PELAGIC SEABIRD MOVEMENT ECOLOGY: ASSESSING DRIVERS OF ALBATROSS (*DIOMEDEIDAE*) MOVEMENT AND THE UTILITY OF BIOLOGGING TOOLS FOR WIDE-RANGING AND THREATENED SEABIRDS

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Abstract

Wide-ranging pelagic seabirds are among the most threatened and most mobile of all marine taxa. Understanding their movement ecology is necessary to develop effective conservation solutions for declines, yet many drivers of their movements throughout the life cycle are poorly understood. Particularly, movements during two critical life stages are known in little detail for many species: the period of post-natal dispersal for fledglings and the non-breeding period for adults. Biologging technologies provide means to study individual at-sea movements during all life stages. However, advances in analytical approaches for examining biologger data have in some cases lagged behind that of the technologies themselves. The objectives of my thesis are to address weaknesses in our understanding of seabird movement ecology and in the approaches used to describe seabird movement from biologger data, using two threatened seabirds, the Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses, as models. In Chapter Two, I describe for the first time the movement and habitat of black-footed albatross fledglings, and compare with those of non-breeding adults. In Chapter Three, I develop an approach to assess detailed activity budgets for non-breeding seabirds, and apply this method to explore drivers of non-breeding movements for both model species. In Chapter Four, I evaluate the limitations of a common approach where period-specific space use for a group, such as a colony, is inferred from a sample of biologger-equipped individuals. In Chapter Five, I build a conceptual framework of the drivers of movement with a focus on the albatross family (*Diomedeidae*), and apply this to identify trends and weaknesses in the literature on albatross movement. My work demonstrates the value of taking a holistic view of seabird movement ecology; interpreting observed movement patterns requires considering multiple interacting factors that drive individuals to move, including intrinsic factors, such as age, breeding phase, and moult status, as well as how “decisions” are made of when and where to move, and what modes of movement are used. Biologging tools afford insights into these drivers of movement, especially when the individual nature of biologger data is considered in analyses, with implications for ecological understanding and conservation.

List of Abbreviations Used

Abbreviation	Description
ANOVA	Analysis of Variance
BAS	British Antarctic Survey
BEC	Bout Ending Criteria
black-footed(s) or BFAL	black-footed albatross *Phoebastria nigripes*
Chl *a*	Chlorophyll *a*
CR	Critically Endangered
DSD	Days Since Departure
ECR	Early Chick Rearing
EN	Endangered
GAMM	Generalized Additive Mixed-effects Model
GLS	Global Location Sensing device
IUCN	International Union for the Conservation of Nature and Natural Resources
In	Inbound transit phase of non-breeding
IQR	Interquartile Range
KDE	Kernel Density Estimation (or Estimate)
Laysan(s) or LAAL	Laysan albatross *Phoebastria immutabilis*
LCR	Late Chick Rearing
LOESS	Locally-weighted scatterplot smoothing
Max	Maximum
MCMC	Markov Chain Monte Carlo
ME	Movement Ecology
Midway or Midway Atoll	Sand Island, Midway Atoll National Wildlife Refuge
Min	Minimum
NPTZ	North Pacific Transition Zone
NT	Near Threatened

Abbreviation	**Description**
Out	Outbound transit phase of non-breeding
OW	Overwinter phase of non-breeding
PBE	Pre-breeding and Eggs
PTT	Platform Terminal Transmitter device
REML	Restricted Maximum Likelihood
SD	Standard Deviation
SE	Standard Error
SST	Sea Surface Temperature
SSM	State-Space Model
Tern or Tern Island	Tern Island, French Frigate Shoals
TZCF	Transition Zone Chlorophyll Front
VU	Vulnerable

