476, Kamuela, HI 96743, USA.

<sup>7</sup> Corresponding author; e-mail: [lindsayc@hawaii.edu](mailto:lindsayc@hawaii.edu)

## ABSTRACT

Laysan albatross (*Phoebastria immutabilis*) began re-colonizing sites across the Pacific in the 1970's after severe population declines, and fledged the first chick on the island of Oahu in 1992. We report the status of Laysan albatross populations at Kaena Point and Kuaokala on the island of Oahu, Hawaii and provide new demographic data for this species. Colonies on Oahu were monitored weekly from 2004 to 2008; all individuals were censused, banded, and genetically identified to gender. There was a population of 365 adults on Oahu in 2008 of which 47% were active breeders. The breeding population increased 27% annually since 1991. The high rate of increase was due primarily to immigration with some local recruitment. Recaptures indicate that seven birds were from French Frigate Shoals, one was from Midway Atoll, and 52 were from Oahu and returning to breed; all other adults were of unknown origin. Hatching rate (62%), fledging rate (78%), and overall reproductive success (48%) were comparable to other colonies despite occasional predation. The rate of adult dispersal was high with up to 10% of birds observed each day on Oahu visiting from Kauai. Adults occasionally changed breeding colonies between seasons, and even visited other islands while actively breeding on Oahu. While small, these colonies are at higher elevations and may serve as refugia in the event of sea level rise and, thus, should continue to be conservation priorities.

## INTRODUCTION

The Laysan albatross (*Phoebastria immutabilis*) has a broad distribution spanning tropical, subtropical, and subarctic zones (8° to 59°N) of the Pacific Ocean from the west coast of North America to Japan (Whittow 1993, Hyrenbach et al. 2002, Shaffer et al. 2005). Their pelagic habitat includes most of the North Pacific Ocean, but they have historically bred on a limited number of remote subtropical islands (Whittow 1993, Tickell 2000). Laysan albatross began colonizing islands from Japan to Mexico in the 1970s, despite their reportedly high natal philopatry. Some sites were re-colonizations of islands where the species had been extirpated, such as Mukojima, Japan (Kurata 1978) and Wake Island in the Western Pacific (Rauzon et al. 2008), and Kauai in the main Hawaiian Islands (Zeillemaker and Ralph 1977, Tickell 2000). In addition to re-colonization of historical nesting sites, Laysan albatross also recently expanded their range to several more islands, including Lehua Islet in the main Hawaiian Islands (VanderWerf et al. 2007), and into the Eastern Pacific on Isla Guadalupe, Clarion, and San Benedicto in Mexico (Gallo-Reynoso and Figueroa-Carranza 1996, Pitman et al. 2004).

Fossil evidence indicates that seabirds were not only present, but abundant in the main Hawaiian Islands before arrival of humans (Olson and James 1982, Moniz-Nakamura 1999, Burney et al. 2001). Seabird populations in the Hawaiian Islands severely declined following the arrival of Polynesians 1,500-1,900 years ago and subsequent arrival of Europeans over 200 years ago (Olson and James 1982, Harrison 1993, Moniz-Nakamura 1999). Laysan albatross populations across the Pacific also severely declined during the early twentieth century as a result of human consumption,

feather collecting, egg collecting, predation from introduced mammals, and military activities (Whittow 1993, Tickell 2000, Rauzon 2001). As a result, Laysan albatross and many other breeding seabirds disappeared entirely from the eight main Hawaiian Islands (Olson and James 1982, Moniz-Nakamura 1999). Today, Laysan albatross breed almost exclusively in the Northwestern Hawaiian Islands (NWHI; 97% of > 600,000 pairs), which are largely free of mammalian predators (Tickell 2000, Naughton et al. 2007).

Laysan albatross are listed as vulnerable by the International Union for the Conservation of Nature (IUCN 2007) due to population fluctuations and high rates of at-sea mortality from bycatch in North Pacific fisheries (Gilman and Freifeld 2002).

Understanding the status of each breeding population of Laysan albatross has become a priority for developing conservation actions because this species is vulnerable and nests in few locations (Naughton et al. 2007). Laysan albatross colonies on Oahu, Kauai, and Lehua in the Hawaiian Islands are currently small, but growing. Populations on these high islands may become increasingly important because they will be better able to withstand projected global climate changes and associated rises in sea level (Baker et al. 2006). Our objectives are to: (1) report the status of the Laysan albatross population on Oahu, including a brief history of the species' occurrence, and (2) provide new demographic data for this species.

## METHODS

### *Study Sites.*

Detailed demographic monitoring of Laysan albatross has occurred at two locations on Oahu in recent years, Kaena Point Natural Area Reserve (Kaena Point NAR), and Kuaokala Game Management Area (Kuaokala GMA) ( Figure 2.1).

Kaena Point NAR (21° 58' N, 158° 27' W) is on the westernmost tip of Oahu and protects 12 ha of arid coastal habitat ranging in elevation from sea level to 25 m.

Mammalian predators, such as cats (*Felis catus*), dogs (*Canis lupus familiaris*), Indian mongoose (*Herpestes javanicus*), and black rats (*Rattus rattus*) are controlled by the U.S. Department of Agriculture (USDA), Wildlife Services through a combination of live trapping, shooting, and poison bait stations; however, these predators still survive at low densities. Two native plant communities are present, a mixed coastal dry shrubland dominated by naupaka (*Scaevola taccada*) and naio (*Myoporum sandwicens*), and a coastal dry mixed shrub and grassland dominated by ilima (*Sida fallax*). Several introduced plants are also common, including koa haole (*Leucaena leucocephala*), kiawe (*Prosopis pallida*), and Guinea grass (*Panicum maximum*), although efforts are underway to remove these species. Laysan albatross use all of these habitat types at Kaena Point NAR, including non-native vegetation.

Kuaokala GMA is ~ 6 km east of Kaena Point NAR at 350 m elevation in the northern Waianae Mountains (21° 56' N, 158° 23' W) and is the highest Laysan albatross colony in the world. The habitat is dominated by introduced ironwood (*Casuarina equisetifolia*), strawberry guava (*Psidium cattleianum*), and introduced grasses. The area where most albatross nest is fenced, and is part of a pig and game bird hunting area

within the Mokuleia Forest Reserve. Most nesting occurs under ironwood trees, where the needles from the trees are used to build nest cups.

### *Monitoring Techniques*

All chicks at Kaena Point NAR and Kuaokala GMA were censused and banded starting in 1992. Regular monitoring of adults and chicks at both colonies began in 2004 for the duration of the breeding season (Nov-Jul), and all birds encountered were captured by hand and banded with a federal metal band with a unique serial number. Monitoring consisted of a weekly census of all birds present in the colony at Kaena Point NAR, and approximately monthly at Kuaokala GMA. Starting in 2006, each bird was also given a field-readable purple plastic band numbered in white from 0001-0999. A small (400 uL) blood sample was collected from the tarsal vein of each bird for use in identifying gender and other genetic analyses. All individuals were classified to gender following protocols outlined in Fridolfsson and Ellegren (1999) and Young et al. (2008). Previously banded birds were reported to the Bird Banding Laboratory which provided information on the origin and, in some cases, age of each bird.

Nesting attempts were monitored from egg-laying through chick fledging. Each time an adult was encountered, its location, status (incubating, brooding, or walking), and association with any other adult or chick were recorded. Chicks were observed approximately weekly from hatching (Feb) until fledging (Jul) each year. Nest number, parent information, hatching date, disease status, and date of either fledging or death were recorded for all chicks. Chicks that survived to fledging age were banded with both a federal metal band and a field-readable plastic band.

## *Analyses*

We estimated the number of Laysan albatross that have been recorded on Oahu since the 1970's by compiling banding records and observations from the published literature, federal banding records, and discussions with biologists and birders.

Individuals were included only if a band number could be obtained to ensure the actual number of individuals, and not just observations, was reported.

Size of the non-breeding population is difficult to estimate in seabirds (Citta et al. 2007), but we attempted to estimate the total current Laysan albatross population on Oahu by summing the numbers of birds that have bred at least once in the past 3 years (to account for birds that skipped up to 2 years), non-breeders that have visited the island at least twice in the past 5 years (since some non-breeders do not visit every year), and chicks hatched on the island that returned and visited the island at least twice in the past 4 years. These time periods were chosen based on attendance patterns of birds in each category and the encounter probability of each category.

We calculated the average rate of increase in the breeding population from 1992 (year the first chick fledged) to 2008 using the formula:  $k = (n_t/n_0)^{1/t}$  where  $k$  is the rate of increase,  $n$  is the number of nesting pairs, and  $t$  is time in years.

## RESULTS

### *Population History*

Laysan albatross have attempted to breed at six locations on Oahu since 1979: Kaena Point NAR, Kuaokala GMA, Kahuku Point, and Dillingham Airfield on Oahu's northern coast, and Kaneohe Marine Corps Base (MCBH) and Moku Manu on the eastern side of Oahu (Figure 2.1). The two sites on Oahu where Laysan albatross have successfully established and maintained colonies are Kaena Point NAR and Kuaokala GMA. The Kahuku Point colony failed to fledge any chicks due to predation by dogs and, in 1996 the remaining adults abandoned breeding there altogether but still regularly visit the site (Mike Ord, Pete Donaldson, Mike Silbernagle, pers. comm.; LCY and EAV, pers. obs.). Laysan albatross attempted to nest at Dillingham Airfield during the late 1980s and 1990s, but due to the strike hazard they posed to aircraft, eggs were removed to discourage nesting (Mark Ono, pers. comm.); adults still regularly visit the site. Laysan albatross still attempt to nest each year near an active runway at MCBH and, at times, in an active firing range (Diane Drigot, pers. comm.). Eggs are removed at this site to discourage nesting and reduce the chance of aircraft strikes. All adults encountered at MCBH since 1985 have been banded by USDA, Wildlife Services personnel and removed from the site; some have been released at Kaena Point NAR.

### *Population Size and Origin of Laysan albatross on Oahu*

The annual growth rate of the Laysan albatross breeding population on Oahu was 27% from 1992 to 2008. This growth was primarily a result of immigration from other colonies, but there was some local recruitment. The number of chicks fledged also



increased over the same time period (Figure 2.2). The total population size on Oahu in 2008 was ~ 365 adults of which 163 (47%) were breeders. Kaena Point NAR is the larger of the two colonies (28-50 nests from 2004 to 2008) and has two to three times the population of Kuaokala GMA (15-23 nests from 2004 to 2008). The sex ratio of adults in the Oahu population was female-biased (59% female), although, the sex ratio of chicks at fledging was 49% female.

A total of 891 Laysan albatross has been recorded on Oahu from 1979 to 2008. Of these, 264 (30%) were chicks hatched on Oahu, 193 (22%) were adults that bred at least once since 2003, and 434 (48%) were non-breeding adults. Most adults on Oahu did not have bands when first observed (78%,  $n = 494/627$ ) and are of unknown origin. Of birds banded as chicks and, thus, of known origin ( $n = 59/627$ ; 9%), seven were from French Frigate Shoals, one was from Midway Atoll, and 52 were Oahu individuals recruiting to their natal colony. Two chicks hatched on Oahu were observed as adults on Kauai (Brenda Zaun, unpubl. data) and have not returned to their natal colony. Birds banded elsewhere as adults were exclusively from Kauai ( $n = 76/365$  adults) and comprised 21% of the current adult population on Oahu. This observation, coupled with chicks from Oahu recruiting to Kauai, provides evidence of both natal and adult dispersal in this species.

### *Reproductive Success and Behavior*

The overall nest success rate on Oahu from 2004 to 2008 was 48% (Figure 2.3). The hatching rate of all eggs laid was 62%, and the fledging rate of all chicks hatched was 78%. The number of nesting attempts steadily increased despite variation in hatching

and fledging success as a result of predation (Figure 2.3). Breeding phenology closely parallels other Laysan albatross colonies with the first birds returning to the colony during 6-11 November, egg laying from 21 November to 16 December, chicks hatching from 25 January to 21 February, and chick fledging occurring primarily in July.

The rate of mate change in Laysan albatross on Oahu was 14% (9/66), based on pairs in which the mate was known for at least 3 years. A mate change was defined as two birds pairing for at least two years then at least one of the birds pairing with a different bird when its previous mate was known to be alive. Eight of nine pairs that changed mates were reproductively successful in their breeding attempt preceding the mate change on Oahu. The chance of changing mates was related to one partner taking a year off and not returning to the colony during that year to reaffirm the pair bond. Five of nine mate changes occurred when one mate returned to the colony and the other did not. Five of the nine birds found a new mate and nested the same season their partner did not return, and four skipped 1 year before breeding with a new mate. In one case a bird returned to its original mate the following year despite breeding with a different bird while its mate was absent.

## DISCUSSION

In 1947 a single Laysan albatross chick was recorded at Moku Manu Islet off Oahu (Fisher 1948) and an abandoned egg was found there the following year (Richardson and Fisher 1950), but it wasn't until 1978 that adults began regularly appearing at several locations around the island (Pyle 1978, 1986, Pratt 1988). Breeding attempts that began in 1979 at Kahuku Point were not successful due to predation and

crushing of nests by off-road vehicles (Eilerts 1987). Laysan albatross colonies on Oahu have grown rapidly since the first chick fledged from Kaena Point NAR in 1992. This success has been made possible by protection and active management of nesting areas, particularly exclusion of off-road vehicles beginning in 1991 and control of alien predators beginning in 1995. These actions have allowed immigrating birds to flourish and the colony to grow despite the continual threat of predation, introduced diseases, and interference from humans (VanderWerf et al. 2005, Young and VanderWerf 2008).

A social attraction project using decoys and sound recordings began in 1993 at Kaohikaipu Island off Oahu's eastern shore in an attempt to attract Laysan albatross to nest on predator-free (and people-free) islets (Borzik et al. 1995). There were no breeding attempts and the project was discontinued, despite visits by adults during the project with the sound system ceasing to function in 1995 (Kress et al. 1999) and removal of the decoys in March 2000. Several hundred Laysan albatross were banded on Oahu during the social attraction project and the project's failure was not due to lack of birds but, perhaps, because of some unsuitable characteristic of Kaohikaipu.

The rapid growth of these colonies cannot be attributed to successful local reproduction alone, because the total number of chicks fledged from 1992 to 2008 was much less than the number of recruits arriving at the colonies. Some birds hatched on Oahu have returned to their natal area and begun breeding, but a much larger proportion of new breeders originated from other islands, and the female-biased sex ratio in the colony is a byproduct of female-biased immigration (Young et al. 2008). Six of seven band recaptures from birds hatched in the NWHI and now present on Oahu were from Whale-skate Island in French Frigate Shoals, which disappeared in 1997 after decades of

erosion, displacing thousands of birds (Beth Flint, pers. comm.). It is possible that colonization events were initiated across the Pacific as the result of displacement of albatross from Whale-Skate Island, and these new colonies now attract dispersing birds from other colonies in the NWHI as a result of social facilitation. Three of six birds from Whale-skate now breeding on Oahu were banded as chicks within one day of each other in 1992, indicating they may have been traveling as a cohort. Travelling as a cohort has not been documented in this species, but is worth investigating as this may provide insights into colonization mechanisms in this, and other, colonial seabird species.

Recent counts of Laysan albatross at Midway, Laysan, and Tern islands in the NWHI, which account for ~93% of the global population, have also indicated stable or growing numbers of breeding birds (Beth Flint, pers. comm.); the increase on Oahu and at other new colonies may be related to this growth. Juvenile dispersal by Wandering albatross (*Diomedea exulans*) is density dependent, leading to higher juvenile dispersal when local population density is high (Inchausti and Weimerskirch 2002). Increases at new colonies may be driven by juveniles dispersing from high density nesting colonies in the NWHI if a similar mechanism is functioning in Laysan albatross. Previous studies on Laysan albatross have reported high natal philopatry, but these early studies (Fisher and Fisher 1969) could have missed immigration or emigration because they were done using a plot design within large colonies, and did not track the fate of individuals that left the plot. The exact cause of the range expansion of Laysan albatross is unknown, but a combination of factors are likely responsible for supplying recruits to new colonies.

Adult dispersal was also documented with non-breeding adults regularly visiting other colonies, at times several times daily through the duration of the breeding season;

breeding adults occasionally switched breeding colonies between years. Up to 10% of the birds observed on Oahu any given day were non-breeding adults visiting from Kauai. Moreover, when both colonies on Oahu were monitored on the same day, 1-2 individuals were often observed at both sites. The same phenomenon has been observed on Kauai, where Oahu non-breeding birds are regularly seen visiting (Brenda Zaun, pers. comm.). One adult banded on Oahu at 1000 hrs HST on 14 January 2006 was observed at 1600 hrs HST the same day at Kilauea Point on Kauai, 137 km away (Brenda Zaun, pers. comm.). Another individual from Kauai was observed on Oahu, and then at Lehua Islet 73 km west of Kauai 8 days later. Most birds moving among colonies are non-breeders and are likely to be young individuals searching for a breeding site, but some are active breeders or birds taking a year off, including one 19-year old adult from French Frigate Shoals observed at Kaena Point NAR in 2008. Each year on Oahu, 1-2 breeding pairs switch from breeding at Kuaokala GMA to breeding at Kaena Point NAR and vice versa. This could be interpreted as low site fidelity, but it is possible the birds functionally treat these sites as a single colony since they are within sight of one another. These observations support the hypothesis that Laysan albatross are aware of nearby colonies and regularly visit them to gather information and prospect for suitable breeding sites and/or mates as has been reported for other seabirds (Danchin et al. 1998).

Observations of the breeding behavior of Laysan albatross on Oahu have also provided new insights into this species' natural history. The high rates of mate change, super-normal clutches, and same-sex pairing (Young et al. 2008) observed on Oahu are all previously unreported for this putatively socially-monogamous, single-egg clutch species. The 14% rate of mate changing is higher than the 9% previously reported for this

species (Fisher 1971, 1976). Mate change in previous studies was reported to be associated with breeding failure (Fisher 1971, Bried et al. 2003), but this was not true on Oahu where the chance of a mate change appeared to be related to one member of a pair taking a year off when the other returned to the colony.

There were several observations of successful single-parent nests in this colony, which has not been reported previously in this species. In 2006, when a female was killed as bycatch by a Taiwanese long-lining vessel, the male partner successfully fledged the week-old chick without assistance from his mate. Additionally, in 2008, one male maintained two separate nests with two different females and successfully fledged both chicks (which accounts for the odd number of 163 breeding birds). These observations indicate that a single parent can fledge a chick, although in both cases the chicks appeared to be underweight and were the last to fledge from the colony. These behaviors have also been observed on Kauai (Brenda Zaun, pers. comm.), indicating they are not unique to Oahu, but typical of this species' natural history.

Regular monitoring that included census of all individuals was possible due to the small size and accessibility of the Laysan albatross colonies on Oahu, and has provided natural history information and observations on this species that are not possible in larger, less accessible colonies (Young and VanderWerf 2008, Young et al. 2008). Estimation of reproductive and population parameters, such as the proportion of breeders and non-breeders, is more feasible for the small population on Oahu than in larger colonies and can serve as a guideline to complement the monitoring occurring at other colonies.

The return of nesting Laysan albatross and other seabirds to the main Hawaiian Islands is the result of years of predator control and habitat restoration projects initiated

by several state and federal agencies. Black-footed albatross (*Phoebastria nigripes*) and 11 other species of seabirds have been observed at Kaena Point NAR and, with continued habitat restoration, and mammalian predator control, some of these species may recolonize the main Hawaiian Islands. A predator-proof fence that would exclude all mammalian predators is now in the planning stages for Kaena Point NAR, which will result in improved protection for nesting Laysan albatross, thousands of nesting Wedge-tailed Shearwaters (*Puffinus pacificus*), and 11 federally endangered plant species (Hawaii Department of Land and Natural Resources 2007). The Laysan albatross colonies at Kaena Point NAR and Kuaokala GMA are small, but may be critically important for the long-term survival of the species because they are among the few high island nesting sites that may serve as refugia should projected rises in sea level inundate primary nesting sites in the Northwestern Hawaiian Islands (Baker et al. 2006). Conservation efforts should continue to focus on protecting these colonies.

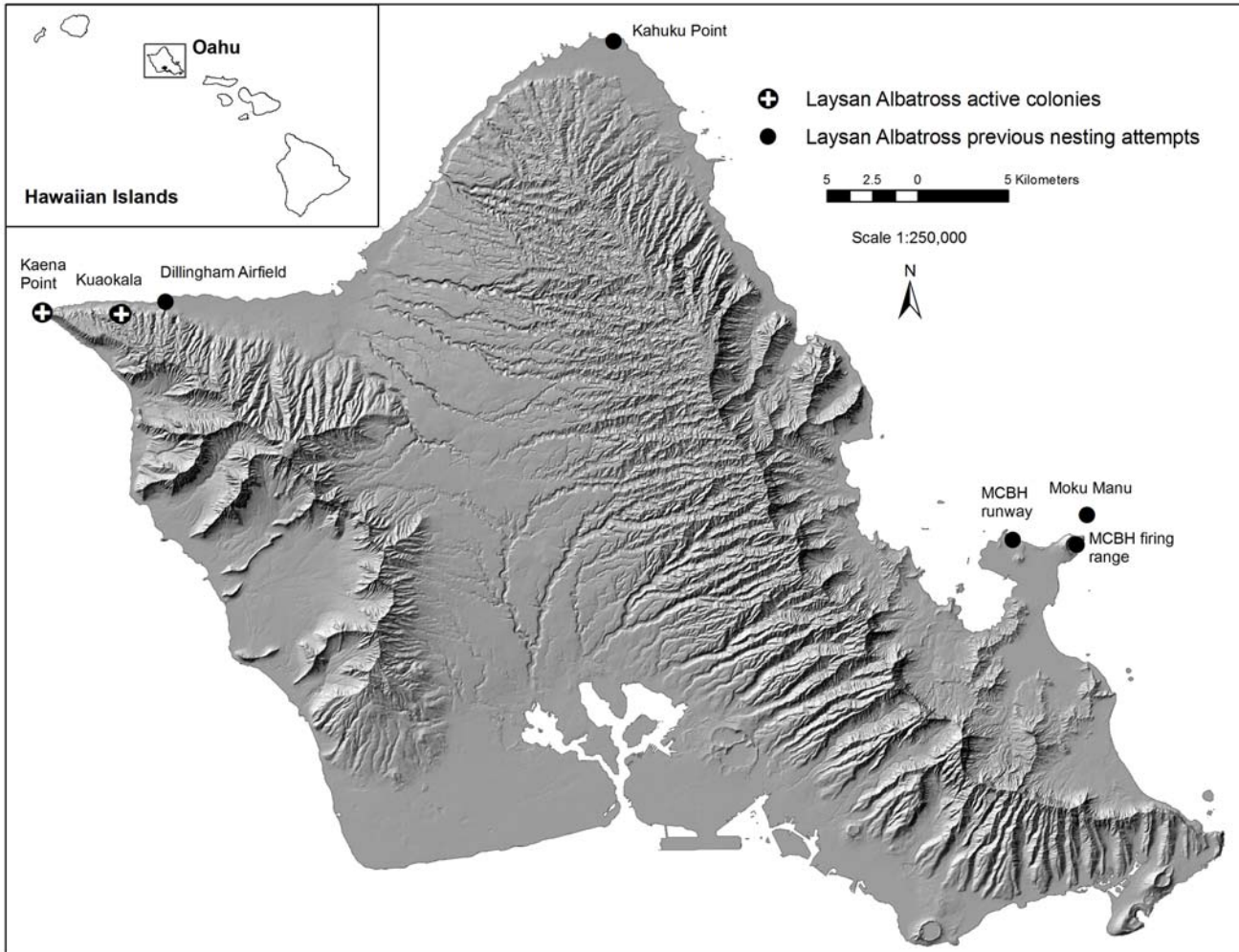


Figure 2.1: Study sites and other locations on Oahu, Hawaii where Laysan albatross have attempted to nest.



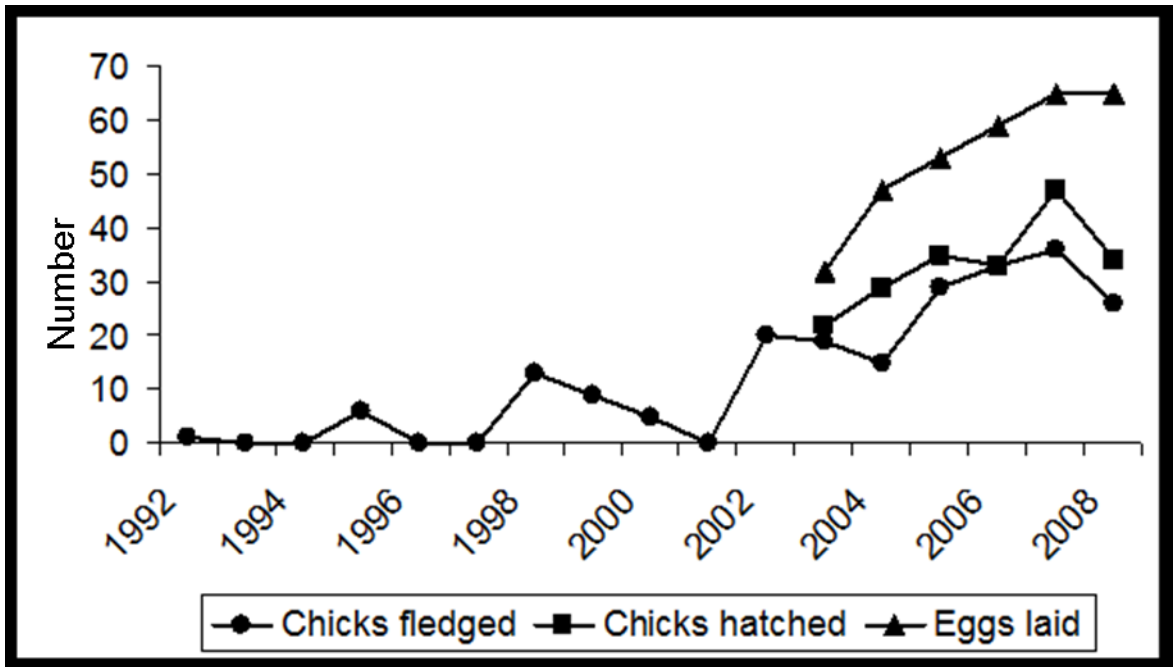


Figure 2.2: Number of chicks fledged each year from Laysan albatross colonies on Oahu, Hawaii since 1992 and numbers of eggs laid and chicks hatched from 2004 to 2008.