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Chapter 1: Introduction

Movement plays a critical role in determining the occurrence and outcomes of ecological interactions, which in turn drive population, community, and ecosystem dynamics (Nathan et al. 2008). Ecological interactions occur between organisms (e.g. courtship, predation, or competition), and between organisms and the abiotic environment (e.g. thermoregulation, or searching for food or mates using physical or chemical cues; Ricklefs 1979). Ecological interactions can also include direct contact with human activities (e.g. poaching or vehicular collisions) and more indirect anthropogenic influences on the environment (e.g. food resource depletion or altered weather patterns from human-induced climate change). The outcomes of ecological interactions can be beneficial or detrimental to the fitness of individuals, and thus impact the persistence of populations, the structure of communities, and the health of ecosystems (Ricklefs 1979). Hence, ecologists and managers share in the need to better understand the complex causes and consequences of movement for their target species (Nathan et al. 2008, Wilson et al. 2015).

In the marine realm, seabirds are conspicuous inhabitants, moving extraordinary distances between breeding colonies, pelagic foraging zones and over-wintering areas. Because they use such large oceanic areas, pelagic seabirds can encounter a wide range of risks to survival and reproduction throughout their movements (Croxall et al. 2012). Small decreases in survivorship and breeding success can have a major impact on populations, as their life history traits (delayed maturity, long lifespan, low annual fecundity and slow overall population growth; Ricklefs 1990, Warham 1990, Tickell 2000) are sensitive to disturbance. While many direct interactions with anthropogenic threats occur at breeding sites (e.g. invasive species, habitat alteration), several significant contemporary challenges encountered by seabirds are in the marine environment (Burger & Shaffer 2008, Croxall et al. 2012). The greatest marine-based threats to seabirds are those from fatal entanglement in fishing gear, ineffective management of fisheries, and pollution (Croxall et al. 2012, IUCN 2015). Due primarily to anthropogenic influences, wide-ranging pelagic seabirds, and especially the albatross family (*Diomedeidae,* Order: *Procellariiformes*), are the most imperilled of all groups of birds, with most species exhibiting alarming declines over recent decades (Croxall et al. 2012, IUCN 2015, Paleczny et al. 2015).

For all threatened seabirds, a more comprehensive understanding of the complex drivers of movement is necessary to advance the study of movement ecology and to develop effective conservation solutions to their many threats. Because seabirds spend the majority of their lives out to sea, many relatively simple ecological questions surrounding their movements and related interactions are challenging to answer (Burger & Shaffer 2008). For example, where and how do breeding adults find food resources for provisioning chicks? Where do fledglings go at sea during the prolonged period of immaturity, why do they go there, and what ecological interactions could impact their recruitment to the breeding population? Similarly, where do adults go at sea during the non-breeding period and what do they do there? The development of sound management plans to address seabird declines also requires answers to these questions; as birds modify their movements and space use in response to shifting energetic constraints throughout the life cycle (Ashmole 1971, Ricklefs 1983), they likely encounter different natural and anthropogenic pressures that impact survival and reproduction (Lack 1968, Shillinger et al. 2012). In order for managers and policy-makers to design and implement effective mitigation strategies that best reflect the movement ecology of threatened seabirds, knowledge of the timing, source and severity of potentially detrimental ecological interactions is indispensible (Ronconi et al. 2012, IUCN 2015, Wilson et al. 2015, Lascelles et al. 2016).

Biologging technologies (i.e. animal-attached electronics) have provided unprecedented opportunities to examine questions about seabird movement ecology. The miniaturization of electronic devices paired with increased capacity to store or transmit large volumes of data has brought rapid advancements and innovation to the field of biologging (Hussey et al. 2015, Wilson et al. 2015). As such, a variety of bird-borne devices have been widely applied in the study of seabird movement, often with the intention of ultimately informing conservation actions and management decisions (Burger & Shaffer 2008, Ronconi et al. 2012). Yet, many aspects of the drivers of movement throughout the life cycle remain poorly understood. In particular, movements during two critical life stages are known in little detail for many species: the period of post-natal dispersal for fledglings and the period of non-breeding for adults. In addition, advances in analytical approaches for examining biologger-derived data have in some cases lagged behind that of the technologies themselves (Demšar et al. 2015). We now have the capability to obtain data on the movement and behaviour of individual seabirds, which can then be applied to make ecological inferences and management recommendations. But these inferences and recommendations are most valuable if the methods used to describe and evaluate movement patterns are robust to the limitations of the data. Therefore, the two major objectives of my thesis are to identify and address weaknesses in: 1) our understanding of seabird movements with a focus on the albatross family and, 2) the approaches used to describe and evaluate seabird movement based on biologger data.

To meet these objectives, I used two threatened seabirds from the North Pacific Ocean as model species, the Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses. These species differ in diet and marine habitat preferences but are similar in size, breeding phenology, and breeding locations, with the majority of birds nesting in the Northwestern Hawaiian Islands (Tickell 2000, Arata et al. 2009). Past biologging studies have investigated detailed habitat use and behaviour of both species during breeding (Fernández et al. 2001, Hyrenbach et al. 2002, 2006, Young et al. 2009, Kappes et al. 2010, 2015, Conners et al. 2015) and more basic at-sea distributions during non-breeding (Hyrenbach & Dotson 2001, Young et al. 2009, Fischer et al. 2009, Block et al. 2011, Hyrenbach et al. 2012). Similar to most seabirds, their movements are relatively restricted around breeding sites during early chick rearing but expand through late chick rearing and fledging (Arata et al. 2009). Their at-sea ranges encompass the entire North Pacific, including offshore waters of Japan, Russia, Canada, the United States, and Mexico, as well as the highly pelagic regions between. Laysan and black-footed albatrosses face typical anthropogenic threats to seabirds both on land and at sea, and are thus considered ‘Near-Threatened’ (IUCN 2015). The highest research priority for the conservation of these species is to investigate movements throughout the entire life cycle in order to identify important marine areas and spatially and temporally explicit threats (Naughton et al. 2007, IUCN 2015). The movements of fledglings had been previously undocumented, and the movements of adults outside the breeding period had been studied in limited detail.

A partnership with the U.S. Fish & Wildlife Service and collaborations with various seabird scientists allowed access to extensive biologger datasets from multiple colonies of Laysan and black-footed albatrosses, on which Chapters Two, Three and Four of this thesis are based. Because of the imperilled state of these species and the availability of biologger data, they act as excellent model species to address weaknesses in our understanding of seabird movement ecology and in the approaches used to describe and evaluate seabird movement based on biologger data. In Chapter Two, I document for the first time the movements and habitat associations of biologger-equipped black-footed albatross fledglings, and compare their patterns with those of non-breeding adults. In Chapter Three, I develop a novel approach to assess detailed activity budgets for non-breeding seabirds, and apply this method to explore drivers of non-breeding movements for Laysan and black-footed albatrosses. In Chapter Four, I use Laysan and black-footed albatrosses as model wide-ranging seabirds to evaluate the inferential limitations of a common approach used by seabird ecologists to infer the space use of a larger group from a sample of biologger-equipped individuals. In Chapter Five, I focus on the albatross family (*Diomedeidae*) to build a conceptual framework of the drivers of movement, and apply this framework to identify trends and weaknesses in the albatross-biologging movement literature. Overall, the findings of my dissertation illustrate a need to expand biologging research beyond the factors that are well understood in order to develop a more holistic understanding of seabird movement. This is necessary to broaden our understanding of movement ecology for wide-ranging marine seabirds, which can in turn inform responsible science-based management. More generally, my work demonstrates the powerful insights afforded by biologging tools into movement ecology, while underscoring the importance of combining approaches and considering the individual nature of the data in analyses.