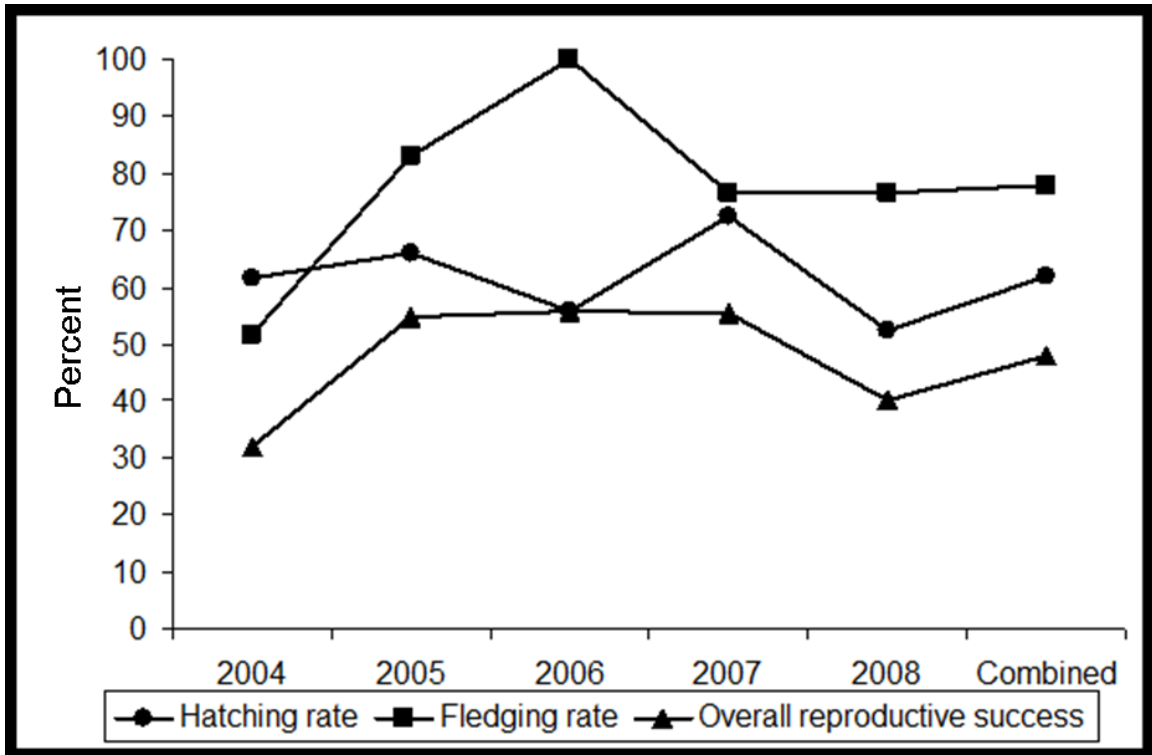


Figure 2.3: Rates of hatching (% of eggs laid that hatch), fledging (% of chicks hatched that fledge), and reproductive success (% of eggs laid that result in fledged chicks) for Laysan albatross on Oahu, Hawaii.

## CHAPTER 3

### BRINGING HOME THE TRASH: DO DIFFERENCES IN FORAGING LEAD TO INCREASED PLASTIC INGESTION IN LAYSAN ALBATROSS?

## ABSTRACT

Under optimal foraging theory, organisms should maximize their energetic gain, while minimizing energy expenditure by altering their movements relative to prey availability. However, with increasing amounts of marine debris, what once may have been ‘optimal’ foraging strategies for top marine predators, are leading to sub-optimal diets comprised in large part of plastics. Indeed, the highly vagile Laysan albatross (*Phoebastria immutabilis*), which forages throughout the North Pacific, are well known for their tendency to ingest plastic parts that appear similar to the foods they consume. Here we examine whether two Laysan albatross populations nesting in the Hawaiian Islands experience different levels of plastic ingestion based upon seasonal changes in their distribution across the Central and Western North Pacific Ocean. Eighty five Global Location Sensing data loggers (geolocators) were deployed on breeding adults for up to two years on Kure Atoll and Oahu Island, 2150 km apart. Regurgitated boluses of undigestible material were collected from chicks at each study colony to compare the amount of plastic vs. natural food fed to them by adults. Chicks from Kure Atoll ingested almost ten times the amount of plastic compared to chicks from Oahu despite both colonies having similar amounts of natural food. Analysis of the tracking data show that adults from both colonies do not have core overlapping distributions when breeding and that adults from Kure had a greater overlap with the putative range for the Western Garbage Patch corroborating the observation of higher plastic loads from chick boluses. In contrast, adults from Oahu had a more central North Pacific distribution that does not overlap with the Garbage Patch, and low plastic loads in boluses reflect this. We also found that albatross distribution varied substantially throughout the year suggesting that Laysan albatrosses either adjusted their foraging behavior according to constraints on

time away from the nest or to variation in resources. However, in the non-breeding season, distributional overlap was greater indicating that the energy required to reach the foraging grounds was less important than the total energy available. These results demonstrate how a marine predator that is not dispersal limited alters its foraging strategy throughout the reproductive cycle to maximize energetic gain and how this has led to differences in plastic ingestion. Determining how and where marine organisms come into contact with marine debris has important conservation implications for how we choose to mitigate the environmental impact of marine debris and can in turn help locate new sources of marine debris.

## INTRODUCTION

When searching for prey, an organism is expected to maximize its energetic gain, while minimizing energy expenditure. To accomplish this, organisms should increase the probability of detecting food patches by altering their movement path relative to the availability of prey (Schoener 1979, Stephens and Krebs 1986). Unlike terrestrial environments, where physical barriers and geography often put constraints on movement, most oceanic environments are essentially unobstructed. As a result, the movements of marine organisms that are not dispersal limited can directly reflect their assessment of resource variation.

In the case of pelagic seabirds that nest on remote oceanic islands (Schreiber and Burger 2001), one would predict that breeding populations on distant islands should maximize energetic gain by exploiting available resources closest to their breeding colony when they are nesting. This central-place foraging during the breeding season could potentially lead to local diet differences between colonies as well as resource depletion and/or competition. When pelagic birds are not breeding, and therefore not constrained to the nest, the foraging patterns of birds from different colonies separated by thousands of kilometers could overlap and instead reflect the actual resource variation throughout their range (Weimerskirch et al. 1993, 2005, 2007, Shaffer et al. 2003).

The at-sea foraging patterns of the highly mobile Laysan albatross (*Phoebastria immutabilis*) have been well documented (Whittow 1993, Fernandez 2001, Hyrenbach et al. 2002, Shaffer et al. 2005, Kappes et al. 2009). There are marked changes throughout their annual reproductive cycle: during incubation and chick rearing stages they practice ‘central-place foraging’, but later, when they are not constrained to the nest, they forage

throughout the North Pacific (Orians 1979, Fernandez 2001, Hyrenbach et al. 2002, Shaffer et al. 2005, Kappes et al. 2009). However, it is unknown whether all breeding colonies exploit the same resources, or habitats, year round, that are well within their dispersal potential, or if colonies utilize 'locally' available resources since previous studies have focused on a single breeding colony. The variable diet and flexible foraging strategy of this species (utilizing both scavenging and live capture (Harrison 1990, Whittow 1993) indicate that it is somewhat of a generalist. As a result, birds in distant colonies should exploit suitable resources closest to the colony during the breeding period, even though they are capable of travelling to virtually any foraging ground in the North Pacific.

Ironically, the flexible foraging strategy of Laysan albatross has potentially lead to a decrease in their foraging efficiency as they are ingesting large amounts of plastic which is in turn fed to their chicks (Fry et al. 1987, Sievert and Sileo 1993, Robards et al. 1997, Auman et al. 1997). It is unclear how often birds encounter or ingest plastic, whether plastic is mistaken for prey, has natural food attached to it, or is consumed to assist in digestion as is sometimes done with pumice (Fry et al. 1987, Sievert and Sileo 1993, Robards et al. 1997, Auman et al. 1997). Unfortunately, plastic ingestion leads to mechanical blockage of the digestive tract, reduced food consumption, satiation of hunger, and potential exposure to toxic compounds. While there have been documented detrimental effects on the growth rates and fledging masses of chicks, it is still unclear what levels of mortality are caused by plastic ingestion (Fry et al. 1987, Sievert and Sileo 1993, Robards et al. 1997, Auman et al. 1997). What is clear is the source of the plastic: there is now so much floating marine debris that has accumulated in the North Pacific

gyre, it known as the ‘great garbage patch’ (Kubota et al. 1994, Damerson et al. 2007, Pichel et al. 2007). This patch consists of two accumulations: the ‘western garbage patch’ off of Japan and ‘eastern garbage patch’ between Hawaii and California (NOAA 2009) that correspond to the putative locations of two sub-gyres within the North Pacific Gyre (Hasunuma and Yoshida 1978), connected by a narrower band of marine debris north of the Hawaiian archipelago (Figure 3.1). Much has been written in the popular press about plastic ingestion by Laysan albatross (Figure 3.2), however, relatively few empirical studies have examined this phenomenon and whether it is species wide, or if this is confined to certain populations.

Here we examine whether Laysan albatross nesting on distant islands attempt to minimize energy expenditure during the breeding season by exploiting resources closer to their breeding colonies and whether this leads to differences in plastic ingestion. In addition to seabird boluses having the potential to monitor plastic in our oceans, determining how and where marine organisms come into contact with marine debris could have implications for how we choose to mitigate its environmental impact.

## METHODS

### *Data logger deployments*

Global Location Sensing data loggers (or geolocators) are small microprocessor-based devices that determine a geographic position on the globe from the establishment of local noon or midnight to estimate longitude and day length at the estimated longitude to derive latitude (Wilson et al. 1992, Hill 1994). Validation studies on albatrosses



indicate that location error using this methodology range from 186-202 km from true location (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005).

We deployed leg mounted 9-g geolocators on Laysan albatrosses breeding at two colonies: Oahu in the main Hawaiian Islands (21° 34'N, 158°16'W), and Kure Atoll 2150 km away in the Northwestern Hawaiian Islands (28°23'N, 178°17'W; Figure 3.3). Model MK3 geolocators manufactured by the British Antarctic Survey (BAS) were attached to a plastic leg band by pre-drilling holes and threading cable ties through the leg band to secure the geocator to it (Figure 3.3). The contact points were then sealed with marine grade epoxy and the leg band with the geocator attached was placed around each bird's tarsus.

On Oahu, 14 pairs ( $N= 28$ ) of incubating or brooding adult Laysan albatrosses at Kaena Point Natural Area Reserve were outfitted with geolocators in February 2005 representing 39% ( $N= 14/36$  nests) of breeding adults that year. The reproductive outcomes of all pairs were tracked from egg laying to fledging to monitor the effects of tagging on reproductive success. On Kure Atoll, 28 pairs, plus one additional breeding adult ( $N= 57$ ) were outfitted with geolocators in May 2005 during the late chick rearing phase. Logistical limitations of working at remote island like Kure Atoll prevented us from deploying the loggers at the same time of year and monitoring the reproductive fate of these birds.

#### *Geocator filtering and spatial data analysis*

Geolocators were retrieved at various time periods from January 2006- June 2007, depending on when tagged birds returned to the colony. Downloaded data were

decompressed using BASTrak v12 software (BAS) and light curves (i.e. to establish sunrise and sunset and thus local noon or midnight) were analysed using Transedit software (BAS) using a sunrise angle of  $-2.5^{\circ}$  for Oahu, and  $-3^{\circ}$  for Kure. Any locations produced from light curves with interruptions or interference around the times of sunset or sunrise (usually as a result of shading of the sensor) were noted during processing and excluded if obviously anomalous. Final position coordinates were generated by BirdTracker (BAS).

Purpose-built routines were created in Matlab 8.0 (The MathWorks, Natick, Massachusetts) and used to filter spurious positions and to integrate remotely-sensed environmental data following established protocols (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005). Given the inaccuracy of latitude estimation during equinoxes (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005 and 2006), location fixes on ten days of either side of the equinoxes were excluded. Three subsequent filters were applied to data once the equinoxes had been removed: one to filter out unrealistic flight speeds (sustained speeds  $>50\text{km/hr}$  over 12 hours) and distances ( $> 500\text{km}$  in 12 hours), a second to remove any remaining points occurring in locations where Laysan albatross have not been recorded previously (latitude and longitudes), and a third to remove any points that occurred over continental land masses (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005 and 2006). Of 14,281 locations produced, 72% ( $N = 10,314$ ) were kept after filtering.

Estimates of bathymetry, and remotely-sensed sea surface temperature (SST), sea surface height (SSH), and primary productivity were calculated for each bird location based on methods described elsewhere (Shaffer et al. 2006, 2009). These data allowed us

to describe the frequency of occurrence that Laysan albatrosses spent within specific water masses, productivity regimes, and depth domains. To assess the degree of spatial overlap at sea of albatrosses from each colony, we derived kernel density distribution estimates (Worton 1989) from unsmoothed (i.e. non-interpolated) locations using the Iknos toolbox (Tremblay unpublished) developed in MatLab. This routine converted geographic coordinates to Cartesian coordinates using a Lambert Cylindrical Equal Area projection (Worton 1989) and created 2-D kernels based on an 80 km grid cell size. The kernel smoothing parameter (h) was based on an adaptive method (Sheather and Jones 1991). We then quantified the spatial overlap of the 95% (foraging range), 75%, 50% (focal region), and 25% (core) kernel polygons representing the distribution of the albatrosses from each colony during each breeding stage and non-breeding period.

#### *Bolus collection and analysis*

Boluses are the non-digestible parts of the albatrosses diet (e.g. squid beaks, otoliths, plastic etc) that are periodically regurgitated and they represent a non-invasive measure of diet (Whittow 1993). Naturally regurgitated boluses were collected from eight chicks on Oahu and 15 from Kure Atoll during the time interval when adults were tracked. Boluses were soaked for 24 hours in water and then sorted according to natural food items (such as flesh, squid beaks and lenses) and plastic items. Wet mass and displacement volume were measured, and plastic items were further categorized into the number and the average mass of pieces per bolus. Mass and volume of natural vs. plastic items in each bolus, as well as the number and average mass of the plastic pieces were compared between Oahu and Kure by using a Mann-Whitney U-test in Minitab 14.

## RESULTS

### *Geolocator recovery rates and effects on reproductive success*

Fourteen and 32 tags were recovered from Oahu and Kure Atoll respectively which amounted to an overall tag recovery rate of 54% ( $N = 46/85$ ). In most cases, geolocators that were not recovered had broken free of the leg band as a result of cable tie failure, despite the bird itself returning. Of the 46 tags recovered, only 22 produced data even after failed batteries were recovered (48%; 10 from Oahu, 11 from Kure). While the cause of the electronic failure of the geolocators is unknown, it is possible that saltwater intrusion occurred as a result of epoxy expansion at higher temperatures which allowed water to leak onto the electrical components. Between tag loss and electrical failure, the cumulative geolocator failure rate was 74% ( $63/85$ ).

Deployment of geolocators had no detectable short-term effect on the birds. Tagged Laysan albatross on Oahu had similar reproductive success (71%,  $N = 10/14$  nests were successful), as well as resight probabilities the following year (86%,  $N = 24/28$  individuals ) compared to non-tagged birds (reproductive success= 55%,  $N = 12/22$ ,  $X^2 = 1.026$ ,  $df = 1$ ,  $p = 0.311$ ; resight probability = 86%,  $N = 30/35$ ,  $X^2 = 0.000$ ,  $df = 1$ ,  $p = 1.000$ ). Multiple birds on Kure Atoll developed minor calluses and chafing on the leg as a result of unsecured cable ties rotating under the leg band. These were temporarily removed immediately after deployment, modified to prevent movement of the cable tie, and re-deployed, which appeared to eliminate further chafing.

### *Spatial associations of each colony*

Laysan albatrosses from both colonies had similar associations with productivity regimes and depth domains that were quantified from bathymetric features, sea surface temperature (SST), sea surface height (SSH) and primary productivity (Figure 3.4). During incubation and early chick rearing, birds from both colonies foraged in pelagic (depth: >4000m), oligotrophic (primary productivity: <600 mg °C m<sup>-2</sup> d<sup>-1</sup>) tropical to sub-tropical waters (SST: <16 °C). During the post-guard stage of chick rearing, birds from both colonies began venturing into cooler, more productive waters further north of their respective colonies. Despite the similarities in the oceanographic features that birds from both colonies were exploiting, significant differences were found in the actual locations of foraging relative to their breeding colonies (Figures 3.5-3.8, Table 3.1).

During incubation and early chick rearing, each colony exploited different habitats and did not overlap in the core usage areas (50% and 25% kernels, Table 3.1, Figure 3.7). Birds from Oahu foraged north of the colony in the area of the transition zone chlorophyll front (TZCF, Figure 3.5, Polovina et al. 2001), but most avoided the area of the ‘eastern garbage patch’. As the breeding season progressed, birds began venturing into the transition domain and subarctic waters, occasionally reaching the Aleutian Island chain. Birds from Kure foraged north/northwest of the colony over the Emperor Seamounts, the area bounded by the Kuroshio and Oyashio current systems and occasionally over the ‘western garbage patch’. As the breeding season progressed, birds moved farther north and west, foraging more in the subarctic frontal zone and the transition domain.

Conversely, during the post-chick guard stage when adults can spend increasing lengths of time away from the nest, or have failed in their nesting attempt, the core areas of Kure and Oahu birds began to overlap, primarily as a result of Oahu birds moving further west and the distributions of both colonies moving farther north. During the non-breeding season, from 38-50% overlap between the two colonies was observed in the 25% and 50% kernel density estimates. While both colonies expanded their foraging radius throughout the season, Oahu birds appeared to have a bi-modal distribution in the non-breeding season with two distinct ‘hot spots’ at parallel locations on either side of the date line (Figure 3.5), whereas Kure birds have a single hot spot significantly west of the date line (Figure 3.6).

#### *Difference in plastic loads*

Every bolus examined in this study contained plastic. The amount of natural food found in the boluses of chicks on Kure and Oahu was similar in volume ( $30.75 \pm 3.72$  ml vs.  $32.18 \pm 5.63$  ml;  $p > 0.628$ ) and mass ( $23.98 \pm 3.00$  g vs.  $26.14 \pm 3.94$  g;  $p > 0.745$ ). However, the amount of plastic in Kure boluses was up to ten times higher than the amount of plastic in Oahu boluses (Figure 3.6): volume ( $53.67 \pm 6.38$  ml vs.  $5.26 \pm 2.50$  ml;  $p = 0.0001$ ), mass ( $38.03 \pm 5.32$  g vs.  $4.37 \pm 2.10$  g;  $p = 0.0001$ ), number of plastic pieces ( $70.6 \pm 11.5$  vs.  $17.4 \pm 5.5$ ;  $p = 0.0004$ ) and the average mass of plastic pieces ( $0.58 \pm 0.065$  g vs.  $0.20 \pm 0.047$  g;  $p = 0.0001$ ).

## DISCUSSION

Distant colonies of Laysan albatross utilize similar oceanographic productivity regimes in widely separated areas, suggesting that this vagile species are able to assess resources on large scales. The similar associations of both colonies with productivity and depth domains indicate that there are predictable oceanographic characteristics of suitable foraging areas that are part of an albatross's search image when they are trying to locate prey (Fernandez et al. 2001, Hyrenbach 2002, Kappes et al. 2009). However, it is their ability to identify suitable areas closest to the colony when they are actively breeding which suggests that their assessment of resource variation also includes an assessment of the energy required to reach the resources, and thus leads to foraging segregation during the reproductive cycle when they are physically constrained to the nest.

During the non-breeding season when birds are not as energetically constrained<sup>6</sup>, some overlap between distant colonies at sea does occur, which may indicate that the energy required to reach the foraging grounds becomes less important than the total energy available on the foraging grounds themselves. Another possible explanation is that the colony on Oahu, which is a 'new colony' comprised almost entirely of immigrants from other colonies (Young et al. 2008) has immigrants from Kure Atoll, and that the bi-modal distribution in the non-breeding season may actually reflect Kure-born birds returning to their ancestral non-breeding foraging grounds. In either case, the results indicate that Laysan albatross are able to assess resource variation and alter their foraging strategies accordingly throughout their reproductive cycle as one would predict in order to maximize energetic efficiency.

The fact that both colonies ingest plastic, unfortunately, suggests that ‘optimal’ foraging produces a sub-optimal diet comprised in large part of non-digestible plastic pieces. Previous studies have shown that the highest concentration of marine debris is in the spring and early summer when the TZCF moves south (Pichel et al. 2007) which, corresponds to the chick rearing season in Laysan albatross (Whittow 1993). Birds breeding on Kure Atoll fed their chicks, on average, ten times more plastic than birds breeding on Oahu indicates that the often overlooked ‘western garbage patch’ where the majority of Kure birds foraged may in fact be a just as much of a threat to marine life as the frequently discussed ‘eastern garbage patch’. Furthermore, every single bolus examined from Kure Atoll contained multiple pieces of fishing paraphenalia, while only two boluses on Oahu contained any evidence of fishing line or tools (despite recreational fishing adjacent to the breeding colony on Oahu), indicating that the threat from fisheries doesn’t just come in the form of bycatch for this species. It is not known whether the western garbage patch contains more trash than the eastern garbage patch, if it is that the size and composition of the pieces are easier for the birds to ingest than those found in the eastern garbage patch, or that Kure birds spent more time foraging in this area.

It has been hypothesized that the two garbage patches are in fact a single contiguous area bounded by prevailing currents, but that the size of the debris pieces between the western and eastern edges is so different that they appear to be two patches. Perhaps the debris in the eastern end of the patch is larger as a result of prevailing winds pushing larger items east, and that smaller items are entrained in the western edge of the patch. Our results support the latter hypothesis as birds from Kure foraging on the western end of the garbage patch had much higher plastic loads than Oahu birds that



foraging towards its eastern end where pieces may be too large to ingest. However, it still does not rule out the possibility that there is also more plastic in the western patch.

Environmental heterogeneity in marine, as well as terrestrial systems, affects animal movements on a range of scales (Weimerskirch 1993, 2005, 2006, Shaffer et al. 2003, Fritz et al. 2003, Pinaud and Weimerskirch 2005). Our results indicate that Laysan albatross are able to assess prey availability on large scales and make foraging decisions based on the energy required to reach feeding grounds throughout their breeding cycle. While the foraging locations during the breeding season are population specific, these predators seem to seek out common ecological characteristics, leading to the use of similar habitats by birds from the two colonies in the non-breeding season when they are not constrained to the nest. Studying movements at a smaller scale in relation to resource distribution, and at multiple colonies over multiple years will be crucial to fully understand scale-dependent adjustments and the ultimate foraging distribution of these animals. Future studies of foraging behavior would also benefit from not only monitoring plastics ingested, but also quantifying natural diet to ascertain regional differences. The large range and potentially long-term retention of ingested plastic indicate that albatross may prove to be a useful species for sampling marine debris and other pollutants in the North Pacific Ocean, and as such, efforts should be made to continue monitoring their plastic ingestion and foraging patterns.

Colony	Region	Incubation- UD 25%, 50%	Chick guard UD 25%, 50%	Post-chick guard UD 25%, 50%	Post-breeding UD 25%, 50%
Oahu	Kure	0, 0	0, 0	23, 28	38, 51
Oahu	E Pac	0, 0	0, 0	0.04, 2.5	4.0, 10.0
Oahu	W Pac	0, 0	0, 0	0, 6.9	9.6, 16.6
Kure	E Pac	0, 0	0, 0	0, 0	0, 0
Kure	W Pac	0, 0	0, 0	18.0, 15.0	0, 1.0

Table 3.1. Overlap of the core (25% and 50% kernel density estimates) ranges of Kure

and Oahu Laysan albatrosses with each other, and with each garbage patch during the incubation, chick guard, post-chick guard and non-breeding periods. Overlap metrics range from 0 to 100%.

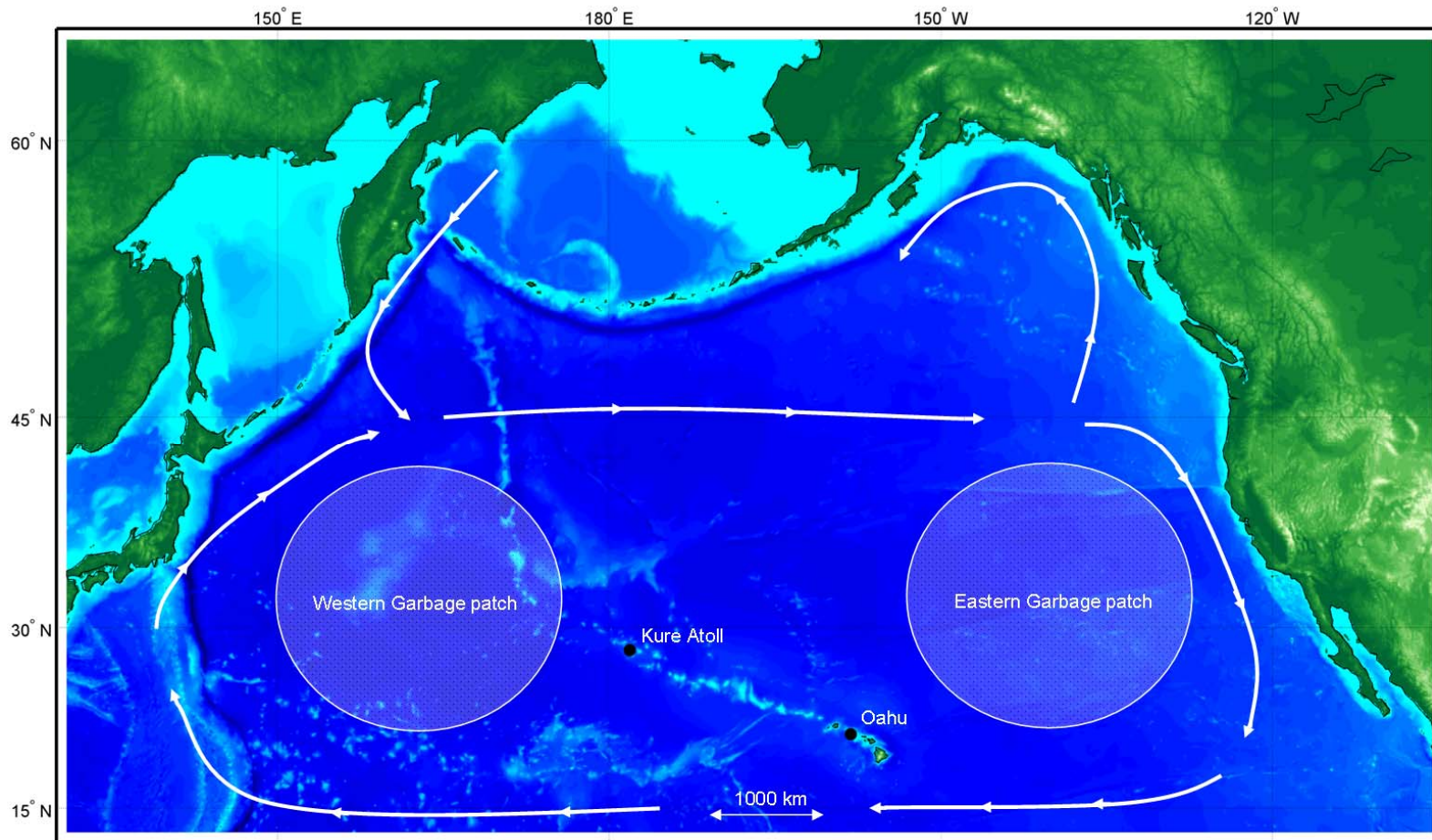


Figure 3.1. Study sites relative to major current systems (white arrows) and putative floating 'garbage patches' (shaded areas) in the North Pacific Ocean.



Figure 3.2: Photograph of a dead Laysan albatross chick with plastic in its stomach



Figure 3.3: Example of geolocator attachment methods on Laysan albatross.

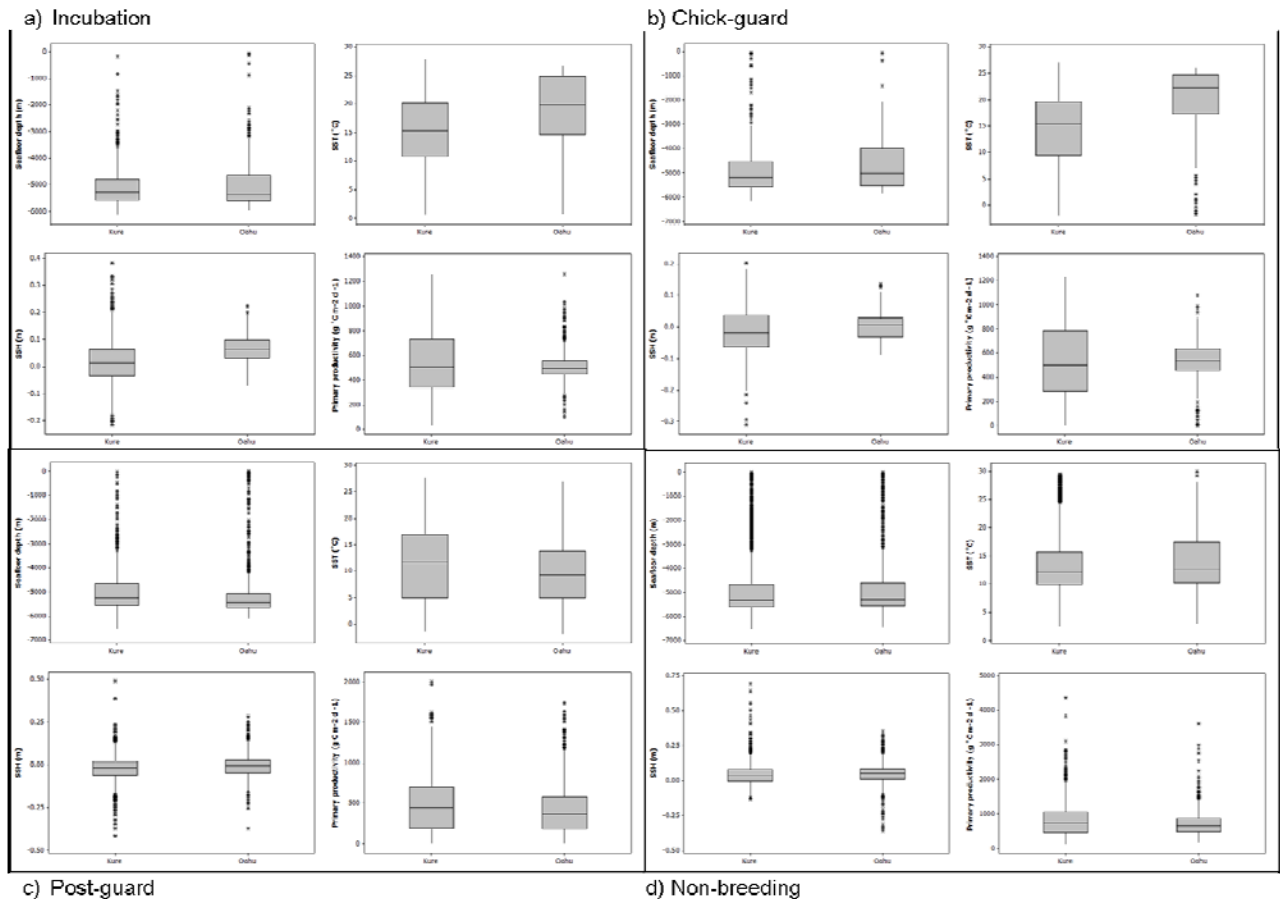


Figure 3.4: Mean oceanographic parameter values for Kure and Oahu populations of Laysan albatross. Boxplots of bathymetry, SST, SSH, and primary productivity during each stage of the breeding season a) Incubation, b) Chick-guard, c) Post-guard and d) Non-breeding seasons.

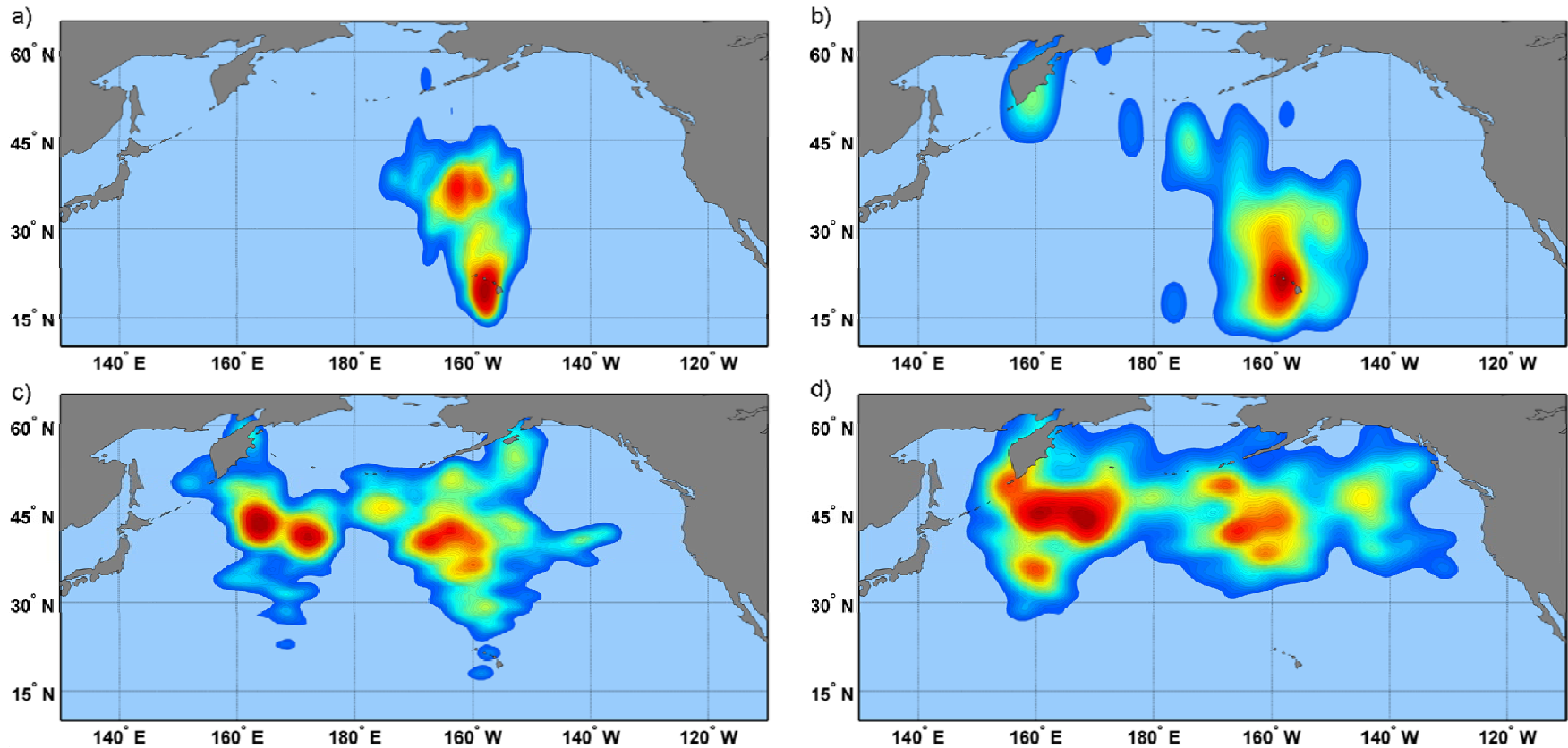


Figure 3.5: Utilization distribution kernels (2% increments from 2%-95% kernel density estimates) for Laysan albatross foraging from Oahu during the a) incubation b) chick guard c) post-guard and d) non-breeding stages. Increasingly warmer tones represent the highest utilization distribution (2%).

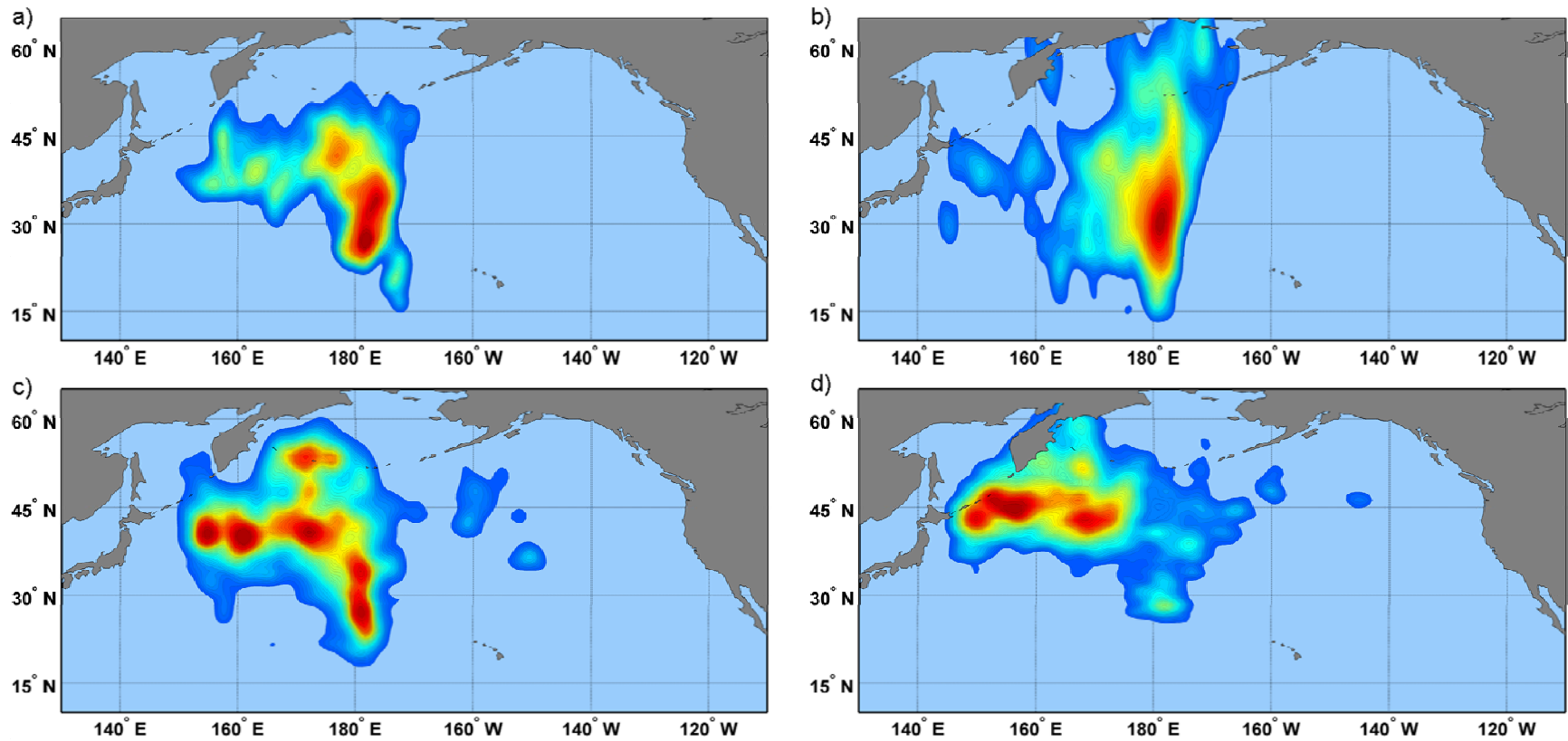


Figure 3.6: Utilization distribution kernels (2% increments from 2%-95% kernel density estimates) for Laysan albatross foraging from Kure during the a) incubation b) chick guard c) post-guard and d) non-breeding stages. Increasingly warmer tones represent the highest utilization distribution (2%).



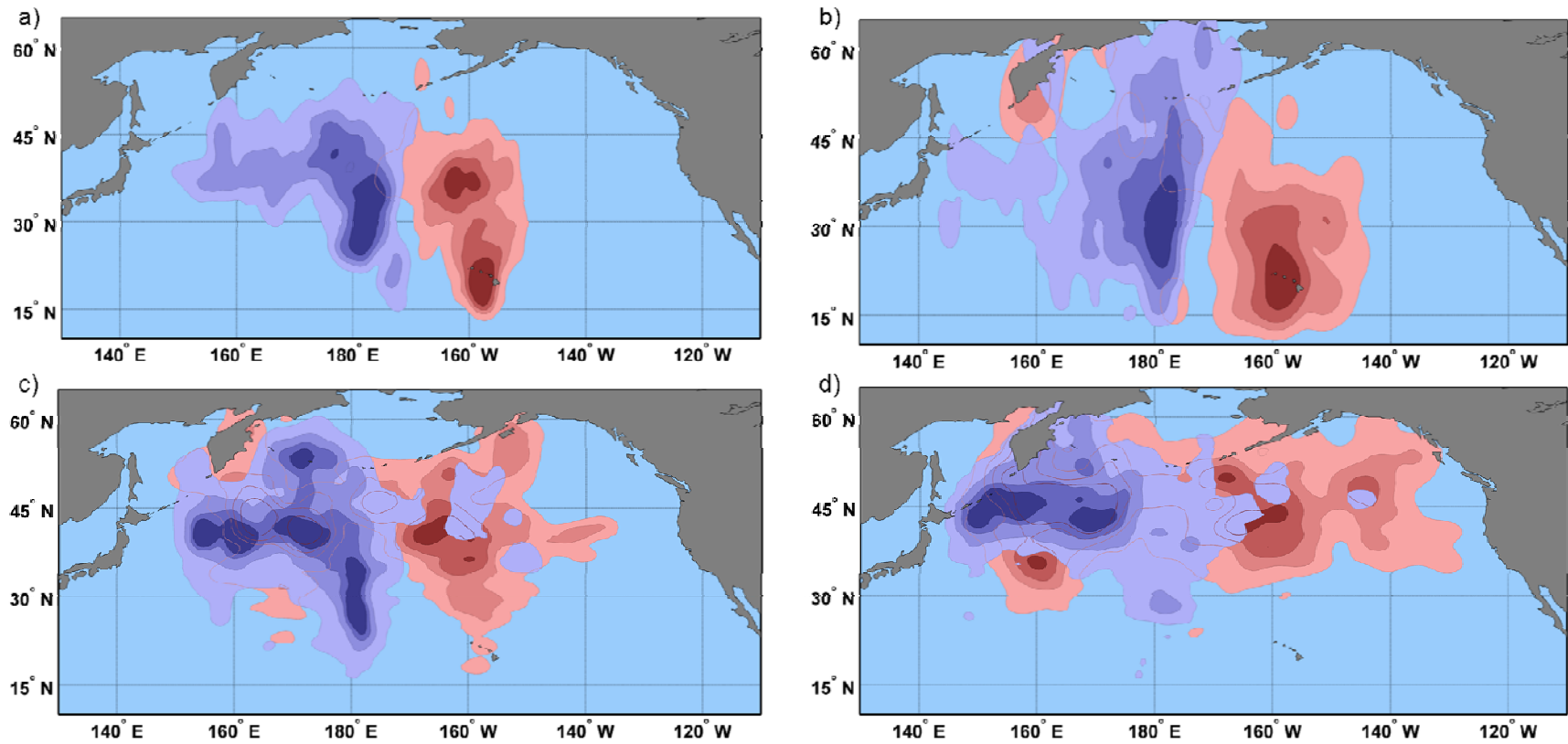


Figure 3.7: Overlap of kernel density estimates (95%, 75%, 50%, and 25%) for Laysan albatross foraging from Kure (blue) vs Oahu (red) during the a) incubation b) chick guard c) post-guard and d) non-breeding stages.

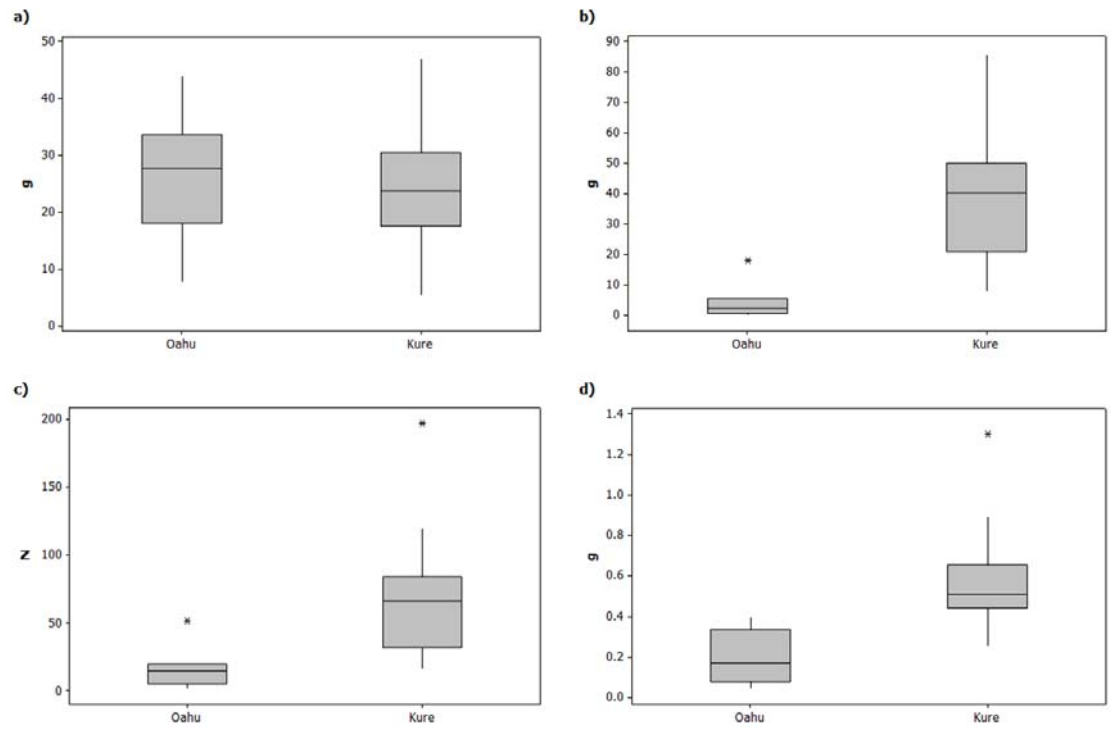


Figure 3.8. Boxplots of a) natural food mass, b) plastic mass, c) # plastic pieces and d) average plastic piece mass from Laysan albatross boluses on Kure and Oahu.

CHAPTER 4  
COLONIZATION HISTORY AND POPULATION GENETICS OF LAYSAN  
ALBATROSS

## ABSTRACT

Identifying biological trends and threats to organisms that make long distance migrations are often the limiting factor in their conservation. Indeed, Laysan Albatross are highly vagile seabirds, foraging throughout the North Pacific Ocean. Despite mark-recapture data indicating natal philopatry, Laysan Albatross have re-colonized several anthropogenically extirpated breeding locations in recent decades. During the same interval, a breeding population in the Northwestern Hawaiian Islands was lost to erosion and it was hypothesized that the colonization events were due to displacement rather than dispersal. Both nuclear and mitochondrial markers were used to test whether natal philopatry corresponded to population structure in Laysan Albatross, and to determine whether recent colonization events were a result of displacement from vanishing breeding habitat. Microsatellite data from five loci indicated weak but significant population structure ( $F_{ST} = 0.01$ ,  $P = 0.001$ ), and mitochondrial control region sequences revealed moderate population structure ( $\Phi_{ST} = 0.05$ ,  $P < 0.001$ ). The results were consistent with male-mediated dispersal and strong, but not absolute, philopatry by females. Mixed stock analyses of the newly-colonized sites indicated contributions from multiple source populations, which contradicted the displacement hypothesis of a single source population and instead supported species-wide dispersal. High genetic diversity ( $\pi = 0.045$ ,  $h = 0.989$ ), rapid colonization, and great dispersal potential bode well for the conservation of Laysan Albatross. However, it may be necessary to protect high-island nesting sites, preserve genetic diversity and maintain breeding populations in the face of projected sea level rises.

## INTRODUCTION

Identifying biological trends and potential threats to organisms that make long distance migrations are often the limiting factor in the conservation of marine animals (Aulsebrook 2000). For example, Laysan Albatross (*Phoebastria immutabilis*) bycatch during North Pacific longlining operations impacts breeding colonies thousands of miles away from foraging grounds (Gilman and Freifeld 2002). The high vagility and remote breeding sites of seabirds has made it difficult to draw the links between anthropogenic activities, and even oceanographic changes, and population trends. In many other taxa, dispersal capability and geographic isolation are often used to form *a priori* hypotheses concerning genetic diversity and variation between and within populations (Bohonak 1999). However, seabirds are not typically limited by barriers to dispersal, as demonstrated through mark-recapture studies, and satellite telemetry (Fisher 1976, Weimerskirch et al. 1985, Jouventin and Weimerskirch 1990, Schjorring 2002). Laysan Albatross fall on the extreme end of this spectrum; they are highly vagile seabirds characterized by an almost entirely pelagic existence (Whittow 1993, Hyrenbach et al. 2002, Shaffer et al. 2005). However, despite an inherently high dispersal potential, and an almost complete lack of dispersal barriers, mark-recapture studies of Laysan Albatross have shown them to be philopatric to their natal nest site (Fisher 1976). This observation has led to predictions of restricted gene flow that have been confirmed in other species of albatross (Abbott and Double 2003a, Alderman et al. 2005, Walsh and Edwards 2005, Bried et al. 2007).

Despite reports of high natal philopatry, in the 1970's Laysan Albatross began colonizing islands from Japan to Mexico and expanding their range beyond the Northwestern Hawaiian Islands (NWHI) where 97% of the species currently nest (Tickell 2000, Naughton et al. 2007). Many of these colonization events were

re-colonizations of anthropogenically extirpated breeding colonies such as those on Mukojima, Japan, Wake Island in the Western Pacific (Kurara 1978), and Kauai in the main Hawaiian Islands (Zeillemaker and Ralph 1977, Tickell 2000). Factors contributing to their historical declines included human consumption, feather collecting, egg collecting, predation from introduced mammals and military activities (Olsen and James 1982, Whittow 1993, Moniz-Nakamura 1999, Tickell 2000). In addition to the re-colonization of historical nesting sites, Laysan Albatross also recently expanded their breeding range to Isla Guadalupe, Clarion and San Benedicto off of Mexico in the East Pacific (Gallo-Reynoso and Figueroa-Carranza 1996, Pitman et al. 2004; Figure 4.1). These colonization events all occurred within the past 20-32 years (<2 albatross generations) and include <400 breeding pairs at each site. The few birds breeding in these new colonies that were banded elsewhere as chicks (<20 individuals/colony) have been almost exclusively from French Frigate Shoals in the NWHI (LCY and B. Zaun unpub data). This site lost an important nesting area, Whale-Skate Island, in the El-Nino event of 1997 after more than 30 years of erosion and displaced hundreds breeding pairs of Laysan Albatross (B. Flint pers comm). As a result of the loss of breeding habitat that coincided with the range expansion and re-colonization events, it has been hypothesized that displacement was in fact responsible for the appearance of these new Laysan Albatross colonies, rather than a low level of natural dispersal that went undetected in mark-recapture studies.

Here I employ both nuclear DNA microsatellites and mitochondrial DNA sequences in a range-wide survey of Laysan albatross rookeries to test whether the natal philopatry documented in mark-recapture studies is reflected in population structure in this species. If population structure is present, and provides sufficient power, the utility of mixed stock analyses in assigning colonizers back to their

colony of origin will be tested. If recent colonization events can be attributed to a single colony's displacement, then the new nesting sites should have a relatively uniform genetic composition in mixed stock analyses. Alternately, if the new nesting sites have multiple origins, this should be apparent in mixed stock analyses as indicated by contributions from multiple source colonies. The Laysan Albatross is listed as vulnerable by the International Union for the Conservation of Nature (IUCN 2007) as a result of recent population fluctuations and the high rates of at-sea mortality as bycatch in North Pacific Fisheries. By resolving the range-wide population structure, and the source(s) of immigrants that have colonized sites throughout the Pacific, I hope to provide a stronger scientific foundation for identification of management units and conservation priorities.

## METHODS

### *Study Sites*

Blood samples were collected from chicks representing the entire extant range of Laysan Albatross. Feathers were collected from Japan, and tissue biopsies were collected from dead animals from Pearl and Hermes Reef and Laysan Island in lieu of blood. Sampling locations, number of samples, and classification of each colony (source, or NWHI vs. new) are documented in Figure 4.1. French frigate shoals, the atoll where a breeding colony disappeared, is represented by Tern Island in this study which is the next closest islet in the atoll.

### *Sample storage and DNA extraction*

Blood stored in Queen's Lysis buffer (Seutin et al. 1991), tissue from freshly dead animals stored in 95% ethanol, and feathers were all kept at -80°C. DNA was extracted from tissue using QIAGEN® DNeasy™ extraction kits

following the manufacturer's protocols and modified during the final two steps for a final elution volume of 175  $\mu\text{L}$  in  $\text{H}_2\text{O}$ . DNA from blood was isolated using ID Labs IDetect<sup>tm</sup> DNA purification kit for whole animal blood following manufacturer's protocols and eluted in 50 $\mu\text{L}$  of  $\text{H}_2\text{O}$ . Final DNA concentrations from both kits ranged from 40ng/  $\mu\text{l}$  – 200 ng/  $\mu\text{l}$ .

#### *Microsatellite amplification and genotyping*

Thirty six microsatellite loci were screened from libraries developed for various albatross species by Burg (1999), Abbott and Double (2003a) and Dubois et al. (2005). Of these 36 loci, only six successfully amplified *P. immutabilis*, one of which was monomorphic and was excluded, leaving five suitable loci (Table 4.1). Amplifications were performed with a PTC-200 MJ Peltier thermalcycler, and PCR temperature profile consisted of denaturation at 94°C for 10 min, then 35 cycles at 94°C for 30 s, annealing at 65°C for 40 s and 72°C for 1 min, followed by a final extension phase at 72°C for 10 min. Reactions were 11  $\mu\text{l}$  total volume containing: 1  $\mu\text{l}$  40-100 ng/  $\mu\text{l}$  genomic DNA, 1.1  $\mu\text{l}$  10x  $\text{NH}_4$  PCR buffer, 0.17  $\mu\text{l}$  50 mM BSA, 0.44  $\mu\text{l}$  50 mM  $\text{MgCl}_2$ , 0.11  $\mu\text{l}$  each of 2 mM dNTP, 0.2  $\mu\text{l}$  each of 10 mM forward and reverse primers and 0.1  $\mu\text{l}$  of 5 U/  $\mu\text{l}$  Taq. Loci were multiplexed on an ABI 3730 XL automated sequencer with one primer of each primer pair fluorescently labeled. Each set of PCR reactions were performed with one positive and one negative control to check for amplification and contamination problems respectively.

#### *Microsatellite analysis*

All loci were scored independently at least twice with GENEMAPPER (Applied Biosystems) and were tested for departures from Hardy Weinberg



equilibrium, linkage disequilibrium, and null alleles in GENEPOP 3.1b (Raymond and Rousset 1997) and CERVUS 2.0 (Marshall *et al.* 1998); no locus showed significant deviations from the above assumptions. A p-level of 0.05 was used in conjunction with a molecular analysis of variance (AMOVA) to determine population structure (F statistics) for microsatellites using ARLEQUIN version 3.0 (Excoffier *et al.* 2005). A Bayesian maximum likelihood analysis using STRUCTURE version 2.0 (Pritchard *et al.* 2000, Pritchard and Wen 2004) was performed to determine the number of effective populations. The results generated were based on running a series of independent simulations from one to five inferred populations (only source populations were included in this analysis). Each run used an admixture model with correlated allele frequencies, no prior population information,  $3 \times 10^6$  iterations after a burn-in of  $2 \times 10^5$  iterations. The program was run independently 10 times for each number of populations ( $K$ ) between one and five to test for convergence of the Markov chain Monte Carlo (MCMC).

#### *mtDNA amplification and sequencing*

Oligonucleotide primers Spec 1 (5'-CAGCTTATGTATAAATGCG-3') and Glu 7 (5'-CGGGTTGCTGATTTCTCG-3') initially developed for the vertebrate mitochondrial DNA (mtDNA) control region of *Thalassarche* albatross species (Abbott and Double 2003b) were used to amplify 189 bp of the control region of *P. immutabilis*. PCR reactions were 25 $\mu$ L in volume and were amplified with 1  $\mu$ L 40-100 ng/ $\mu$ L genomic DNA, 1.5  $\mu$ L 10x NH<sub>4</sub> PCR buffer, 0.17  $\mu$ L 50 mM BSA, 1.5  $\mu$ L 50 mM MgCl<sub>2</sub>, 0.375  $\mu$ L each of 2 mM dNTP, 0.75  $\mu$ L each of 10 mM forward and reverse primers and 0.2  $\mu$ L of 5 U/ $\mu$ L Taq DNA polymerase (Invitrogen). Amplifications were performed with a PTC-200 MJ Peltier thermal

cycler (MJ Research), and PCR temperature profile consisted of denaturation at 94°C for 10 min, then 35 cycles at 94°C for 30 s, annealing at 64.3°C for 40 s and 72°C for 1 min, followed by a final extension phase at 72°C for 4 min. Five microlitres of the PCR product was then added to 1 U of ExoSAP-IT® kit (USB Corporation, Cleveland, OH, USA) and incubated for 15 min at 37°C followed by 15 min at 80°C in order to purify PCR products. Products were sequenced at the Greenwood Core Facility at the University of Hawaii at Manoa in both forward and reverse directions using an Applied Biosystems 377XL DNA Sequencer.

### *Sequence analysis*

Sequences were manually edited using Sequencher 4.7 (Gene Codes Corporation). The problem of including inadvertently sequenced nuclear copies of mitochondrial genes (NUMTs; Sorenson and Quinn 1998) or of nuclear heteroplasmy (Abbott et al. 2005) was reduced in this study by using primers developed to minimize amplification of nuclear material (Abbott et al. 2005), comparing both forward and reverse sequences, and checking for the presence of double peaks characteristic of NUMTs. No duplication or heteroplasmy were detected. Within each population, genetic diversity was estimated in DNAsp version 4.20 (Rozas et al. 2003) using the nucleotide diversity index  $\pi$  (Nei, 1987, equation 10.5) as well as Tajimas D and Fu's F to test for demographic changes. Genetic differentiation between populations was quantified using the  $\Phi_{ST}$  statistic computed from both haplotype frequencies and the number of mutations between the haplotypes using the program ARLEQUIN (Excoffier et al. 2005) with 1000 MCMC simulations to determine statistical significance. An AMOVA was also done in ARLEQUIN that uses both the frequency and sequence divergence between haplotypes to estimate the extent of genetic differentiation between

populations. A minimum spanning network of haplotypes with a 95% confidence limit was constructed in TCS 1.21 (Clement et al. 2000) for source populations with at least two individuals sharing a haplotype to assess the un-rooted haplotype genealogy inferred from the mtDNA sequence data.

Program MIGRATE version 1.7.6 (Beerli 1997) was used to estimate maximum-likelihood migration rates from the five source colonies into all other colonies with mtDNA sequences. This approach, based on coalescence using MCMC searches, is advantageous over conventional  $F_{ST}$ -based approaches in that it accounts for unequal effective population sizes and asymmetrical gene flow (Beerli and Felsenstein 1999, 2001, Whitlock and McCauley 1999) both of which are likely occurring in newly colonized sites in this data set. The default settings of migrate were used with the exception of changes made to the number of short and long Markov chains and the number of trees sampled which were increased (20 short chains sampling 10 000 trees and five long chains sampling 100 000 trees, following an initial 'burn-in' period of 10 000 trees). A Mantel tests comparing gene flow estimates based on coalescent and  $F_{ST}$ -based approaches were run using MANTEL ver.32 (<http://life.bio.sunysb.edu/morph/>) and a 2-sample t-test was done in Minitab to compare the average number of migrants for both source and newly established colonies.

To estimate the proportional contribution of each established source colony in the NWHI to each new colony, a MCMC mixed stock analysis using the program BAYES was performed (<ftp://ftp.afsc.noaa.gov/sida/mixture-analysis/Bayes/>; Pella and Masuda 2001) following protocols for sequence data from Reece et al. (2006). Estimated source colony contributions to new colonies were calculated based on 469-6640 resamplings (as determined by BAYES for each population) of one stock mixture expected to recruit individuals from either

source colony along with their standard deviations. Bayesian mixed stock analyses used equal contributions from source populations as an initial (prior) distribution. A linear regression was used to test whether Bayesian estimated contributions from each source colony to each new colony depended on source colony population size or distance from the colonization site.

## RESULTS

### *Genetic diversity and neutrality*

The control region of the mitochondria produced 188 haplotypes in 358 individuals with several ancestral shared haplotypes that differed in frequency between source populations (Figure 4.2), but many that were also unique to a single population (Table 4.2, Appendix 1). The haplotype network constructed using a statistical parsimony approach (Figure 4.2) revealed multiple shared haplotypes among populations and no distinct clades among source populations. Both haplotype and nucleotide diversity were high for all populations (Table 4.2). Microsatellite loci showed moderate allele numbers from four-11 alleles per locus, and had observed heterozygosity values ranging from  $H_o = 0.188 - 0.859$  (Table 4.1). All loci were in Hardy Weinberg equilibrium and did not show signs of linkage disequilibrium or null alleles. However, since the presence of new colonies confirms gene flow it should be noted that new colonies are by definition not in Hardy Weinberg equilibrium (HWE) due to migration and could be experiencing genetic drift due to small founding population sizes.

### *Population growth*

While no Tajima's D or Fu's F values were significant (Table 4.2), their overall negative values, particularly the high Fu's F, were consistent with models

of population expansion. A graph of the mismatch distribution (Figure 4.3) produced a smooth and unimodal curve that also fit the predicted model of population expansion.

#### *Structure of all populations*

The overall genetic partitioning with microsatellite data was  $F_{ST} = 0.01$  ( $P < 0.01$ ), and the overall value for mitochondrial data was  $\Phi_{ST} = 0.05$  ( $P < 0.0001$ ). Pairwise population  $F_{ST}$  and  $\Phi_{ST}$  values were calculated for all populations with microsatellites and mtDNA respectively (Table 4.3).

Pairwise comparisons in microsatellite data produced only one significant comparison between source colonies (Tern and Laysan), but the low  $F_{ST}$  value (0.002) suggests high current gene flow (Hedrick 1999). Between new colonies and source colonies, most showed significant structure between Kure, Midway, Pearl and Hermes and Laysan Island. However, all  $F_{ST}$  values were  $< 0.02$  which still indicates some level of gene flow (Hedrick 1999). Within new colonies, there was virtually no structure indicating high levels of gene flow. STRUCTURE analysis of genotypes from source populations identified only one inferred population ( $K = 1$ ) indicating little population subdivision in microsatellite markers for this species.

In contrast, pairwise comparisons in mitochondrial data produced statistically significant population structure between source populations, particularly between Midway Atoll and all other colonies ( $\Phi_{ST} = 0.06-0.18$ ). There was also significant structure between Tern and Laysan Island among source populations ( $\Phi_{ST} = 0.04$ ). Between new colonies and source colonies, Midway was again distinct in every comparison ( $\Phi_{ST} = 0.11-0.24$ ), and structure was found

between Lehua and Mexico, and Kure Atoll and Tern Island ( $\Phi_{ST} = 0.02-0.05$ ).

There were no significant comparisons between any of the new colonies.

#### *Migration and source populations*

Estimates of gene flow from a  $\Phi_{ST}$  approach showed no correlation with those derived from a coalescent based approach in MIGRATE (Mantel  $r^2 = 0.220$ ;  $P = 0.73$ ). Moreover, 12/15 pairwise comparisons that showed significant population structure in mtDNA  $\Phi_{ST}$  had  $>4$  migrants per generation (Tables 3 and 4) indicative of high levels of gene flow using the coalescent approach. New populations did not have significantly more migrants per generation ( $486 \pm 58$ ) than source populations ( $394 \pm 122$ ,  $P = 0.526$ ). Japan was the only population to show low levels of gene flow ( $<1$  migrant/generation from 4/5 source populations) which is consistent with lack of population growth that has been observed in the colony since its inception in 1976 (Tomohiro Deguchi, pers. comm.).

Bayesian mixed stock analyses indicated that new colonies were genetically diverse assemblages comprised of individuals from multiple source colonies in the NWHI. This was also confirmed in the coalescent analysis with high number of migrants coming from each source colony into each new colony. Primary contributions differed to some degree in each colony, with the exception of Midway Atoll which showed low contributions to all new colonies (3 – 15%; Table 4.5) despite hosting about 72% of the world's breeding population of Laysan Albatross (Naughton et al. 2007). These results are consistent with the high genetic structure that was found in pairwise comparisons between Midway Atoll and all other colonies. Contributions from all other colonies (5 – 51%; Table 4.5) had overlapping standard errors, but indicate that most source colonies contribute to most new colonies and thus rejecting the displacement hypothesis of

single source colony contribution. The estimated contributions from each source colony to each new colony did not show a significant regression on either distance or source colony size (Table 4.6) indicating that source colony size and distance were not accurate predictors of new colony contribution. Based on the mixed stock analysis, all colonies have low rates of emigration rather than a single colony having a high rate of emigration.

## DISCUSSION

The goals of this study were to test hypotheses about the effects of natal philopatry on population structure and to determine whether colonization events could be attributed to dispersal or displacement in Laysan Albatross. The results indicate that despite a lack of barriers to dispersal, and high vagility, high natal philopatry appears to lead to population structure in Laysan Albatross. However, unlike the strong population genetic signatures that have been documented in other Albatross species (Abbott and Double 2003a, Alderman et al. 2005, Bried et al. 2007) or the lack of population structure found in others (Abbott and Double 2003b, Burg and Croxall 2004, Huyvaert and Parker 2006) the Laysan Albatross has modest population structure apparently driven by female philopatry. Contributions from multiple source colonies to newly colonized sites were contrary to the expectation of a displacement hypothesis of single source colony contribution. Instead, these data indicate low levels of dispersal from all colonies as the source of colonization events.

The high haplotype and nucleotide diversities observed in this study indicate that the control region may be useful as a genetic monitoring tool in documenting changes in Laysan Albatross populations and corresponding genetic diversity. The levels of both haplotype and nucleotide diversity in *P. immutabilis*

populations were higher than in many other avian taxa (Awise and Walker 1998, Qu et al. 2005) but were consistent with that found in other species of albatross (Burg and Croxall 2001, Abbott and Double 2003a, Alderman et al. 2005, Walsh and Edwards 2005) despite several albatross species having low nuclear diversity (Milot et al. 2007). The high number of haplotypes was also consistent with population expansion, which often enhances the retention of novel mutations and creates an excess of haplotypes differing by one or a few mutations (Watterson 1984, Slatkin and Hudson 1991, Rogers and Harpending 1992). The unimodal observed mismatch distribution (Figure 4.3) also fit closely with the model of population expansion (Rogers and Harpending 1992, Avise 2000). However, accurate population estimates from pre and post harvesting periods are not available, and so it is possible that the population reduction did not in fact create a genetic bottleneck. Indeed, the number of differences in the mismatch distribution is more indicative of earlier population expansion (prior to human contact) rather than a recent one which suggests that much of the observed genetic diversity and patterns of expansion are a result of many generations of population expansion in addition to the recently observed range expansion.

The pattern of genetic structuring among Laysan Albatross colonies likely reflects both historical and contemporary gene flow. The mtDNA analysis demonstrated modest but significant populations structure ( $\Phi_{ST} = 0.05$ ). Midway Atoll proved to be distinct in every pairwise combination, and the high  $\Phi_{ST}$  values from these comparisons (0.06—0.24) would also serve to influence the overall mitochondrial structure despite weak  $\Phi_{ST}$  values in most other pairwise comparisons, which is also evident in the haplotype network (Figure 4.2). The observed structure is likely a combination of historical population subdivision (since contemporary gene flow is obviously occurring).



In contrast, there was only weak differentiation between populations in terms of allele frequencies at microsatellite loci, particularly among source populations. This discrepancy between the markers is likely a result of their ability to detect structure on different time scales as well as differences in migration rates between the sexes. The greater mtDNA structure found in this study is indicative of female natal philopatry and male mediated dispersal. Sex-biased dispersal is a common pattern observed in many other avian species (Dobson 1982, Clark et al. 1997, Newton 2003). Notably, the adult sex ratio in the new colony on Oahu, Hawaii is significantly female biased as a result of greater female immigration (Young et al. 2008). While these results may initially appear to be contradictory, several females from Kauai have been observed to mate with males on Oahu, and then return to Kauai (LCY per obs). Hence the male mediated gene flow does not require males to disperse, if females are highly vagile yet philopatric (see Bowen et al. 2005).

With respect to contemporary gene flow, which is represented better by microsatellites in this study, there are multiple examples on Kauai and Oahu of fledglings that relocate from their natal colony and subsequently breed at the new colonies (LCY and B. Zaun unpub data). On Oahu approximately 10% of nesters are from Kauai (LCY unpub data) which is contrary to previous studies finding virtually no inter-island natal dispersal in this species (Fisher 1976). There is also evidence of movements by adults between colonies. For example, approximately fifteen percent of all adults resighted on Oahu each year were banded elsewhere; the majority (66%) from the next closest colony on Kauai (137 km), but some from as far away as Midway Atoll (2052 km). Contemporary observations of the rapid increase in population size following the founding in these two colonies

suggest a large contribution by immigrants, rather than growth via self-recruitment (see Birt-Friesen et al. 1992, Austin et al. 1994).

The degree of genetic differentiation among populations can be greatly influenced by the age structure of the populations themselves (Whitlock 1992). In the case of Laysan Albatross, where newly colonized, as well as old populations exist, the founding events represent a potential source of genetic drift that would serve to differentiate the populations (Whitlock and McCauley 1990). While pairwise comparisons between new colonies were presented, it should be noted that newly colonized sites have population structure that likely reflects the source and number of founding individuals (Giles and Goudet 1997) rather than true population genetic separations since not enough time has passed for genetic changes to accumulate at these sites. Moreover, new colonies reflect populations that severely violate the assumptions of HWE since migration, and likely drift, are occurring, and as such, using these comparisons to infer gene flow should be done with caution. As these colonies mature and generations pass,  $F_{ST}$  values are likely to change over time as mutations accumulate and alleles become fixed. Giles and Goudet (1997) found that populations of different age classes as a result of population turnover that are connected by gene flow, will be more differentiated than populations that are equally demographically mature and at equilibrium between gene flow and genetic drift. They also found that the  $F_{ST}$  of young populations as well as old populations should be higher than that of intermediately aged populations due to founding events and decreased recruitment respectively both of which keep populations out of equilibrium. While there were not any populations that would represent an 'intermediate' age class in this study, the result of both young and old (source) colonies having population structure was confirmed.

The moderate population structure observed in Laysan Albatross is indicative of low level gene flow as demonstrated in the coalescent migration analysis, and the colonization events that occurred across the Pacific empirically confirm this. However, the presence of population structure between source colonies in mtDNA did allow for a mixed stock analysis to test the displacement hypothesis. The hypothesis that new colonies were comprised entirely of birds displaced from French Frigate Shoals (represented by Tern Island) was not supported by the mixed stock or the migration analyses, which instead revealed that new colonies were comprised of varying mixtures of birds from all source populations in the NWHI. While a certain proportion of the recruits in new colonies are likely displaced individuals from French Frigate Shoals, there are probably displaced birds that colonized closer sites in the NWHI as a result of conspecific attraction provided by existing breeding colonies which is a common phenomenon in colonial nesting birds (Wagner and Danchin 2003). The lack of correlation between source colony population size, or distance to the colonization site indicates that some other factor, perhaps nest site limitation or distance to foraging grounds, is responsible for the differences in source colony contribution to newly colonized sites.

Recent counts of Laysan Albatross at Midway, Laysan, and Tern Island in the NWHI, which account for ~93% of the global population, have reported growing numbers of breeding birds (Naughton et al. 2007) and the appearance of new colonies may be related to this growth. In the Wandering Albatross (*Diomedea exulans chionoptera*), juvenile dispersal is density dependent, leading to higher juvenile dispersal when the local population density is high (Inchausti and Weimerskirch 2002). If a similar mechanism were functioning in Laysan Albatross, then increases at new colonies may be driven by juveniles dispersing

from high density nesting colonies in the NWHI. Midway Atoll, however, contributed significantly fewer recruits to all new colonies despite its large size. While the exact reason for this is unknown, the abundant nesting habitat as well as the size of the colony, when compared to other source colonies, could serve to provide strong incentive for young birds to return as opposed to disperse.

Seabirds provide an interesting challenge when studying gene flow and population dynamics: many are highly philopatric, but also highly vagile which are two seemingly opposing forces when concerning gene flow. A review by Friesen et al. (2007) on mechanisms of population differentiation in seabirds found that two factors predicted most genetic and phylogeographic structure: non-breeding distribution and foraging range during the breeding season. Species that were year-round residents of their breeding colonies, or those that had population specific post breeding foraging ranges, had higher population structure than those that did not exhibit these characteristics. Laysan Albatross do not exhibit either of these characteristics and had low levels of population structure which is consistent with the hypothesis put forward by Friesen et al. (2007). The structure exhibited by Laysan Albatross is likely due to natal philopatry as has been demonstrated in the Galapagos petrel, *Pterodroma phaeopygia* (Friesen et al. 2006), Xantus's murrelet, *Synthliboramphus hypoleucus* (Friesen et al. 2007) and other seabird species. When choosing a suitable place to breed, often the best information a young bird has is that based on its own survival at the natal colony.

High genetic diversity, ability to rapidly colonize new locations and great dispersal potential bode well for the future of Laysan albatross and could explain this species success relative to other albatross species. However there are still a myriad of threats to Laysan albatross, from fisheries bycatch to global warming, that will likely increase in magnitude in the future. Consequently, it is important

to prioritize management actions aimed at preserving the genetic diversity and maintaining existing colonies. Due to its size and genetic isolation, Midway Atoll should be maintained as a distinct management unit. With the remaining colonies of Laysan albatross being genetically similar, efforts should be made to preserve colonies at the extreme edges of the range (Japan and Mexico) as well as colonies on high islands (Lehua, Kauai and Oahu) that could provide refugia in the event of future sea level rises (Baker et al. 2006). The research conducted here, in conjunction with mark-recapture studies, indicate that displaced birds and natural colonizers will find and use these refuges and that providing predator-free refuges on high islands in the Hawaiian archipelago could help mitigate potential habitat loss in the future.

Table 4.1: Characteristics of dinucleotide microsatellite loci. Size is the size in base pairs of smallest allele, Het(obs) is the observed proportion of heterozygotes, Het(exp) is the expected heterozygosity, and Null is the per locus possible frequency of null alleles.

Name	No. Alleles	Size	Het(obs)	Het(exp)	Null
11H7	11	189	0.859	0.822	-0.0277
12H8	4	164	0.364	0.403	0.0602
D9	4	81	0.188	0.181	-0.0253
D21	4	162	0.521	0.530	0.0032
Tc65	8	137	0.533	0.503	-0.0545

Table 4.2: Population genetics statistics for Laysan Albatross populations<sup>†</sup> throughout the Pacific.

	Kure	Midway	Pearl and Hermes	Laysan	Tern	Japan	Lehua	Kauai	Oahu	Mexico	Overall
# Sequences obtained	45	41	23	24	52	15	23	37	42	54	358
Total # Haplotypes	38	24	21	23	43	12	19	29	32	38	188
# Unique haplotypes	21	17	7	11	22	5	7	9	13	19	131
Haplotype diversity ( <i>h</i> )	0.986	0.851	0.992	0.996	0.988	0.971	0.984	0.986	0.986	0.983	0.989
Nucleotide diversity ( $\pi$ )	0.043	0.030	0.041	0.044	0.043	0.037	0.059	0.043	0.050	0.043	0.045
Theta	8.048	5.634	7.613	8.395	8.159	6.971	11.028	8.098	9.382	8.177	8.349
Tajimas D <sup>‡</sup>	0.120	0.015	-0.118	0.603	-0.100	-0.388	0.274	0.316	0.316	0.054	-0.732
Fu's F <sup>‡</sup>	-0.496	0.651	-12.580	0.494	-0.794	-3.308	-5.574	-0.124	0.100	-1.548	-264.852
# Individuals amplified with MS	46	49	29	26	49	16	27	45	75	53	417
# Microsatellite alleles	27	24	25	27	28	18	26	29	30	29	31

<sup>†</sup> Wake Island was not included in this table as with only two samples these statistics could not be calculated.

<sup>‡</sup> No Tajima's D and Fu's F statistics were significant at  $p \leq 0.05$

Table 4.3: Pairwise population†  $\Phi_{ST}$  values for mtDNA control region (above the diagonal) and  $F_{ST}$  values for microsatellites (below diagonal) of Laysan Albatross. Source populations are contained in the upper left box. \* $p < 0.05$ ; \*\* $p < 0.01$  denote statistically significant pairwise comparisons.

	Kure	Midway	Pearl and Hermes	Laysan	Tern	Japan	Lehua	Kauai	Oahu	Mexico
Kure	-	0.1084**	0.0327	0.0107	0.0188	0.0456	0.0537*	0.0248	0.022	0.0404**
Midway	0.0028	-	0.1540**	0.178**	0.0557**	0.1121**	0.1892**	0.1714**	0.1399**	0.1441**
Pearl and Hermes	0.0058	0.009	-	0.0154	0.0086	-0.1262	0.0106	0.0064	-0.0023	-0.0099
Laysan	-0.0004	-0.01	0.0113	-	0.035*	0.0359	-0.0019	0.0011	-0.0037	0.0096
Tern	-0.0016	0.0076	0.0175	0.002*	-	0.0045	0.0467**	0.018	0.0137	0.02*
Japan	0.0205	0.0246	0.0078*	0.0138**	0.0343	-	0.0407	0.04	0.0158	0.0016
Lehua	0.0242**	0.0262*	0.0064**	0.021*	0.0161	0.0005	-	0.0061	0.0044	0.019
Kauai	0.0141**	0.0125*	-0.0015*	0.0173**	0.0188	0.0104	0.0084	-	-0.0037	0.0044
Oahu	0.0109*	0.0133*	-0.0025**	0.0158**	0.0276	0.0016	0.0113*	-0.0018	-	0.00009
Mexico	0.0166**	0.0036	-0.0007	0.0045	0.0083	0.011	-0.0021	0.0035	0.0072	-

† Wake Island was not included in this table as with only two samples these statistics could not be calculated.

Table 4.4: Migration estimates from source populations (rows) into recipient populations† (columns) based on a coalescent approach using the computer program MIGRATE for mtDNA. The first value is the best estimate given by migrate, the second set of values in parentheses are the range representing the 95% confidence interval.

	Kure	Midway	Pearl and Hermes	Laysan	Tern	Japan	Lehua	Kauai	Oahu	Mexico
Kure	-	4.6 (4.0 - 7.5)	7.7 (4.5 - 11.5)	0.6 (0 - 6.2)	27.7 (17.8 - 47.1)	1.0 (0.4 - 1.7)	0.3 (0 - 4.5)	0.4 (0 - 2.2)	13.0 (7.3 - 22.2)	2.6 (2.0 - 3.8)
Midway	0.5 (0 - 1.1)	-	5.0 (2.1 - 11.7)	4.5 (0.8 - 9.8)	15.0 (10.6 - 18.5)	0.1 (0 - 0.4)	17.5 (10.0 - 24.8)	33 (22.3 - 41.1)	14.1 (6.0 - 18.4)	7.5 (6.4 - 9.5)
Pearl and Hermes	0.2 (0 - 1.2)	3.3 (2.1 - 4.6)	-	50.1 (34.9 - 63.1)	0.4 (0 - 1.1)	1.6 (1.3 - 2.1)	13.2 (8.9 - 18.6)	4.5 (2.5 - 9.4)	0.4 (0 - 1.0)	0.04 (0 - 0.1)
Laysan	6.2 (4.0 - 8.7)	0.2 (0 - 0.4)	0.1 (0 - 0.5)	-	0.9 (0 - 1.6)	0.4 (0.1 - 0.7)	3.7 (1.1 - 8.2)	1.4 (0.6 - 3.2)	2.6 (1.0 - 4.5)	2.7 (2.2 - 3.4)
Tern	17.4 (11.2 - 24.5)	3.5 (2.0 - 5.9)	4.5 (2.7 - 7.3)	22.8 (10.7 - 45.2)	-	0.1 (0 - 0.3)	3.7 (1.8 - 6.6)	6.8 (3.6 - 11.6)	0.9 (0.1 - 3.8)	26.0 (10.9 - 29.5)
Japan	19.5 (7.4 - 45.5)	1.3 (0.8 - 2.4)	7.6 (4.7 - 11.9)	3.7 (0 - 12.3)	4.2 (2.7-6.8)	-	14.0 (3.1 - 21.2)	5.5 (2.6 - 10.4)	2.6 (1.1 - 4.1)	1.5 (0 - 2.4)
Lehua	7.9 (7.2 - 14.6)	0.5 (0.2 - 1.1)	0.2 (0 - 0.9)	22.9 (10.7 - 42.5)	32.4 (23.2 - 46.2)	0.02 (0 - 0.3)	-	1.0 (0.1 - 3.6)	13.7 (9.5 - 18.2)	0.7 (0.4 - 1.1)
Kauai	0.4 (0 - 1.18)	2.9 (1.4 - 4.2)	8.5 (3.1 - 12.5)	15.3 (7.4 - 25.2)	11.9 (3.9 - 15.7)	0.2 (0.1 - 0.5)	23.7 (9.5 - 31.8)	-	8.1 (4.1 - 13.7)	0.5 (0.2 - 0.7)
Oahu	8.2 (5.3 - 10.5)	2.7 (1.3 - 3.9)	6.5 (3.5 - 10.0)	10.2 (4.5 - 25.7)	1.5 (0.8 - 2.3)	0.1 (0 - 0.4)	3.8 (1.6 - 7.1)	4.8 (2.2 - 8.0)	-	0.4 (0.2 - 0.6)
Mexico	19.0 (8.0 - 23.1)	3.9 (2.5 - 6.2)	9.9 (6.6 - 17.2)	24.6 (11.2 - 49.3)	13.2 (10.1 - 18.0)	0.1 (0 - 0.6)	35.7 (24.6 - 39.4)	13.4 (9.4 - 20.5)	3.0 (1.2 - 6.6)	-
Total	79.3	22.9	50	154.7	107.2	3.62	115.6	70.8	58.4	41.94

† Wake Island was not included in this table as with only two samples these statistics could not be calculated.



Table 4.5: Proportional contribution of source populations to newly colonized populations of Laysan Albatross spanning the Pacific based on results obtained in BAYES.

Source population	New colony		Lehua	SE	Kauai		SE	Oahu		SE	Mexico		SE	Wake	
	%	SE†			%	SE		%	SE		%	SE		%	SE
Kure	0.41	0.36	0.05	0.10	0.07	0.12	0.20	0.23	0.03	0.06	0.14	0.23			
Midway	0.07	0.15	0.04	0.10	0.03	0.07	0.03	0.06	0.02	0.05	0.18	0.28			
Pearl and Hermes	0.19	0.28	0.49	0.30	0.51	0.31	0.07	0.12	0.03	0.05	0.36	0.34			
Laysan	0.24	0.30	0.31	0.26	0.28	0.28	0.30	0.32	0.68	0.26	0.19	0.28			
Tern	0.09	0.15	0.10	0.10	0.12	0.15	0.40	0.30	0.25	0.25	0.14	0.22			

† SE is standard error

Table 4.6: Regression of proportional contribution of source populations to newly colonized populations of Laysan Albatross using source colony size and source colony distance as predictive variables using Minitab version 13.

New colony	R <sup>2</sup>	P
Japan	0.59	0.41
Lehua	0.18	0.83
Kauai	0.29	0.71
Oahu	0.80	0.20
Guadalupe	0.31	0.69
Wake	0.16	0.84

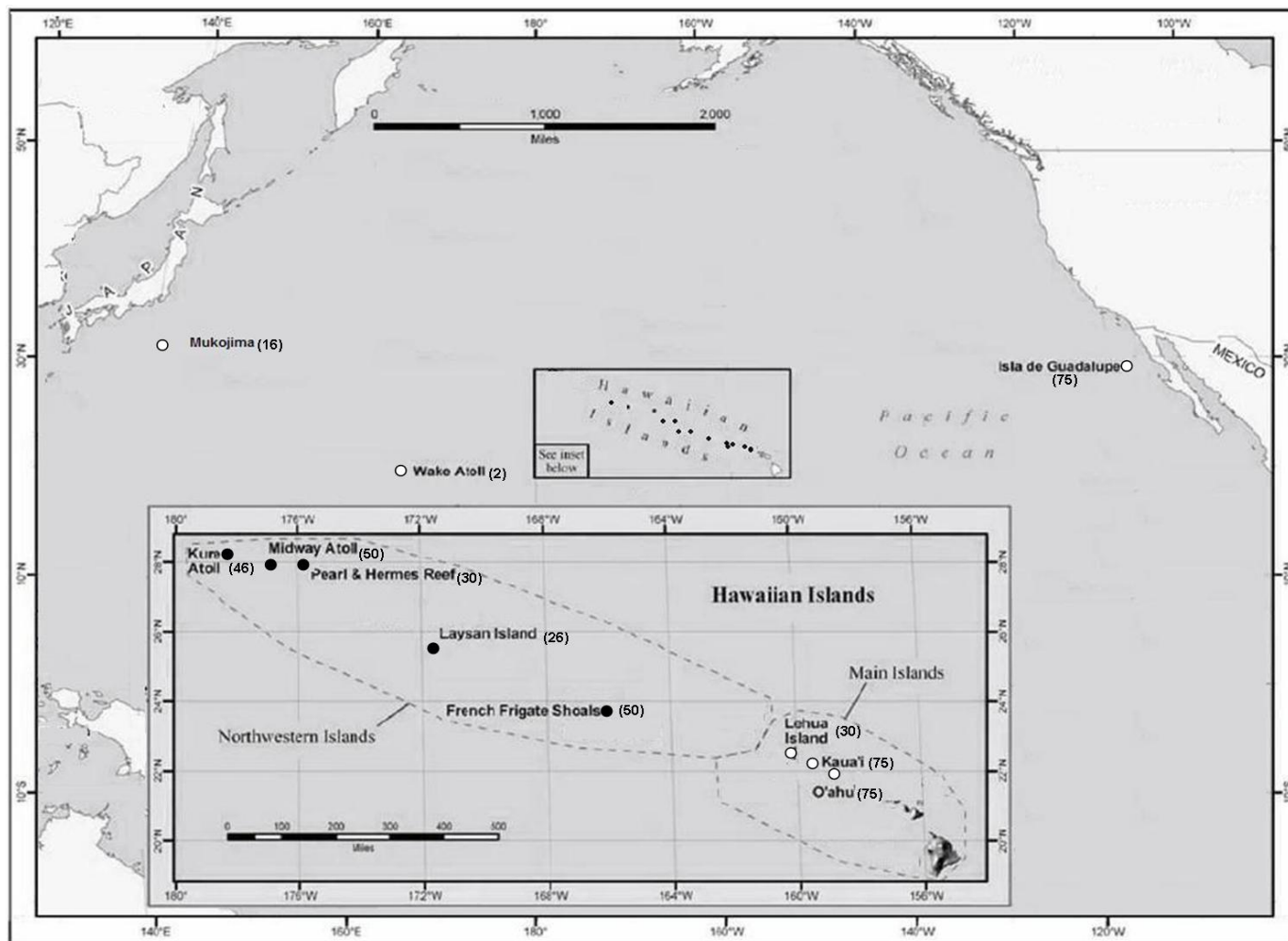


Figure 4.1: Sampling locations and number of samples (in brackets) collected from each Laysan Albatross colony. Closed circles denote source colonies, and open circles denote new colonies.

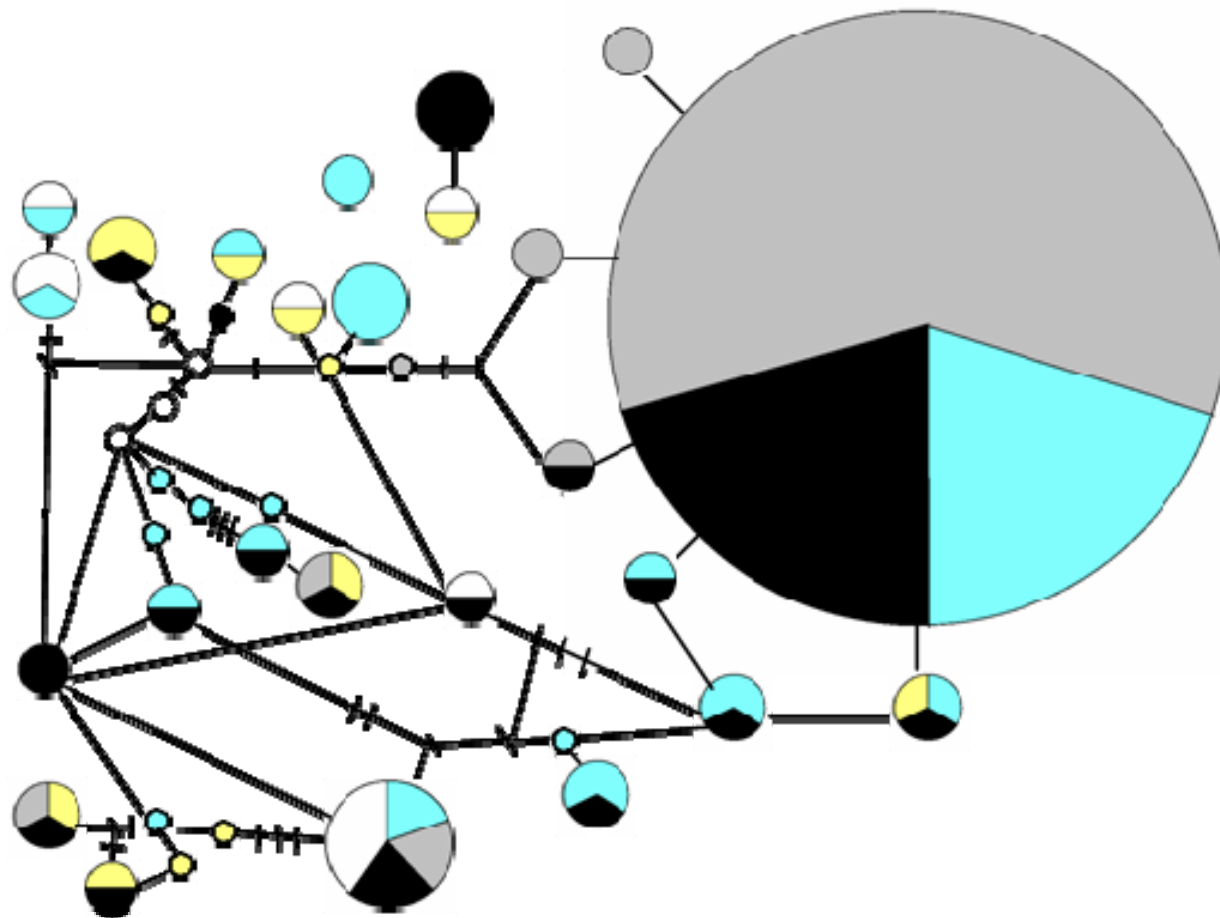


Figure 4.2: Statistical parsimony network of shared haplotypes from source populations of the mtDNA control region sequences for Laysan Albatross. The diameter of the circles is proportional to the number of individuals represented by that haplotype. Each branch represents a single base pair mutation and black dashes are hypothetical/unsampled haplotypes. Colours correspond to populations: black is Kure Atoll, grey is Midway Atoll, white is Pearl and Hermes reef, yellow is Laysan Island and blue is Tern Island.

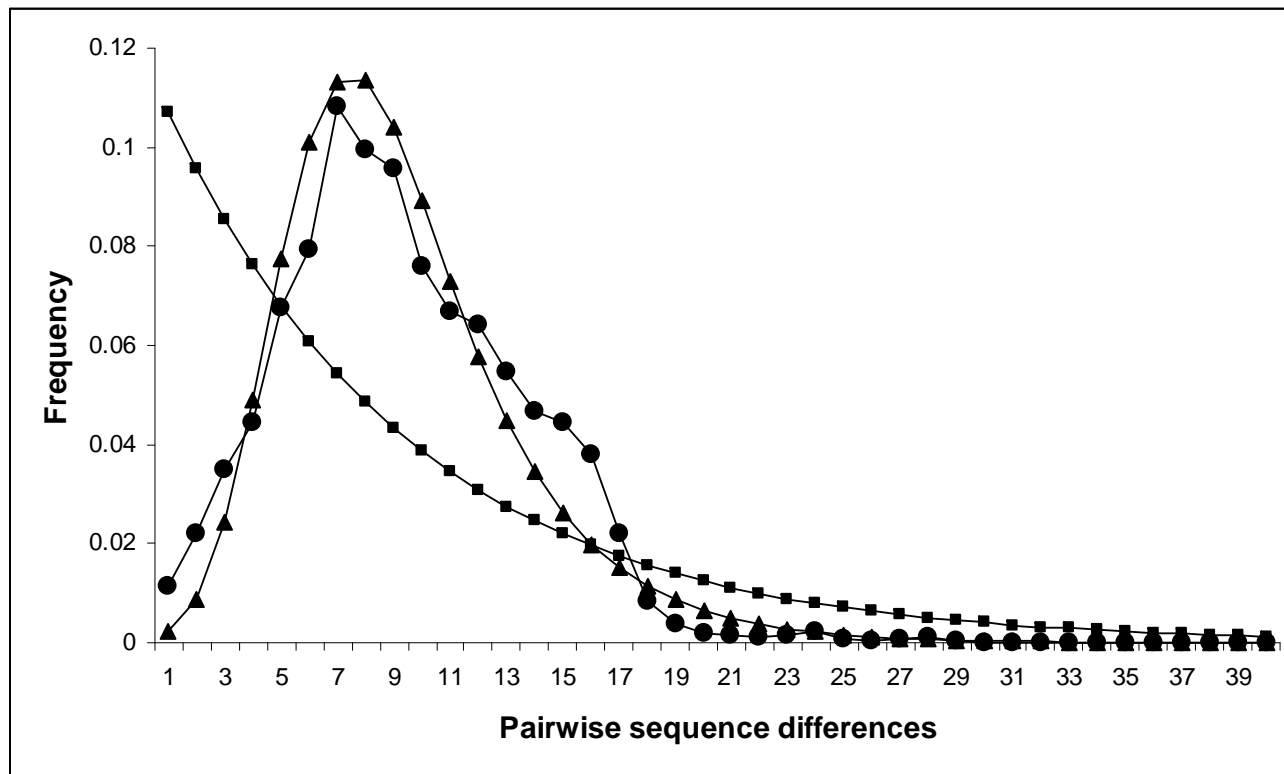


Figure 4.3: The observed mismatch distribution (circles) of all populations of the mtDNA control region sequences for Laysan Albatross compared to models expected under population growth (triangles) and constant population size (squares)

## CHAPTER 5

### DO DIFFERENCES IN FORAGING LEAD TO DIFFERENCE IN RISK OF FISHERIES BYCATCH IN LAYSAN ALBATROSS?

## ABSTRACT

Albatross species worldwide have been experiencing widespread declines attributed to incidental bycatch in commercial fisheries. As a result, estimating the risk of bycatch is important in determining conservation priorities. The objectives of this study were to determine the degree of overlap of the foraging ranges of Laysan albatross tracked at sea from Kure Atoll and Kaena Point, Oahu with commercial fishing effort, whether this overlap changes throughout their reproductive cycle and whether differences in colony overlap translate into actual bycatch differences by doing a genetic mixed stock analysis. Eighty five Laysan albatross breeding on Oahu and Kure Atoll, 2150 km away were tracked for two years using geolocators. Tracking data was integrated with data on fishing effort and distribution of commercial longline fisheries from 22 nations in the North Pacific targeting tuna (*Thunnus spp*) and other billfish. A mixed stock analysis was performed on genetic bycatch samples, but contributions could not be precisely resolved due to low statistical power. Tracking data indicated that birds from both colonies were most vulnerable to fisheries bycatch during the incubation periods when their core foraging areas overlapped completely with areas of highest fishing effort, and during the non-breeding season when areas of high fishing effort were found throughout their range. Since Laysan albatross have obligate bi-parental care, any adult mortality during the breeding period could extend to chicks which will not receive adequate amounts of food from a single parent. Birds from both colonies spent little time in US EEZ, but spent large amounts of time in the Kuroshio Extension east of Japan and the Kuril islands off of Russia where extensive pelagic longline fishing operations occur. As a result of the high risk of fisheries interactions occurring in international waters, conservation efforts should focus on ensuring that international fleets employ seabird mitigation measures.

## INTRODUCTION

Albatross species worldwide have been facing widespread population declines owing to incidental bycatch in commercial fisheries (Brothers et al. 1999, Gilman and Freifeld 2002, Butchart et al. 2004). Albatrosses as a family are particularly susceptible to bycatch due to their late maturity (5-8 years), low annual fecundity and high adult survivorship (Tickell 2000). As a result, factors that reduce adult survivorship, such as bycatch mortality, have disproportionately large effects on the viability of a population as they remove individuals in the population with the highest reproductive potential. While species-based conservation priorities are relatively well developed for many albatrosses, population-based management has received less attention due to uncertainty regarding the genetic differences between populations, and lack of knowledge of behavioral characteristics, such as differences in spatial and temporal movements between separate colonies. Therefore, if high fishing pressure occurs in key areas where, for example, the majority of a population aggregate for foraging purposes, there is a potential for population specific increased rates of bycatch.

The three species of albatross found in the North Pacific Ocean, Black-footed (*Phoebastria nigripes*), Laysan (*P. immutabilis*) and Short-tailed (*P. albatrus*) are all taken as bycatch in commercial fisheries (Gilman and Freifeld 2002). Veran et al. (2007) speculate that population level impacts of fisheries bycatch may already be occurring for Black-footed albatross, and similar factors may be affecting Laysan and Short-tailed albatross. From 1994-1999, combined annual mortality of Laysan and Black-footed albatross was approximately 990 birds in the demersal longline fishery in the Alaskan Exclusive Economic Zone (EEZ), and 2500 birds in the Hawaiian EEZ pelagic longline

fishery (National Marine Fisheries Service 2006a). Undocumented bycatch in pelagic longline fisheries occurring in international waters probably contributes thousands of both Laysan and Black-footed albatross to these totals (Cousins et al. 2000). Vessels from numerous nations operating in fisheries throughout the North Pacific are not required to employ seabird avoidance measures or carry observers on board, and as a result, it is difficult to assess the levels of bycatch and whether they have decreased over time. Fortunately, significant progress has been made in reducing seabird bycatch in longlining operations in North American waters as a result of government-led initiatives to implement bycatch avoidance measures (Melvin et al. 2001; Smith and Morgan 2005; National Marine Fisheries Service 2006a) and improved observer coverage.

Fisheries observers currently provide the majority of seabird bycatch estimates. Since observer coverage can range from none to complete for a fleet, estimates of global or even regional bycatch rates are variable at best. As a result, indirect methods of bycatch estimation, such as using the spatial overlap of albatross distributions with commercial fisheries as a proxy for potential bycatch risk, have developed (Fischer et al. 2009, Suryan et al. 2007). While these methods are not a substitute for a comprehensive observer program, information garnered from these techniques can serve to supplement observer data when available, or be used instead of when observer data are not available for a specific fishery or region. When spatial data are coupled with genetic assignment tests to determine the natal colony of animals already killed as bycatch, a more complete picture of the bycatch risk for each population can be obtained to determine if spatial patterns of overlap match bycatch patterns. Genetic assignment tests and mixed stock analyses has become a popular technique to determine the origin of other marine species



caught as bycatch (Manel et al. 2005) but has been slow to catch on in assigning provenance to seabirds killed as bycatch (Walsh and Edwards 2005, Abbott et al. 2006).

The objectives of this study are to determine whether the foraging ranges of widely separated colonies of Laysan albatross tracked at sea differ in their degree of overlap with commercial fishing effort, whether this overlap changes throughout their reproductive cycle and if differences in colony overlap translate into actual bycatch differences by doing a genetic mixed stock analysis on birds killed as bycatch. This is the first study to compare potential bycatch risk at the population level and how this risk varies spatially and temporally. By utilizing both at-sea tracking data and genetic data from birds killed as bycatch, we hope to identify specific periods in the reproductive cycle, locations and/or fisheries which would provide the highest conservation return from potential mitigation.

## METHODS

### *Genetic bycatch sample analysis*

Genetic samples (blood, tissue and/or feathers) were collected from chicks representing the entire extant range of Laysan albatross. Eighteen tissue samples were obtained from Laysan albatross killed as bycatch in high seas drift net squid fisheries from the collection of the Burke Museum (Table 5.1). Thirteen additional samples from birds killed as bycatch in the Hawaii longline fishery (2002-2004) were obtained from J. Bisson at the National Oceanic and Atmospheric Administration (NOAA) observer program.

DNA was extracted from tissue using QIAGEN® DNeasy™ extraction kits following the manufacturer's protocols and modified during the final two steps for a final elution volume of 175 uL in H<sub>2</sub>O. DNA from blood was isolated using ID Labs IDetect™ DNA purification kit for whole animal blood following manufacturers protocols and eluted in 50uL of H<sub>2</sub>O. Oligonucleotide primers Spec 1 (5'-CAGCTTATGTATAAATGCG-3°) and Glu 7 (5°-CGGGTTGCTGATTTCTCG-3°) initially developed for the vertebrate mitochondrial DNA (mtDNA) control region of *Thalassarche* albatross species (Abbott and Double 2003b) were used to amplify 189 bp of the control region of *P. immutabilis* following PCR protocols outlined in chapter 4.

Sequences were manually edited using Sequencher 4.7 (Gene Codes Corporation) by comparing both forward and reverse sequences, and checking for the presence of double peaks characteristic of nuclear duplication events. No duplication or heteroplasmy were detected. Genetic differentiation between populations was quantified using the  $\Phi_{ST}$  statistic computed from both haplotype frequencies and the number of mutations between the haplotypes using the program ARLEQUIN 3.1 (Excoffier et al. 2005) with 1000 MCMC simulations to determine statistical significance.

To estimate the proportional contribution of each established source colony in the NWHI to bycatch, a MCMC mixed stock analysis using the program BAYES 1.0 was performed (<ftp://ftp.afsc.noaa.gov/sida/mixture-analysis/Bayes/>; Pella and Masuda 2001) following protocols for sequence data from chapter Estimated source colony contributions to bycatch were calculated based on 2158 resamplings (as determined by BAYES) of bycatch samples expected to recruit individuals from each source colony

along with their standard deviations. Bayesian mixed stock analyses used equal contributions from source populations as an initial (prior) distribution.

#### *At-sea tracking of albatross*

We deployed leg mounted 9-g geolocation tags (model MK3 manufactured by British Antarctic Survey) on Laysan albatross breeding at two colonies: 28 tags on breeding birds on Oahu in the main Hawaiian Islands (21° 34'N, 158° 16'W), and 57 tags on breeding birds at Kure Atoll 2150 km away in the Northwestern Hawaiian Islands (28° 23'N, 178° 17'W; Figure 3.1). Geolocators were retrieved from January 2006 to June 2007, depending on when tagged birds returned to the colony. Downloaded data was decompressed using BASTrak v12 software (BAS) and light curves were analysed using Transedit software (BAS) using a sunrise angle of -2.5° for Oahu, and -3° for Kure. Any locations produced from light curves with interruptions or interference around the times of sunset or sunrise (usually as a result of shading of the sensor) were noted and excluded if obviously anomalous. Final position coordinates were generated by BirdTracker (British Antarctic Survey).

Matlab 8.0 (The MathWorks, Natick, Massachusetts) was used to filter positions and integrate environmental data following established protocols (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005). Given the inaccuracy of latitude estimation during equinoxes, location fixes on ten days of either side of the equinoxes were excluded (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005 and 2006). Three subsequent filters were applied to data once the equinoxes had been removed: one to filter out unrealistic flight speeds (sustained speeds >50km/hr over 12

hours) and distances (> 500km in 12 hours), a second to remove any remaining points occurring in locations where Laysan albatross have not been recorded previously (latitude and longitudes), and a third to remove any points that occurred over continental land masses (Wilson et al. 1992, Hill 1994, Phillips et al. 2004, Shaffer et al. 2005 and 2006). Of 14,281 locations produced, 72% ( $N = 10,314$ ) were kept after filtering. Detailed protocols of tag deployment and analyses can be found in chapter 3.

### *Fisheries data*

Monthly effort and catch statistics for tuna (*Thunnus* spp.), billfish (*Makaira* spp. and *Tetrapturus* spp.), and broad-bill swordfish (*Xiphias gladius*) fisheries in the North Pacific Ocean were obtained for 2005-2007 from the Oceanic Fisheries Programme of the Secretariat of the Pacific Community (SPC; <http://www.spc.int/oceanfish>). This compiled dataset will be referred to as ‘North Pacific pelagic longlining operations’ throughout the manuscript. These statistics are compiled from pelagic longlining vessels based out of 22 countries around the Pacific. Effort was spatially aggregated into 5° x 5° cells and was estimated based on the total hooks set across all catch species, and the number and weight caught of each species.

To assess the degree of spatial overlap at sea of albatrosses from each colony with fishing effort, we derived kernel density distribution estimates (Worton 1989) from unsmoothed (i.e. non-interpolated) locations using the Ikonos toolbox (Tremblay unpublished) developed in MatLab. This routine converted geographic coordinates to Cartesian coordinates using a Lambert Cylindrical Equal Area projection (Worton 1989) and created 2-D kernels based on an 80 km grid cell size. The kernel smoothing parameter ( $h$ ) was based on an adaptive method (Sheather and Jones 1991). We then

quantified the spatial overlap of the 95% (foraging range), 50% (focal region), and 25% (core area) kernel polygons representing the distribution of the albatrosses from each colony during each period in the reproductive cycle. We then determined for each colony the period in their reproductive cycle that had the highest overlap with fishing effort and the approximate locations where the overlap was occurring.

## RESULTS

### *Genetic source colonies of birds caught as bycatch*

The mtDNA control region sequences included 188 haplotypes in 358 source individuals with several ancestral shared haplotypes that differed in frequency between source populations, but many that were also unique to a single population (Table 5.2, Appendix 1). Detailed population genetic information on this species can be found in chapter 4. The overall genetic partitioning was  $\Phi_{ST} = 0.05$  ( $P < 0.0001$ ). The presence of genetic structure between source populations allowed for a mixed stock analysis to be performed.

Bayesian mixed stock analyses indicated that the bycatch mixture was a genetically diverse assemblage comprised of individuals from multiple source colonies in the Northwestern Hawaiian Islands (Table 5.2). Primary contributions differed to some degree in each colony, but had overlapping standard errors, indicating that estimating the precise contribution of each source colony to bycatch was not possible with this data set.

*Distribution of tracked albatrosses from Oahu and fisheries*

During the incubation phase, Laysan albatross tracked from Oahu foraged north of the colony in the area of the transition zone chlorophyll front (Polovina et al. 2001) and away from the continental shelf (Figure 5.1). Detailed descriptions of foraging patterns relative to oceanographic features from this data set can be found in chapter 4. During the incubation period (November-January), breeding birds had significant overlap with North Pacific pelagic longlining operations. The core foraging areas (25% and 50% kernel estimates) completely overlapped with the area of highest fishing effort and the majority of the distribution (95% contour) overlapped with moderate to high fishing effort. During incubation, the areas of highest overlap were found from 155°-160°W, 15°-25°N, and 160°-165°W, 30°-35°N which corresponded to the area of the transition zone chlorophyll front and the core foraging area of Laysan albatross from Oahu.

During the chick-guard stage (February), overlap was lowest of the entire reproductive cycle with only one area of high fishing effort overlapping significantly with the 95% distribution contour and the rest overlapping with areas of low fishing pressure. Despite this period having the lowest overlap with fisheries, a breeding female tracked as part of this study was caught as bycatch by a Taiwanese vessel approximately 1263 km northeast of the Oahu, seven days after her geolocator was deployed during the chick-guard stage. The geolocator, as well as the bird's leg band, were returned to the authors by the Taiwanese government who had fisheries observers onboard the vessel.

As the breeding season progressed, Laysan albatross from Oahu began venturing into the transition domain and subarctic waters, occasionally reaching the Aleutian Island chain and venturing further west to the Kuroshio Extension. During the post-guard stage

(March-June), Laysan albatross on Oahu had a higher spatial overlap than in the chick guard stage, but still relatively low compared to the incubation stage. The birds then expanded their foraging radius relative to earlier periods in the reproductive cycle, with the strongest overlap with areas of high fishing effort occurring directly north of the colony at approximately 25°-30°N in the 95% contour. The non-breeding season (July-October) had the second highest amount of overlap with fishing effort, and again, the greatest overlap occurred with the highest level of fishing effort in the 25% and 50% kernel contours at 170°-175°E, 40°-45°N and 160°-165°E, 35°-40°N with moderate amounts of fishing effort in the 95% density contour. However, more than half of their range extended farther north of the fishery which significantly reduced the overlap with fishing effort.

#### *Distribution of tracked albatrosses from Kure and fisheries*

During the incubation period, Laysan albatross from Kure Atoll foraged north/northwest of the colony over the Emperor Seamounts and the area bounded by the Kuroshio and Oyashio current systems. During early chick rearing, Laysan albatross from Kure Atoll foraged almost due north of the colony, and as the brooding season progressed to the post-guard stage, the 95% contour of their distribution moved farther west, with birds foraging more in the subarctic frontal zone, the transition domain and into the areas bounded by the Kuroshio and Oyashio current systems. During the entire breeding season, the core foraging areas represented by the 25% and 50% contours remained stable and only began extending to the west toward the end of the breeding season. As a result, fisheries overlap was approximately the same for all three periods in the reproductive

cycle. The area of highest overlap occurred with high fishing effort in the 25% and 50% contours at approximately 175°-180°E and 25°-35°N during the incubation period.

Overlap with areas of moderate fishing effort occurred at 175°-180°W and 30°-40°N in the 25% and 50% contours, also during incubation. The distribution of birds tracked on Kure Atoll in the non-breeding season moved significantly north and west and out of the areas of highest fishing effort. As a result, no overlap was seen with fishing effort in the core foraging areas, and moderate overlap was observed in the 95% contour.

## DISCUSSION

Our results indicate that at least some colonies of Laysan albatross experience different levels of exposure to commercial fishing operations throughout their reproductive cycle. Because of distinct colony-based differences in foraging locations, individual birds also run different risks of becoming fisheries bycatch based on where they breed. The international North Pacific pelagic longline fishery for tuna (*Thunnus* spp.), billfish (*Makaira* spp. and *Tetrapturus* spp.), and broad-bill swordfish (*Xiphias gladius*) appears to present the highest risk for birds from both colonies (compared to Alaska based fisheries) due to their year-round operations in the lower latitudes often used by birds provisioning for their chicks. Laysan albatross spent relatively little time in the shelf and continental margins of the US EEZ where the majority of commercial fishing effort examined in previous studies has occurred (Fisher et al. 2009). While the specific locations that presented the highest risk for bycatch, based on potential overlap differed between birds nesting on Oahu and Kure Atoll, with Oahu having a much higher



risk for fisheries overlap than Kure, the periods in the reproductive cycle that presented the highest risk did not differ.

For Laysan albatross nesting on Oahu, the lowest risk of fisheries bycatch was during the non-breeding season when their distribution moved significantly north and out of the area of overlap with the fishery. However, while the core foraging areas did not enter the US EEZ during this time, the 95% density contour did overlap with potential Alaska based fisheries which take Laysan albatross as bycatch. Little time was spent in Alaskan waters during the breeding stages, and so overlap was primarily with pelagic longlining operations. The overlap, and thus potential risk, was highest in the incubation stage and in the non-breeding season which are continuous with each other. The maximum overlap with fishing effort occurred during the incubation period when the core foraging areas of the birds overlapped completely with the areas of highest fishing effort. Laysan albatross forage closer to the colony in warmer waters during this time as they must return to the nest frequently to relieve their mate (see chapter 3), and these warm waters are where the target species for this fishery are most abundant.

Laysan albatross nesting on Kure Atoll also had the highest overlap during the incubation period as a result of foraging closer to their nest sites. In parallel to birds from Oahu, Kure Atoll birds had less overlap with fisheries during the non-breeding season when they moved farther north out of the normal distribution of the target species range for this fishery. However, despite the overlap of core foraging areas and areas of highest fishing effort being lower than that of birds on Oahu, birds from Kure Atoll spent significantly more time in the western Pacific than birds from Oahu, potentially increasing their overlap with fisheries that were not examined in this study. Birds from

Kure Atoll spent little or no time in the US EEZ during the year, confounding the evaluation of their overlap with fishing effort.

The finding that birds from both colonies are at greatest risk for bycatch during the breeding season has troubling conservation implications. Birds killed during the breeding season are not only lost, but any chicks alive at the time of their death will likely be lost since Laysan albatross have obligate bi-parental care (Whittow 1993). Furthermore, the surviving parent may expend more effort attempting to raise a chick without the help of a mate and may potentially have lower survivorship (Weimerskirch et al. 1994a & b, Hyrenbach et al. 2002). Previous studies have shown that the provisioning patterns of procellariiformes alternate between ‘long’ and ‘short’ trips as a trade off between self maintenance (long trips) chick growth (short trips; Weimerskirch et al. 1994b, Hyrenbach et al. 2002). Survival analyses also indicate that breeding birds have slightly lower survival than non-breeding birds that are skipping a year, demonstrating the cost to reproduction (Fisher 1975). As a result of the k-selected life history of this species, birds killed as bycatch during the breeding season may disproportionately influence the population dynamics on a colony compared mortality in the non-breeding season.

Bycatch risks for Laysan albatrosses exist beyond the fisheries examined during this study, and indeed may be highest in areas and/or fisheries that are not documented. In addition to overlap with the fishery examined in this study, the birds forage frequently in the Russian and Japan EEZ’s which are countries known for their massive fishing fleets. Because fishing effort data were not examined from those two nations, which, along with China, are not members of the SPC, it is likely that overlap with fishing effort

was much higher than is reported here. Although Laysan albatrosses tracked during this study appeared to be at a lesser risk of interactions with fisheries inside the Alaskan EEZ compared to previous studies that only tracked birds for a portion of the year (Fisher et al. 2009), the foraging range of birds tracked in this study extended well into the Kuroshio Extension east of Japan and the Kuril islands off of Russia where extensive pelagic longline fishing operations occur (Cousins 2000). The extension of the foraging range of Laysan albatross from both Kure Atoll and Oahu to the western Pacific, particularly during the non-breeding season confirms previous ship based estimates of their pelagic range (Fisher and Fisher 1972, Robbins and Rice 1974, Kuroda 1988, Wahl et al. 1989, Fernandez et al. 2001).

Pelagic longline fishery data compiled by 22 participating nations was selected for analysis in this study because this fishery poses a number of threats to Laysan albatross. First, because tuna and billfish are more commonly associated with subtropical or tropical waters and convergent fronts (Polovina et al. 2000, 2001), there is a greater chance of Laysan albatross coming into contact with these fisheries during the breeding season when they forage in warmer waters. Since the breeding season extends from November to June, birds forage in proximity to this fishery for the majority, if not the entire year. Second, and perhaps more importantly, not all member nations in this fishery employ seabird bycatch mitigation measures, thus increasing the chance of birds being caught as bycatch when they do encounter these vessels. Finally, it has been demonstrated in pelagic longline tuna fisheries in Hawaii, that longlining presents a high bycatch risk for Laysan albatross due to their tendency to swallow bait on hooks and drown underwater (Cousins et al. 2000).

Our results indicate that Laysan albatross are at highest risk from fisheries interactions during the early breeding season and that monitoring potential demographic shifts that occur as a result of mortality in breeding birds may help to better quantify the impacts of bycatch during this period. Since birds from both colonies move into areas where fishing effort was not analyzed for in this study, obtaining fisheries data from the Alaskan fisheries and Asian nations would greatly improve our ability to assess bycatch risk and identify areas of high overlap. Finally, since the population structure observed was not enough to produce significant differences in the mixed stock analysis, developing species-specific microsatellite, or using other mtDNA markers could improve the resolution of the population structure of this species. Further resolving the population sub-division would improve our ability to perform assignment tests on birds killed as bycatch and help answer the question of whether bycatch is disproportionately affecting certain populations. As a result of the potential risks from international fisheries that were presented in this study, future mitigation measures should focus on international fisheries in addition to those based in US waters and future studies should attempt to quantify overlap with Asian fisheries.

Table 5.1: Burke Museum accession number for bycatch samples obtained.

UWBM 65658  
 UWBM 65659  
 UWBM 65662  
 UWBM 65665  
 UWBM 65667  
 UWBM 65668  
 UWBM 65669  
 UWBM 65670  
 UWBM 65671  
 UWBM 65673  
 UWBM 65681  
 UWBM 65685  
 UWBM 61816  
 UWBM 61845  
 UWBM 61857  
 UWBM 61859  
 UWBM 61860  
 UWBM 61863

Table 5.2: Proportional contribution of source populations bycatch samples of Laysan Albatross based on results obtained in BAYES.

Source population	Bycatch	
	Proportion	SE†
Kure	0.15	0.33
Midway	0.10	0.06
Pearl and Hermes	0.42	0.38
Laysan	0.14	0.28
Tern	0.19	0.11

† SE is standard error

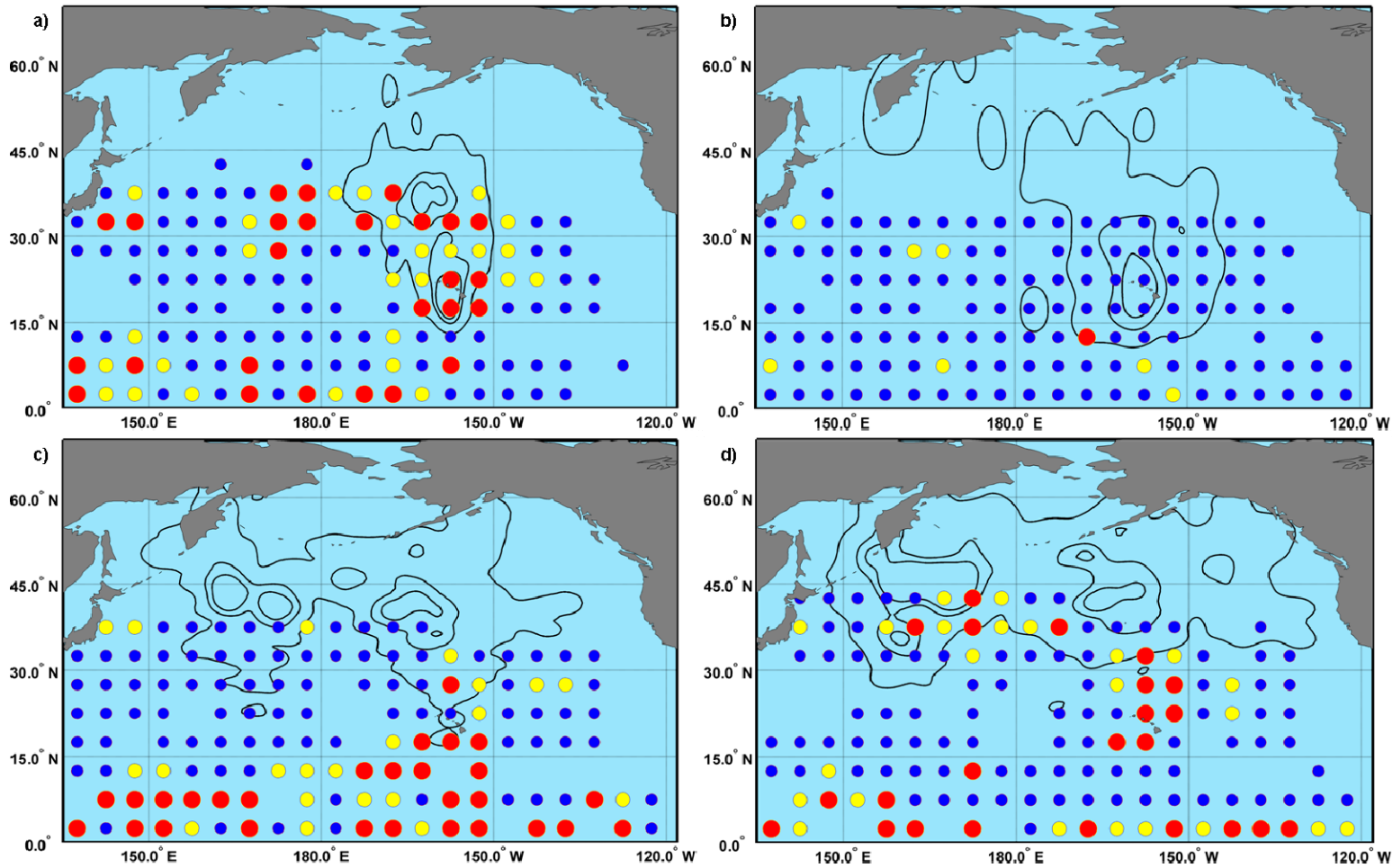


Figure 5.1: Overlap between 25%, 50% and 95% kernel density estimates of Laysan albatross foraging distribution from Oahu and the spatial distribution of observed or reported longline fishing effort (1000s of hooks) in the North Pacific during the a) incubation b) chick guard c) post-guard and d) non-breeding stages. Red circles represent fishing effort < 25,000 hooks/ 5° grid, yellow circles < 10,000, and blue circles < 5,000 hooks per 5° latitude and longitude grid.

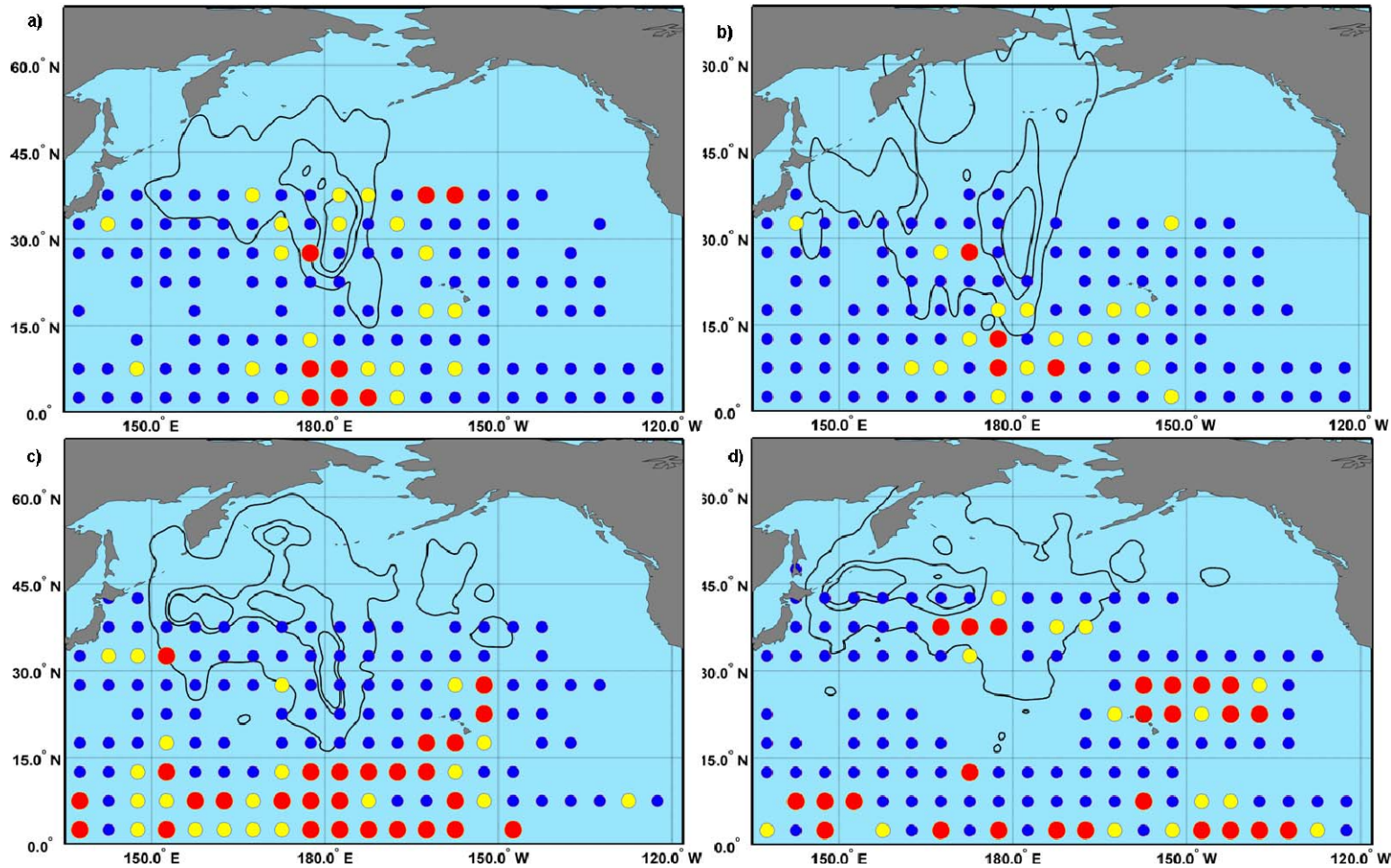


Figure 5.2: Overlap between 25%, 50% and 95% kernel density estimates of Laysan albatross foraging distribution from Kure Atoll and the spatial distribution of observed or reported longline fishing effort (1000s of hooks) in the North Pacific during the a) incubation b) chick guard c) post-guard and d) non-breeding stages. Red circles represent fishing effort < 25,000 hooks/ 5° grid, yellow circles < 10,000, and blue circles < 5,000 hooks per 5° latitude and longitude grid.

## CHAPTER 6

### SUMMARY

This dissertation represents the first comprehensive examination of the ecological and genetic population characteristics of the Laysan albatross (*Phoebastria immutabilis*) and how this information can be used to set conservation priorities. While some of the hypotheses put forward in the introduction of this dissertation were supported, others contradicted what we have known about the biology of Laysan albatross.

#### FORAGING ECOLOGY OF LAYSAN ALBATROSS

Distant colonies of Laysan albatross utilize oceanographic regimes of similar productivity in widely separated areas, indicating that this vagile species is able to assess resource variation on large scales. The similar associations of the two colonies studied with productivity and depth domains indicate that there are predictable oceanographic characteristics of suitable foraging areas that may be part of an albatross's search image when they are locating prey. However, it is their ability to identify suitable areas closest to the colony, when they are breeding, which suggests that their assessment of resource variation also includes an assessment of the energy required to reach the resources, and thus leads to foraging segregation during the reproductive cycle when they are physically constrained to the nest. During the non-breeding season when birds are not as energetically constrained, some overlap between distant colonies does occur, which may indicate that the energy required to reach the foraging grounds becomes less important than the total energy available on the foraging grounds themselves.



The plastic loads in stomachs of birds between the two colonies were also vastly different, with birds from Kure Atoll feeding their chicks as much as ten times more plastic than birds on Oahu. These results were quite surprising as it was thought that plastic ingestion was relatively high in all colonies. It had also been assumed previously that widely separated colonies of Laysan albatross were foraging in similar areas, which we now know is not true at certain points in the reproductive cycle.

Environmental heterogeneity in marine, as well as terrestrial systems, affects animal movements on a range of scales (Weimerskirch et al. 1993, Shaffer et al. 2003, Pinaud and Weimerskirch 2007). Results indicate that Laysan albatross are able to assess prey availability on large scales and make foraging decisions based on the energy required to reach feeding grounds throughout their breeding cycle. While the foraging locations during the breeding season are population specific, these predators seek out common ecological characteristics, leading to the use of similar habitats by birds from the two colonies in the non-breeding season when they are not constrained to the nest. Studying movements at a smaller scale in relation to resource distribution, and at multiple colonies over multiple years will be crucial to fully understand scale-dependent adjustments and the ultimate foraging distribution of these animals. Future studies of foraging behavior would also benefit from not only monitoring plastics ingested, but also quantifying natural diet to ascertain regional differences. The large range and potentially long-term retention of ingested plastic indicate that the Laysan albatross may prove to be a key species for sampling marine debris and other pollutants in the North Pacific Ocean and, as such, efforts should be made to continue monitoring their plastic ingestion and foraging patterns.

## POPULATION GENETICS OF LAYSAN ALBATROSS

The goals of this chapter were to test hypotheses about the effects of natal philopatry on population structure and to determine whether colonization events could be attributed to dispersal or displacement in Laysan albatross. The results indicate that despite a lack of barriers to dispersal and high vagility, high natal philopatry appears to lead to population structure in Laysan albatross. However, unlike the strong population genetic signatures that have been documented in other albatross species, or the lack of population structure found in other seabirds, the Laysan albatross has intermediate population structure apparently driven by a combination of female philopatry and population unique haplotypes. Contributions from multiple source colonies to newly colonized sites were contrary to the expectation of a displacement hypothesis of single source colony contribution. Instead, these data indicate low levels of dispersal from all colonies as the source of colonization events.

High genetic diversity, ability to rapidly colonize new locations and great dispersal potential bode well for the future of Laysan albatross and could explain this species' success relative to other albatross species. However there are still a multitude of threats to Laysan albatross, from fisheries bycatch to climate change, that will likely increase in magnitude in the future. Consequently, it is important to prioritize management actions aimed at preserving the genetic diversity of existing colonies.

## SIGNIFICANCE OF THE RESEARCH AND CONSERVATION IMPLICATIONS

The results of this dissertation research have numerous applications for science-based management priorities for Laysan albatross. Genetic results indicate that Midway

Atoll should be a distinct management unit. With the remaining colonies of Laysan albatross being genetically similar, efforts should be made to preserve colonies at the extreme edges of the range (Mukojima and Isla Guadalupe) that will provide birds with an environmental buffer against potential oceanographic changes. Most importantly, colonies on high islands (Necker, Nihoa, Lehua, Kauai and Oahu in addition to Mukojima and Guadalupe) could provide refugia in the event of future sea level rises (Baker et al. 2006) and should be the focus of protective measures, even though their current population sizes are small.

In terms of susceptibility to fisheries bycatch, the risk of Laysan albatross from each colony coming into contact with fishing vessels and thus potentially being caught as bycatch will depend on the colonies' locations, and their resident birds foraging patterns. Species wide patterns include overlap with the pelagic longlining fishery for billfish in the North Pacific, posing the greatest threat to Laysan albatross of the fisheries examined in this study.

The North Pacific billfish fishery data, based on data submitted by 22 participating nations and includes multiple target species, poses a threat to Laysan albatross for a number of reasons. Billfish are frequently found in warmer waters, so there is a greater chance of birds coming into contact with these fisheries during the breeding season when they forage in warmer, oligotrophic waters. Since the breeding season extends from November to June, birds forage in proximity to this fishery for the majority of the year. In addition, this is an international fishery and not all member nations employ seabird bycatch mitigation measures, increasing the chance of albatross bycatch. Finally, this fishery is a pelagic longline fishery which uses the gear type that

has the highest bycatch risk for Laysan albatross due to their tendency to swallow bait on hooks.

The point in the reproductive cycle when Laysan albatross are at the highest risk for being caught as bycatch appears to be the entire breeding season. This is because adults are foraging in warmer waters closer to the colony where the target species for this fishery are being targeted. Indeed, the areas of highest fishing effort in almost every case corresponded with the core foraging area of birds throughout the reproductive cycle. During the non-breeding season, birds moved significantly north and out of the areas of greatest fishing effort where the target species for this fishery are not found.

It is hoped that the research conducted here, in conjunction with previous research, can provide resource managers charged with protecting Laysan albatross with the information needed to make informed conservation decisions.

#### FUTURE RESEARCH OPPORTUNITIES

As should be the case with most research, this study resolved several issues, but raised more questions than it answers. I envision several research avenues that could enhance our understanding of the population biology and potential meta-population dynamics in Laysan, and other albatross species.

The first, currently being pursued by the author as well as several government agencies, is to set up and conduct long-term colony-based studies. By determining the sex of birds being followed and supplementing these data with at-sea tracking studies, a comprehensive picture of sex-based survival rates, foraging patterns and colony and thus species specific growth rates can be obtained. Since the behavior of Laysan albatross is much more flexible than previously thought, as evidenced through high rates of female

pairing, tracking annual oceanographic changes and colony based difference in foraging behavior, these animals will likely alter their behavior to compensate for long term environmental changes. Determining when and how they respond to climate changes will be critical to understanding large-scale oceanographic changes occurring throughout the North Pacific, and how these affect not only the albatross, but other seabird species as well. Obtaining these demographic values will also assist in determining population trends and the effects of bycatch and other anthropogenic threats on this species.

The second avenue that I believe promises to provide a wealth of research opportunities is moving towards more hypothesis-based approach with at-sea tracking studies that incorporate diet and/or actual prey movement data into the results. Albatross tracking has emerged as a popular field of study because, relative to smaller seabird species, albatross are easy to track. And while many exciting studies have documented the foraging patterns of these animals, incorporating more hypothesis based studies that attempt to answer ‘why’ birds forage in different locations should become a priority.

Finally, developing species-specific microsatellite markers could improve the resolution of the population structure of this species. Further resolving population subdivisions would improve our ability to determine the provenance of birds killed as bycatch, and determine the origin of new colonizers. Obtaining museum specimens from the early 1900’s and comparing historical vs contemporary levels of diversity could also serve to improve our estimate of pre feather harvesting population sizes and levels of genetic diversity, both of which could significantly enhance conservation efforts.

While much has been learned concerning Laysan albatross, there is still much that can be done not only on this species, but for many of our tropical seabird species. Laysan

albatross provide a wealth of opportunities to study ecological, behavioral, evolutionary and conservation related topics that have relevance across taxa--the surface has only been scratched.

Appendix 1: Geographic distribution of mtDNA control region haplotypes in Laysan

Albatross.

Haplotype ID	Japan	Kure	Midway	Pearl & Hermes	Laysan	Tern	Lehua	Kauai	Oahu	Mexico	Wake
LACR_1	0	1	0	0	2	0	0	0	1	5	0
LACR_2	0	0	0	0	0	0	0	0	0	1	0
LACR_3	0	1	1	0	1	0	0	0	0	2	0
LACR_4	2	1	0	0	0	0	0	1	1	2	0
LACR_5	0	0	0	0	0	0	0	0	0	1	0
LACR_6	0	0	0	0	0	1	0	0	0	2	0
LACR_7	0	0	0	0	0	0	0	0	0	2	0
LACR_8	0	0	0	0	0	0	0	0	0	1	0
LACR_9	0	0	0	0	0	0	0	0	0	1	0
LACR_10	0	0	0	0	0	3	0	1	0	1	0
LACR_11	0	0	0	0	0	0	0	0	0	1	0
LACR_12	0	0	0	0	0	1	0	0	2	1	0
LACR_13	0	0	0	0	1	0	0	1	1	2	0
LACR_14	0	0	0	0	0	0	0	0	0	1	0
LACR_15	0	0	0	0	0	1	0	0	0	1	0
LACR_16	0	0	0	0	0	0	0	0	0	1	0
LACR_17	0	0	0	0	0	0	1	0	0	3	0
LACR_18	0	0	0	1	0	0	0	2	1	1	0
LACR_19	0	0	0	0	0	0	0	0	0	2	0
LACR_20	0	1	0	0	0	1	0	1	1	2	0
LACR_21	0	5	16	0	0	5	0	0	1	1	0
LACR_22	0	0	0	0	0	0	0	0	0	1	0
LACR_23	0	0	0	0	0	1	0	0	0	1	0
LACR_24	0	0	0	0	0	0	0	0	0	1	0
LACR_25	0	0	0	0	0	0	0	0	0	1	0
LACR_26	0	0	0	0	0	0	0	0	0	1	0
LACR_27	0	0	0	0	0	0	0	0	0	1	0
LACR_28	0	0	0	1	1	0	2	2	1	3	0
LACR_29	0	0	0	0	0	0	0	0	0	1	0
LACR_30	0	0	0	0	0	0	0	0	0	1	0
LACR_31	0	0	0	0	0	0	0	0	0	1	0
LACR_32	0	0	0	0	0	0	0	0	0	1	0
LACR_33	0	1	0	0	1	0	1	0	3	1	0
LACR_34	0	0	0	0	0	0	0	0	0	1	0
LACR_35	0	0	0	0	0	0	0	0	0	1	0
LACR_36	0	1	0	0	1	1	0	1	0	1	0
LACR_37	0	0	0	0	0	1	0	0	0	1	0
LACR_38	0	0	0	0	0	0	0	0	0	1	0
LACR_39	0	0	0	0	0	0	0	0	0	1	0
LACR_40	1	0	0	0	0	0	0	0	0	0	0
LACR_41	1	0	0	0	1	0	0	0	1	0	0
LACR_42	2	0	0	0	0	0	0	0	0	0	0
LACR_43	1	0	0	0	0	0	0	0	1	0	0
LACR_44	1	0	0	0	0	0	0	0	0	0	0

LACR_45	1	0	0	0	0	0	0	0	0	0	0	0
LACR_46	1	0	0	0	0	0	0	1	0	0	0	0
LACR_47	1	0	0	0	0	0	0	2	0	0	0	0
LACR_48	1	0	0	0	0	0	0	0	0	0	0	0
LACR_49	2	1	0	1	0	0	1	0	0	0	0	0
LACR_50	1	0	0	0	0	1	0	0	0	0	0	0
LACR_51	0	1	0	0	0	1	0	0	0	0	0	0
LACR_52	0	1	0	0	0	0	0	0	0	0	0	0
LACR_53	0	1	0	0	0	0	0	0	0	0	0	0
LACR_54	0	1	0	0	0	0	0	0	0	0	0	0
LACR_55	0	1	1	0	0	0	0	0	0	0	0	0
LACR_56	0	1	0	0	0	0	0	0	0	0	0	0
LACR_57	0	1	0	0	0	0	0	0	0	0	0	0
LACR_58	0	1	0	0	0	0	0	0	0	0	0	0
LACR_59	0	3	0	0	0	0	0	0	0	0	0	0
LACR_60	0	1	0	0	0	0	0	0	0	0	0	0
LACR_61	0	2	0	0	0	0	0	2	1	0	0	0
LACR_62	0	1	0	0	0	0	0	0	0	0	0	0
LACR_63	0	1	1	1	0	0	0	0	0	0	0	0
LACR_64	0	1	0	0	0	2	1	1	2	0	0	0
LACR_65	0	1	0	0	0	1	0	0	0	0	0	0
LACR_66	0	1	0	0	0	0	0	0	0	0	0	0
LACR_67	0	1	0	0	0	0	0	0	0	0	0	0
LACR_68	0	1	0	0	0	0	0	0	0	0	0	0
LACR_69	0	1	0	0	0	0	0	0	0	0	0	0
LACR_70	0	1	0	0	0	0	0	0	0	0	0	0
LACR_71	0	1	0	0	0	0	0	0	0	0	0	0
LACR_72	0	1	0	0	0	0	0	0	0	0	0	0
LACR_73	0	1	1	2	0	1	0	0	0	0	0	0
LACR_74	0	1	0	0	0	0	0	0	0	0	0	0
LACR_75	0	1	0	0	0	0	0	0	0	0	0	0
LACR_76	0	1	0	0	0	0	0	0	0	0	0	0
LACR_77	0	1	0	0	0	0	0	0	1	0	0	0
LACR_78	0	1	0	0	0	0	0	0	0	0	0	0
LACR_79	0	1	0	0	0	0	0	0	0	0	0	0
LACR_80	0	1	0	0	0	0	0	0	0	0	0	0
LACR_81	0	0	0	0	1	0	0	3	0	0	0	0
LACR_82	0	0	0	0	0	0	0	1	0	0	0	0
LACR_83	0	0	0	0	0	0	0	1	0	0	0	0
LACR_84	0	0	0	0	0	0	1	1	2	0	0	0
LACR_85	0	0	0	0	0	0	0	1	0	0	0	0
LACR_86	0	0	0	0	0	0	1	2	0	0	0	0
LACR_87	0	0	0	0	0	0	0	1	0	0	0	0
LACR_88	0	0	0	0	0	0	0	1	0	0	0	0
LACR_89	0	0	0	0	0	1	0	1	0	0	0	0
LACR_90	0	0	0	0	1	0	0	1	0	0	0	0
LACR_91	0	0	0	1	0	0	0	1	0	0	0	0
LACR_92	0	0	0	1	0	0	0	1	0	0	0	0
LACR_93	0	0	0	0	0	0	0	1	0	0	0	0
LACR_94	0	0	0	0	0	0	0	1	0	0	0	0
LACR_95	0	0	1	0	0	0	0	1	0	0	0	0
LACR_96	0	0	0	0	0	0	0	1	0	0	0	0



LACR_97	0	0	0	1	0	1	1	2	0	0	0
LACR_98	0	0	0	0	0	0	0	1	0	0	0
LACR_99	0	0	0	0	0	0	0	0	1	0	0
LACR_100	0	0	0	0	0	1	0	0	2	0	0
LACR_101	0	0	0	0	0	0	0	0	2	0	0
LACR_102	0	0	1	0	0	0	0	0	1	0	0
LACR_103	0	0	0	0	0	0	0	0	1	0	0
LACR_104	0	0	0	0	0	0	0	0	1	0	0
LACR_105	0	0	0	0	0	0	0	0	1	0	0
LACR_106	0	0	0	0	0	0	0	0	1	0	0
LACR_107	0	0	0	0	0	0	0	0	1	0	0
LACR_108	0	0	0	0	0	0	0	0	1	0	0
LACR_109	0	0	0	0	0	0	0	0	3	0	0
LACR_110	0	0	0	0	0	0	0	0	1	0	0
LACR_111	0	0	0	0	0	0	0	0	1	0	0
LACR_112	0	0	0	0	0	1	0	0	2	0	0
LACR_113	0	0	0	0	0	0	0	0	1	0	0
LACR_114	0	0	0	0	0	0	0	0	1	0	0
LACR_115	0	0	0	0	0	0	0	0	1	0	0
LACR_116	0	0	0	0	1	0	0	0	0	0	0
LACR_117	0	0	0	0	1	0	0	0	0	0	0
LACR_118	0	0	0	0	1	0	0	0	0	0	0
LACR_119	0	0	0	0	1	0	0	0	0	0	0
LACR_120	0	0	0	0	1	1	1	0	0	0	0
LACR_121	0	0	0	0	1	0	0	0	0	0	0
LACR_122	0	0	0	0	1	0	0	0	0	0	0
LACR_123	0	0	0	0	1	0	1	0	0	0	0
LACR_124	0	0	0	1	1	0	0	0	0	0	0
LACR_125	0	0	0	0	1	0	0	0	0	0	0
LACR_126	0	0	0	0	1	0	0	0	0	0	0
LACR_127	0	0	0	0	1	0	0	0	0	0	0
LACR_128	0	0	0	0	1	0	0	0	0	0	0
LACR_129	0	0	0	0	1	0	0	0	0	0	0
LACR_130	0	0	0	1	0	0	1	0	0	0	0
LACR_131	0	0	0	0	0	0	2	0	0	0	0
LACR_132	0	0	0	1	0	0	1	0	0	0	0
LACR_133	0	0	0	0	0	0	2	0	0	0	0
LACR_134	0	0	0	0	0	0	2	0	0	0	0
LACR_135	0	0	0	0	0	0	1	0	0	0	0
LACR_136	0	0	0	0	0	0	1	0	0	0	0
LACR_137	0	0	0	0	0	0	1	0	0	0	0
LACR_138	0	0	0	0	0	0	1	0	0	0	0
LACR_139	0	0	1	0	0	0	0	0	0	0	0
LACR_140	0	0	1	0	0	0	0	0	0	0	0
LACR_141	0	0	2	0	0	0	0	0	0	0	0
LACR_142	0	0	2	0	0	0	0	0	0	0	0
LACR_143	0	0	1	0	0	0	0	0	0	0	0
LACR_144	0	0	1	0	0	0	0	0	0	0	0
LACR_145	0	0	1	0	0	0	0	0	0	0	0
LACR_146	0	0	1	0	0	0	0	0	0	0	0
LACR_147	0	0	1	0	0	0	0	0	0	0	0
LACR_148	0	0	1	0	0	0	0	0	0	0	0

LACR_149	0	0	1	0	0	0	0	0	0	0	0	0
LACR_150	0	0	1	0	0	0	0	0	0	0	0	0
LACR_151	0	0	1	0	0	0	0	0	0	0	0	0
LACR_152	0	0	1	0	0	0	0	0	0	0	0	0
LACR_153	0	0	1	0	0	0	0	0	0	0	0	0
LACR_154	0	0	1	0	0	0	0	0	0	0	0	0
LACR_155	0	0	1	0	0	0	0	0	0	0	0	0
LACR_156	0	0	0	1	0	0	0	0	0	0	0	0
LACR_157	0	0	0	2	0	1	0	0	0	0	0	0
LACR_158	0	0	0	1	0	0	0	0	0	0	0	0
LACR_159	0	0	0	1	0	1	0	0	0	0	0	0
LACR_160	0	0	0	1	0	0	0	0	0	0	0	0
LACR_161	0	0	0	1	0	0	0	0	0	0	0	0
LACR_162	0	0	0	1	0	0	0	0	0	0	0	0
LACR_163	0	0	0	1	0	0	0	0	0	0	0	0
LACR_164	0	0	0	1	0	0	0	0	0	0	0	1
LACR_165	0	0	0	1	0	0	0	0	0	0	0	0
LACR_166	0	0	0	0	0	1	0	0	0	0	0	0
LACR_167	0	0	0	0	0	1	0	0	0	0	0	0
LACR_168	0	0	0	0	0	1	0	0	0	0	0	0
LACR_169	0	0	0	0	0	1	0	0	0	0	0	0
LACR_170	0	0	0	0	0	1	0	0	0	0	0	0
LACR_171	0	0	0	0	0	1	0	0	0	0	0	0
LACR_172	0	0	0	0	0	1	0	0	0	0	0	0
LACR_173	0	0	0	0	0	2	0	0	0	0	0	0
LACR_174	0	0	0	0	0	1	0	0	0	0	0	0
LACR_175	0	0	0	0	0	1	0	0	0	0	0	0
LACR_176	0	0	0	0	0	1	0	0	0	0	0	0
LACR_177	0	0	0	0	0	1	0	0	0	0	0	0
LACR_178	0	0	0	0	0	1	0	0	0	0	0	0
LACR_179	0	0	0	0	0	1	0	0	0	0	0	0
LACR_180	0	0	0	0	0	2	0	0	0	0	0	0
LACR_181	0	0	0	0	0	1	0	0	0	0	0	0
LACR_182	0	0	0	0	0	1	0	0	0	0	0	0
LACR_183	0	0	0	0	0	1	0	0	0	0	0	0
LACR_184	0	0	0	0	0	1	0	0	0	0	0	0
LACR_185	0	0	0	0	0	1	0	0	0	0	0	0
LACR_186	0	0	0	0	0	1	0	0	0	0	0	0
LACR_187	0	0	0	0	0	1	0	0	0	0	0	0
LACR_188	0	0	0	0	0	0	0	0	0	0	0	1

## LITERATURE CITED

Abbott, C.L., Double, M.C. Trueman, J.W.H., Robinson, A., & Cockburn, A. (2005) An unusual source of apparent mitochondrial heteroplasmy: duplicate mitochondrial control regions in *Thalassarche* albatrosses. *Molecular Ecology* 14: 3605-3613.

Abbott, C.L. & Double, M.C. (2003a) Genetic structure, conservation genetics and evidence of speciation by range expansion in shy and white-capped albatrosses. *Molecular Ecology* 12: 2953-2962.

Abbott, C.L. & Double, M.C. (2003b) Phylogeography of shy and white-capped albatrosses inferred from mitochondrial DNA sequences: implications for population history and taxonomy. *Molecular Ecology* 12: 2747-2758.

Abbott, C.L., Double, M.C., Gales, R., Baker, G.B., Lashko, A., Robertson, C.J.R., & Ryan, P.G. (2006) Molecular provenance analysis for shy and white-capped albatrosses killed by fisheries interactions in Australia, New Zealand, and South Africa. *Conservation Genetics* 7: 531-542.

Alderman, R., Double M.C., Valencia, J., & Gales, R.P. (2005) Genetic affinities of newly sampled populations of wandering and black-browed albatross. *Emu* 105: 169-179.

Anderson, S., & McArdle, B. (2002) Sink rate of baited hooks during deployment of a pelagic longline from a New Zealand fishing vessel. *New Zealand Journal of Marine and Freshwater Research* 36: 185-195.

Arditi, R., & Dacorogna, B. (1985) Optimal foraging in non-patchy habitats. *Mathematical Biosciences* 76: 127-145.

Arditi, R., & Dacorogna, B. (1988) Optimal foraging on arbitrary food distributions and the definition of habitat patches. *American Naturalist* 131: 837-846.

Auman, H.J., Ludwig, J.P., Giesy, J.P., & Colborn, T. (1997) Plastic ingestion by Laysan Albatross chicks on Sand Island, Midway Atoll, in 1994 and 1995. In: Robertson G, Gales R, editors. *Albatross Biology and Conservation*. Chipping Norton: Surrey Beatty & Sons. pp 239-244

Austin, J.J., White, R.W.G., & Oveden, J.R. (1994) Population-genetic structure of a philopatric, colonially nesting seabird, the short-tailed shearwater (*Puffinus tenuirostris*). *Auk* 111.

Avise, J.C. (2000) Stability, equilibrium and molecular aspects of conservation in marine species. *Hydrobiologia* 420: XI-XII.

Avise, J.C., & Walker, D. (1998) Pleistocene phylogeographic effects on avian populations and the speciation process. *Proceedings of the Royal Society B-Biological Sciences* 265: 457-463.

Baker, J. D., Littman, C. L., & Johnston, D. W. (2006) Potential effects of sea level rise on the terrestrial habitats of endangered and endemic megafauna in the Northwestern Hawaiian Islands. *Endangered Species Research* 4: 1-10.

Ballance, L.T., Pitman, R.L., & Reilly, S.B. (1997) Seabird community structure along a productivity gradient: Importance of competition and energetic constraint. *Ecology* 78: 1502-1518.

Beerli, P. (1997) Migrate: documentation and program, part of LAMARC. Version 2.1.3. Revised 23 December 2004. Available from <http://evolution.gs.washington.edu/lamarc/>

Beerli, P. & Felsenstein, J. (1999) Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach. *Genetics* 151: 763- 773.

Beerli, P. & Felsenstein, J. (2001) Maximum likelihood estimation of a migration matrix and effective population sizes in n populations by using a coalescent approach. *Proceedings of the National Academy of Sciences* 98: 4563-4568.

Belda, E.J., & Sanchez, A. (2001) Seabird mortality on longline fisheries in the western Mediterranean: Factors affecting bycatch and proposed mitigating measures. *Biological Conservation* 98: 357-363.

Birt-Friesen, V.L., Montevecchi, W.A., Gaston, A.J. et al. (1992) Genetic structure of thick-billed murre (*Uria lomvia*) populations examined using direct sequence analysis of amplified DNA. *Evolution* 46: 267-272.

Bisson, J. (2007) Diet dynamics and trophic relations of Laysan and Black-footed Albatrosses associated with pelagic longline fishing. Masters Thesis. University of Hawaii at Manoa. Honolulu, HI

Blight, L.K., & Burger, A.E. (1997) Occurrence of plastic particles in seabirds from the eastern North Pacific. *Marine Pollution Bulletin* 34: 323-325.

Bohonak, A.J. (1999) Dispersal, gene flow, and population structure. *Quarterly Review of Biology* 74: 21-45.

Borzik, R.V., Ramil, D., & Tessaglia D. L. (Editors) (1995) Egg Rock update 1995. Newsletter of the Seabird Restoration Program of the National Audubon Society, Ithaca, New York, USA.

Bowen, B.W., Bass, A.L., Soares, L., Toonen, R.J. (2005) Conservation implications of complex population structure: lessons from the loggerhead turtle (*Caretta caretta*).

Molecular Ecology 14: 2389-2402.

Bried, J., Micolaut, M., Dubois, M-P, Jouventin, P. (2007). Population biology of the wandering albatross (*Diomedea exulans*) in the Crozet and Kerguelen archipelagos, southern Indian Ocean, approached through genetic and demographic methods. Journal Zoology 277: 20-29.

Bried, J. & Jouventin, P. (2002) Site and mate choice in seabirds: an evolutionary approach. In: Biology of Marine Birds (eds. E.-A. Schreiber & J. Burger) pp. 263-305. CRC Press, Boca Raton.

Bried, J., Pontier, D., & Jouventin, P. (2003) Mate fidelity in monogamous birds: a re-examination of the *Procellariiformes*. Animal Behaviour 65: 235-246.

Brothers, N. (1991) Albatross mortality and associated bait loss in the Japanese longline fishery in the Southern Ocean. Biological Conservation 55: 255-268.

Brothers, N., Cooper, J., & Lokkeborg, S. (1999) The incidental catch of seabirds by longline fisheries: worldwide review and technical guidelines for mitigation. FAO Fisheries Circular 937: 100 pp.

Burg, T.M. (1999) Isolation and characterization of microsatellites in albatrosses. *Molecular Ecology* 8: 338-341.

Burg, T.M. & Croxall, J.P. (2001) Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Molecular Ecology* 10: 2647-2660

Burg, T.M., & Croxall, J.P. (2004) Global population structure and taxonomy of the wandering albatross species complex. *Molecular Ecology* 13: 2345-2355.

Burney, D. A., James, H. F., Burney, L. P., Olson, S. L., Kikuchi, W., Wagner, W. L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F. V., Gage II, R., & Nishek, R. (2001) Fossil evidence for a diverse biota from Kaua`i and its transformation since human arrival. *Ecological Monographs* 71: 615-641.

Butchart, S.H.M., Stattersfield, A.J., Bennun, L.A., Shutes, S.M., Akcakaya, H.R., Baillie, J.E.M., Stuart, S.N., Hilton-Taylor, C., & Mace, G.M. (2004) Measuring global trends in the status of biodiversity: Red list indices for birds. *PLoS Biology* 2: 2294-2304.

Cherel, Y., & Klages, N. (1998) A review of the food of albatrosses. In: *Albatross: biology and conservation* (eds. G. Robertson & R. Gales) pp. i-xii, 1-300 Chapter pagination 113-136. Surrey Beatty & Sons Pty Limited.



Cherel, Y., Weimerskirch, H., & Duhamel, G. (1995) Interactions between longline vessels and seabirds in Kerguelen waters and a method to reduce seabird mortality. *Biological Conservation* 75: 63-70.

Cherel, Y., Weimerskirch, H., & Trouve C. (2000) Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Marine Ecology Progress Series* 207: 183-199.

Citta, J., Reynolds, M. H., & Seavy, N. (2007) Seabird monitoring assessment for Hawai'i and the Pacific Islands. Hawai'i Cooperative Studies Unit, Technical Report HSCU-007. University of Hawai'i at Hilo, Hilo, Hawaii, USA.

Clarke, A.L., Saether, B-E, & Roskaft, E. (1997) Sex biases in avian dispersal: a reappraisal. *Oikos* 79: 429-438.

Clement, M., Posada, D., & Crandall, K.A. (2000) TCS: A computer program to estimate gene genealogies. *Molecular Ecology* 9: 1657-1659.

Cousins, K.L., Dalzell, P. & Gilman, E. (2000) Managing pelagic longline-albatross interactions in the North Pacific Ocean. *Marine Ornithology* 28: 157-174.

Dalziell, J., & De Poorter, M. (1993) Seabird mortality in longline fisheries around South Georgia. *Polar Record* 29: 143-145.

Dameron, O.J., Parke, M., Albins, M.A., Brainard, R. (2007) Marine debris accumulation in the Northwestern Hawaiian Islands: an examination of rates and processes. *Marine Pollution Bulletin* 54: 423-433. doi: 10.1016/j.marpolbul.2006.11.019.

Danchin, E., Boulinier, T., & Massot, M. (1998) Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. *Ecology* 79: 2415-2428

Dobson, F.S. (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behavior* 30: 1183-1192.

Dubois, M-P., Jarne, P., Jouventin, P. (2005) Ten polymorphic microsatellite markers in the wandering albatross *Diomedea exulans*. *Molecular Ecology Notes* 5: 905-907.

Eilerts, B. (1987) April field trip report Kaena Point Natural Area Reserve. *Elepaio* 47: 70.

Excoffier, L., Laval, G., Schneider, S. (2005) Arlequin ver 3.0—An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* 1: 47-50.

Fernandez, P., & Anderson, D.J. (2000) Nocturnal and diurnal foraging activity of Hawaiian albatrosses detected with a new immersion monitor. *Condor* 102: 577-584.

Fernandez, P., Anderson, D.J., Sievert, P.R., & Huyvaert, K.P. (2001) Foraging destinations of three low-latitude albatross (*Phoebastria*) species. *Journal of Zoology* (London) 254: 391-404.

Fisher, H. I. & Fisher, M. L. (1969) The visits of Laysan Albatrosses to the breeding colony. *Micronesica* 5: 173-221.

Fisher, H. I. (1948) Laysan Albatross nesting on Moku Manu Islet, off Oahu. *Pacific Science* 2: 66.

Fisher, H. I. (1971) The Laysan Albatross: its incubation, hatching, and associated behaviors. *Living Bird* 10: 19-78.

Fisher, H. I. (1976) Some dynamics of a breeding colony of Laysan Albatrosses. *Wilson Bulletin* 88: 121-142.

Fisher, H.I. (1975) Mortality and survival in the Laysan albatross, *Diomedea immutabilis*. *Pacific Science* 29: 279-300.

Fisher, H.I. & Fisher, J.R., (1972) The oceanic distribution of the Laysan albatross, *Diomedea immutabilis*. *Wilson Bulletin* 84: 7-27.

Fisher, K.N., Suryan, R.M., Roby, D.D., & Balogh, G.R. (2009) Post-breeding season distribution of black-footed and Laysan albatrosses satellite-tagged in Alaska: Inter-specific differences in spatial overlap with North Pacific fisheries. *Biological Conservation*. 142: 751-760.

Fretwell, S., & Lucas, H. (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.

Fridolfsson, A. K. & Ellegren, H. (1999) A simple and universal method for molecular sexing of non-ratite birds. *Journal of Avian Biology* 30: 116-121.

Friesen, V.L., Burg, T.M., & McCoy, K.D. (2007) Mechanisms of population differentiation in seabirds. *Molecular Ecology* 16: 1765-1785.

Friesen, V.L., González, J.A., & Cruz-Delgado, F. (2006) Population genetic structure and conservation of the Galápagos petrel (*Pterodroma phaeopygia*) *Conservation Genetics*, 7: 105-115.

Fritz, H., Saïd, S., Weimerskirch, H. (2003) Evidence for scale-dependent hierarchical adjustments of movement patterns in long range foraging animals. *Proceedings of the Royal Society, London (B)* 270: 1143-1148.

Fry, D.M., Fefer, S.I., Sileo, L. (1987) Ingestion of plastic debris by Laysan albatrosses and wedge-tailed shearwaters in the Hawaiian Islands. *Marine Pollution Bulletin* 18: 339-343.

Furness, R.W. (2003) Impacts of fisheries on seabird communities. *Scientia Marina* 67: 33-45.

Gallo-Reynoso, J. P. & Figueroa-Carranza, A. L. (1996) The breeding colony of Laysan Albatrosses on Guadalupe, Mexico. *Western Birds* 27: 70-76.

Giles, B.E. & Goudet, J. (1997) Genetic differentiation in *Silene dioica* metapopulations: estimation of spatiotemporal effects in a successional plant species. *American Naturalist* 149: 507-526.

Gilman, E. & Freifeld, H. (2002) Seabird mortality in the North Pacific longline fisheries. *Endangered Species Update* 20: 35-46.

Gilman, E., Boggs, C., & Brothers, N. (2003) Performance assessment of an underwater setting chute to mitigate seabird bycatch in the Hawaii pelagic longline tuna fishery. *Ocean & Coastal Management* 46: 985-1010.

Gould, P. & Hobbs, R. (1993) Population dynamics of the Laysan and other albatrosses in the North Pacific. *International North Pacific Fisheries Commission Bulletin* 53: 485-497.

Gould, P., Ostrom, P., Walker, W., & Pilichowski, K. (1998) Laysan and black-footed albatrosses: trophic relationships and driftnet fisheries associations on non-breeding birds. *Robertson, Graham; Gales: i-xii, 1-300 Chapter pagination 199-207.*

Harrison, C. S. (1993) *Seabirds of Hawaii*. Cornell University Press, Ithaca, New York, USA

Hasunuma, K., Yoshida, K. (1978) Splitting the subtropical gyre in the western North Pacific. *Journal of the Oceanographic Society of Japan* 34: 160-172.

Haury, L., McGowan, J., & Wiebe, P. (1979) Patterns and processes in the time-space scales of plankton distribution. In: *Spatial Pattern in Plankton Communities* (ed. J. Steele) pp. 277-327. Plenum Press, New York.

Hawaii Department of Land and Natural Resources. (2007) *Draft Environmental Assessment for the Kaena Point Ecosystem Restoration Project*. Hawaii Division of Forestry and Wildlife, Honolulu, Hawaii, USA.

Hedrick, P.W., (1999) Perspective: Highly variable genetic loci and their interretation in evolution and conservation. *Evolution* 53: 313-318.

Hill, R.D. (1994) Theory of geolocation by light levels. In: Le Boeuf BJ, Laws RM editors. *Elephant seals: population ecology, behaviour and physiology*. Berkeley, CA: University of California Press. pp 227-236.

Huyvaert, K.P., Parker, P.G. (2006) Absence of population genetic structure among breeding colonies of the waved albatross. *Condor* 108: 440-445.

Hyrenbach, K.D., & Dotson, R.C. (2001) Post-breeding movements of a male black-footed albatross *Phoebastria nigripes*. *Marine Ornithology* 29: 7-10.

Hyrenbach, K.D., Fernandez, P., & Anderson, D.J. (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233: 283-301.

Inchausti, P. & Weimerskirch, H. (2002) Dispersal and metapopulation dynamics of an oceanic seabird, the Wandering Albatross, and its consequences for its response to long-line fisheries. *Journal of Animal Ecology* 71: 765-770.

International Union for the Conservation of Nature (IUCN) (2007) IUCN Red List of threatened species. <[www.iucnredlist.org](http://www.iucnredlist.org)> (accessed 10 September 2008)

Jouventin, P., & Weimerskirch, H. (1990) Satellite tracking of wandering albatrosses. Nature 343: 746-748.

Kappes MA, Shaffer SA, Tremblay Y, Foley DG, Palacios DM, Robinson PW, Bograd SJ, Coast DP (2009) Hawaiian albatrosses track interannual variability of marine habitats in the North Pacific. Progress in Oceanography .In press.

Kiyota, M. (2002) Incidental take of seabirds in longline fisheries: Nature of the issue and measures for mitigation. Journal of the Yamashina Institute for Ornithology 34: 145-161.

Krebs, C. (2001) Ecology: The Experimental Analysis of Distribution and Abundance. Benjamin-Cummings.

Kress, S.W., Borzik, R.V., & Hai, P. (Editors) (1999) Egg Rock update 1999. Newsletter of the Seabird Restoration Program of the National Audubon Society, Ithaca, New York, USA.

Kubota, M. (1994) A mechanism for the accumulation of floating marine debris north of Hawaii. Journal of Physical Oceanography 24: 1059- 1064.

Kurata, Y. (1978) Breeding records of the Laysan Albatross *Diomedea immutabilis* on the Ogasawara Islands (a preliminary report) Journal of Yamashina Institute for Ornithology 10: 185-189.



Kuroda, N. (1988) A distributional analysis of *Diomedea immutabilis* and *D. Nigripes* in the North Pacific. *Journal of the Yamashina Institute for Ornithology* 20: 1-20.

Mackas, D., & Boyd, C. (1979) Spectral analysis of zooplankton spatial heterogeneity. *Science* 204: 62-64.

Manel, S., Gaggiotti, O.E., & Waples, R.S. (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution* 20: 136-142.

Marshall, T.C., Slate, J., Kruuk, L.E.B., & Pemberton, J.M. (1998) Statistical confidence for likelihood-based paternity inference in natural populations. *Molecular Ecology* 7: 639-655.

Melvin, E.F., Parrish, J.K., Dietrich, K.S., & Hamel, O.S., 2001. Solutions to seabird bycatch in Alaska's demersal longline fisheries. Washington Sea Grant Program. Project A/FP-7, Seattle, WA, p. 45.

Milot, E., Weimerskirch, H., Duchesne, P., & Bernatchez, L. (2007) Surviving with low genetic diversity: the case of albatrosses. *Proceedings of the Royal Society B-Biological Sciences* 274: 779-787.

Moniz-Nakamura, J. J. (1999) The archaeology of human foraging and bird resources on the island of Hawai'i: the evolutionary ecology of avian predation, resource intensification, extirpation, and extinction. Dissertation. University of Hawaii, Honolulu, USA

Moreno, C.A., Arata, J.A., Rubilar, P., Hucke-Gaete, R., & Robertson, G. (2006) Artisanal longline fisheries in Southern Chile: Lessons to be learned to avoid incidental seabird mortality. *Biological Conservation* 127: 27-36.

National Marine Fisheries Service (2006a) Summary of seabird bycatch in Alaskan groundfish fisheries, 1993-2004. National Marine Fisheries Service, Seattle, WA.

National Marine Fisheries Service (2006b) North Pacific Groundfish Observer Manual. North Pacific Groundfish Observer Program. Alaska Fisheries Science Center, Seattle, WA.

Naughton, M. B., Romano, M. D., & Zimmerman, T. D. (2007) A conservation action plan for Black-footed Albatross (*Phoebastria nigripes*) and Laysan Albatross (*P. immutabilis*) Version 1.0. USDI, Fish and Wildlife Service, Portland, Oregon, USA.

Nei, M. (1987) *Molecular Evolutionary Genetics*. Columbia University Press, New York, NY

Newton, I. (2003) The speciation and biogeography of birds. Academic Press, San Diego, CA

NOAA website <http://coastwatch.pfel.noaa.gov> accessed 04/10/2009

Olson, S. L. & James, H. F. (1982) Prodrum of the fossil avifauna of the Hawaiian Islands. Smithsonian Contributions to Zoology 365: 1-59.

Orians, G., & Pearson, N. (1979) On the theory of central place foraging. In: Horn D, Mitchell, R., Stairs, G., editors. Analysis of ecological systems. Columbus, OH: Ohio State University Press. pp. 157-177

Pella, M. & Masuda, J. (2001) Bayesian methods for analysis of stock mixtures from genetic characters. NOAA Fisheries Bulletin 99: 151-167.

Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., Briggs, D.R. (2004) Accuracy of geolocation estimates for flying seabirds. Marine Ecology Progress Series 266: 265-272.

Pichel WG, Churnside JH, Veenstra TS, Foley DG, Friedman KS, Brainard RE, Nicoll JB, Zheng A, Clemente-Colon P (2007) Marine debris collects within the North Pacific Subtropical Convergence Zone. Marine Pollution Bulletin 54: 1207-1211.

Pinaud, D. & Weimerskirch, H. (2007) At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *Journal of Animal Ecology*. 76: 9-19.

Pinaud, D., Weimerskirch, H. (2005) Scale-dependent habitat use in a long-ranging central place predator. *Journal of Animal Ecology* 74: 852-863.

Pitman, R. L., Walker, W. A., Everett, W. T., & Gallo-Reynoso, J. P. (2004) Population status, foods and foraging of Laysan Albatrosses *Phoebastria immutabilis* nesting on Guadalupe Island, Mexico. *Marine Ornithology* 32: 159-165.

Platt, T. (1972) Local phytoplankton abundance and turbulence. *Deep-Sea Research* 19: 183-187.

Polovina, J.J., Howell, E., Kobayashi, D.R., Seki, M.P. (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* 29: 469-483.

Polovina, J.J., Kobayashi, D.R., Parker, D.M., Seki, M.P., & Balazs, G.H (2000) Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning fishing grounds in the in the central North Pacific, 1997-1998. *Fisheries Oceanography* 9, 71-82.

- Pratt, T. K. (1988) Recent observations March-May 1988. *Elepaio* 48: 65-66.
- Prince, P.A., Rothery, P., Croxall, J.P., & Wood, A.G. (1994) Population dynamics of black-browed and grey-headed albatrosses *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 136: 50-71.
- Pritchard, J.K., Stephens, M., & Donnelly, P. (2000) Inference of population structure using multilocus genotype data. *Genetics* 155: 945-959.
- Pritchard, J.K. & Wen, W. (2004) Documentation for Structure: Version 2. University of Chicago, Chicago, IL, USA.
- Pyle, R. L. (1978) Hawaii bird observations March through July 1978. *Elepaio* 39: 60-64.
- Pyle, R. L. (1986) Recent observations December 1985-February 1986. *Elepaio* 46: 135-136.
- Qu, Y.H., Ericson, P.G.P., Lei, F.M., & Li, S.H. (2005) Postglacial colonization of the Tibetan plateau inferred from the matrilineal genetic structure of the endemic red-necked snow finch, *Pyrgilauda ruficollis*. *Molecular Ecology* 14: 1767-1781.
- Rauzon, M. J. (2001) *Isles of Refuge*. University of Hawaii Press, Honolulu, USA.

- Rauzon, M. J., Boyle, D., Everett, W. T., & Gilardi, J. (2008) The status of birds on Wake Atoll. *Atoll Research Bulletin* 561: 1-41.
- Raymond, M. & Rousset, F. (1997) GENEPOP (version 3.1b). An updated version of GENEPOP version 1.2: population genetics software for exact tests and ecumenicism. *Journal of Heredity* 86: 248-249.
- Reece, J.S., Ehrhart, L.M., & Parkinson, C.L. (2006) Mixed stock analysis of juvenile loggerheads (*Caretta caretta*) in Indian River Lagoon, Florida: implications for conservation planning. *Conservation Genetics* 7: 345-352
- Richardson, F. & Fisher, H. I. (1950) Birds of Moku Manu and Manana Islands off Oahu, Hawaii. *Auk* 67: 21.
- Robards, M.D., Gould, P.J., Piatt, J.F. (1997) The highest global concentrations and increased abundance of oceanic plastic debris in the North Pacific: evidence from seabirds. In: Coe JM, Rogers DB editors. *Marine Debris: Sources, Impacts, and Solutions*. New York: Springer-Verlag. pp 71-80.
- Robbins, C.S. & Rice, D.W., 1974. Recoveries of banded Laysan albatrosses (*Diomedea immutabilis*) and black-footed albatrosses (*D. nigripes*). In: King, W.B. (Ed.), *Pelagic Studies of Seabirds in the Central and Eastern Pacific Ocean*, Smithsonian Contributions to Zoology. Smithsonian Institution Press, Washington, DC, pp. 232-277.

Rogers, A.R., Harpending, H. (1992) Population growth makes waves in the distribution of pair-wise genetic differences. *Molecular and Biological Evolution* 9: 552-569.

Rozas, J., Sanchez-Delbarrio, J.C., Messeguer, X., Rozas, R. (2003) DnaSP, DNA polymorphism analyses by the coalescent and other methods. *Bioinformatics* 19: 2496-2497.

Sagar, P.M., Stahl, J.C., & Molloy, J. (1998) Sex determination and natal philopatry of southern Buller's Mollymawks (*Diomedea bulleri bulleri*). *Notornis* 45: 271-278.

Schjorring, S. (2001) Ecologically determined natal philopatry within a colony of great cormorants. *Behavioral Ecology* 12: 287-294.

Schjorring, S. (2002) The evolution of informed natal dispersal: Inherent versus acquired information. *Evolutionary Ecology Research* 4: 227-238.

Schoener, T. (1979) Generality of the size-distance relation in models of optimal feeding. *American Naturalist* 114: 902-914.

Schreiber, B.A., Burger, J. (2001) *Biology of Marine Birds*. Boca Raton, FL: CRC Press.

Seutin, G., White, B.N., & Boag, P.T. (1991) Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* 69: 82-90.

Shaffer, S.A., Tremblay, Y., Awkerman, J.A., Henry, R.W., Teo, S.L.H., Anderson, D.J., Croll, D.A., Block, B.A., & Costa, D.P. (2005) Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147: 833-843.

Shaffer, S.A., Costa, D.P., Weimerskirch, W. (2003) Foraging effort in relation to the constraints of reproduction in free-ranging albatrosses. *Functional Ecology* 17: 66-74

Shaffer, S.A., Tremblay, Y., Awkerman, J.A., Henry, R.W., Teo, S.L.H., Anderson, D.J., Croll, D.A., Block, B.A., & Costa, D.P. (2005) Comparison of light- and SST-based geolocation with satellite telemetry in free-ranging albatrosses. *Marine Biology* 147: 833-843.

Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., Sagar, P.M., Moller, H., Taylor, G.A., Foley, D.G., Block, B.A., Costa, D.P. (2006) Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proceedings of the National Academy of Science*. 103: 12799-12802.

Sheather, S.J., Jones, M.C. (1991) A reliable data-based bandwidth selection method for kernel density estimation. *Journal of the Royal Statistical Society, Series B* 53: 683-690.

Shuntov, V.P. (1974) *Seabirds and the biological structure of the ocean*. US Department of Commerce, Springfield.



Sievert, P.R., Sileo, L. (1993) The effects of ingested plastic on growth and survival of albatross chicks. In: Vermeer K, Briggs K.T, Morgan KH, Siegal-Causey D, editors. The status, ecology, and conservation of marine birds of the North Pacific Ottawa: Canadian Wildlife Service Specie Publication. pp 212-17.

Slatkin, M. & Hudson, R.R. (1991) Pairwise comparisons of mitochondrial DNA sequences in stable and exponentially growing populations. *Genetics* 129: 555-562.

Slatkin, M., & Excoffier, L. (1996) Testing for linkage disequilibrium in genotypic data using the expectation-maximization algorithm. *Heredity* 76: 377-383.

Smith, J.L. & Morgan, K.H. (2005) An Assessment of Seabird Bycatch in Longline and Net Fisheries in British Columbia. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia. p. 51.

Sorenson, M.D. & Quinn, T.W. (1998) Numts: a challenge for avian systematics and population biology. *The Auk* 115: 214-221.

Spear, L.B., Ainley, D.G., & Webb, S.W. (2003) Distribution, abundance and behaviour of Buller's, Chatham Island and Salvin's Albatrosses off Chile and Peru. *Ibis* 145: 253-269.

Spear, L.B., Balance, L.T., & Ainley, D.G. (2001) Response of seabirds to thermal boundaries in the tropical Pacific: the thermocline versus the Equatorial Front. *Marine Ecology-Progress Series* 219: 275-289.

Steele, J. (1979 ) Patchiness. In: *The Ecology of the Seas* (eds. D. Cushing & J. Walsh). Blackwell Scientific Publications Oxford.

Stephens, D.W., & Krebs, J.R. (1986) *Foraging Theory*. Princeton: Princeton University Press.

Suryan, R.M., Dietrich, K.S., Melvin, E.F., Balogh, G.R., Sato, F., & Ozaki, K. (2007). Migratory routes of short-tailed albatrosses: use of exclusive economic zones of North Pacific Rim countries and spatial overlap with commercial fisheries in Alaska. *Biological Conservation* 137: 450-460.

Tickell, W.L.N. (2000) *Albatrosses*. Yale University Press, Cambridge.

Tuck, G.N., Polacheck, T., & Bulman, C.M. (2003) Spatio-temporal trends of longline fishing effort in the Southern Ocean and implications for seabird bycatch. *Biological Conservation* 114: 1-27.

Tuck, G.N., Polacheck, T., Croxall, J.P., & Weimerskirch, H. (2001) Modelling the impact of fishery by-catches on albatross populations. *Journal of Applied Ecology* 38: 1182-1196.

VanderWerf, E.A., Swindle, K.A. & Young, L.C. (2005) Pox virus in Laysan Albatross at Ka`ena Point, O`ahu: how can we help? *Elepaio* 65: 1-7.

VanderWerf, E.A., Wood, K.R., Swenson, C., LeGrande, M., Eijzenga, H., & Walker, R. L. (2007) Avifauna of Lehua Islet, Hawai'i: conservation value and management needs. *Pacific Science* 61: 39-52.

Veran, S., Gimenez, O., Flint, E., Kendall, W.L., Doherty Jr., P.F., & Lebreton, J.-D. (2007) Quantifying the impact of longline fisheries on adult survival in the black-footed albatross. *Journal of Applied Ecology* 44: 942-952.

Wagner RH, Danchin É (2003) Conspecific copying: a general mechanism of social aggregation. *Ani. Behav* 65: 405-408

Wahl, T.R., Ainley, D.G., Benedict, A.H., & DeGrange, A.R. (1989) Associations between seabirds and water-masses in the northern Pacific Ocean in summer. *Marine Biology* 103: 1-11.

Walsh, H.E., & Edwards, S.V. (2005) Conservation genetics and Pacific fisheries bycatch: Mitochondrial differentiation and population assignment in black-footed albatrosses (*Phoebastria nigripes*). *Conservation Genetics* 6: 289-295.

Watterson, G.A. (1984) Allele frequencies after a bottleneck. *Theoretical Population Biology* 26: 387-407.

Weimerskirch, H., & Wilson, R. (2000) Oceanic respite for wandering albatrosses. *Nature* 406: 955-956.

Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, F., Ceunot-Chaillet, F., Hindermeier, X., & Judas, J. (1994b) Alternate long and short foraging trips in pelagic seabird parents. *Animal Behavior* 47: 472-476.

Weimerskirch, H., Doncaster, C.P., & Cuenotchaillet F. (1994a) Pelagic seabirds and the marine environment - foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society of London Series B-Biological Sciences* 255: 91-97.

Weimerskirch, H., Jouventin, P., Mougín, J.L., Stahl, J.C. & Vanbeveren, M. (1985) Banding recoveries and the dispersal of seabirds breeding in French Austral and Antarctic territories. *Emu* 85: 22-33.

Weimerskirch, H., Salamolard, M., Sarrazin, F., & Jouventin, P. (1993) Foraging strategy of wandering albatrosses through the breeding season - a study using satellite telemetry. *The Auk* 110: 325-342.

Whitlock, M.C. (1992) Temporal fluctuations in demographic parameters and the genetic variance among populations. *Evolution* 46: 608-615.

Whitlock, M.C. & McCauley, D.E. (1990) Some population genetic consequences of colony formation and extinction: genetic correlations within founding groups. *Evolution* 44: 1717-1724.

Whitlock, M.C. & McCauley, D.E. (1999) Indirect measures of gene flow and migration:  $F_{ST}$  not equal  $1/(4Nm + 1)$ . *Journal of Heredity* 82: 117-125.

Whittow, G.C. (1993) Laysan albatross (*Phoebastria immutabilis*). In Pool A, Gill F (eds) *The birds of North America* no 66. The Academy of Natural Sciences and The American Ornithologists' Union, Washington, DC

Wilson, R.P., Ducamp, J.J., Rees, G., Culik, B.M., Niekamp, K. (1992) Estimation of location: global coverage using light intensity. In: Priede IM, Swift SM editors. *Wildlife telemetry: remote monitoring and tracking of animals*. Chichester: Ellis Horward. pp 131-134.

Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home ranges. *Ecology* 70: 164-168.

Young, L.C. & VanderWerf, E.A. (2008) Prevalence of avian pox virus and effect on fledging success in Laysan Albatross. *Journal of Field Ornithology* 79: 93-98.

Young, L.C., Zaun, B.J., & VanderWerf, E.A. (2008) Successful same sex pairing in Laysan Albatross. *Biology Letters* 4: 323-325.

Zeillemaker, C.F. & Ralph, C.J. (1977) First breeding record of Laysan Albatross on Kauai. *Elepaio* 38: 51-53.