Chapter 2: Post-Breeding Distribution And Habitat Associations Of Fledgling And Adult Black-Footed Albatrosses In The North Pacific

Abstract

Past biologging studies of marine animals have primarily targeted adults, biasing our understanding of at-sea habitat use and movement ecology toward older life stages. Anthropogenic threats persist throughout the at-sea ranges of all life stages and it is therefore of interest to ecologists and managers alike to understand spatiotemporal distributions and possible niche differentiation among age-classes. In albatrosses, particularly little is known about the juvenile life stage when fledglings depart the colonies and venture to sea with no prior experience or parental guidance. Here I describe the movements of 18 fledgling black-footed albatross *Phoebastria nigripes* tracked from Midway Atoll between 2006 and 2008 using satellite telemetry. I then compare fledgling movements and habitat associations with those of 16 adults tracked from the same colony between 2008 and 2009 using coarser-scale light-based geolocation. Following device deployment, all fledglings spent several days in the calm atoll waters, then dispersed northward until reaching 750-900 km from the colony. At this point, fledgling distributions approached the productive North Pacific Transition Zone (NPTZ). Rather than reaching the high chlorophyll *a* densities on the leading edge of this zone, however, fledglings remained in restricted areas of low productivity and warm surface waters in the subtropical gyre. In contrast, adult albatrosses tracked concurrently from the same breeding colony ranged widely throughout the cool and highly productive pelagic regions and northern periphery of the Pacific Ocean basin among the shelf regions off Japan and the Aleutian Islands. The dichotomy in habitat use between fledglings and adults tracked from Midway suggests some degree of ontogenetic niche separation in this species. This research begins to fill a large knowledge gap in at-sea habitat use during a little known yet critical life stage of albatrosses, and contributes to a more comprehensive understanding of differential mortality pressure between age-classes and overall conservation status of the near-threatened black-footed albatross.

Introduction

Management and conservation of animal populations require an understanding of where organisms are found in space and time, and the associated habitat characteristics influencing this spatiotemporal distribution (Costa et al. 2012). However, for most far-ranging migratory species, this spatial information can be difficult to obtain. With roughly 1,800 migratory bird species globally, gathering comprehensive information on the distribution of any species throughout the entire annual and life cycle poses a common challenge (Şekercioğlu et al. 2004). This is especially true of long-distance migratory marine species, for which direct observation over long periods for the majority of the life cycle is logistically impossible (Hazen et al. 2012).

Many pelagic bird species range across extraordinary oceanic distances spanning multiple management jurisdictions and anthropogenic threats, and thus can encounter a wide range of risks to survival and reproduction throughout their lifetime (Shaffer et al. 2006, Egevang et al. 2010). Of all seabird families, albatrosses are the most threatened, with 15 of 22 species listed as Threatened by the IUCN and the remainder Near Threatened (IUCN 2015). Investigations of at-sea distributions throughout all seasons and life stages are therefore critical in building a spatially and temporally integrated survey useful for conservation and management applications.

Little information exists on the juvenile life stages of albatrosses, despite representing nearly half the total population of any species (Weimerskirch et al. 2006). When fledging occurs, juvenile albatrosses depart to sea, seemingly without parental influence (Tickell 2000). Hence, they must develop and refine their skills at flying as well as their ability to successfully search for and capture prey without guidance from experienced adults. It is unclear how fledglings are able to assess and integrate environmental cues necessary for navigating in the pelagic environment and finding food, such as celestial or olfactory information, or currents and dynamic features associated with biological productivity and prey availability. It is therefore not surprising that mortality rates of albatrosses are generally highest during the first few years of life at sea (Fisher 1975, Warham 1990, Weimerskirch et al. 1997a).

Information on the spatial distribution of juveniles is difficult to obtain due to high mortality rates and an extended multi-year at-sea period following fledging, precluding the retrieval of expensive electronic tracking devices. Our current understanding of juvenile albatross postnatal dispersal and at-sea behaviour is based on six species from seven published studies (Walker & Elliott 2006, Weimerskirch et al. 2006, Thomas & Holland 2010, Alderman et al. 2010, Deguchi et al. 2013, Riotte-Lambert & Weimerskirch 2013, Thiebot et al. 2014). These studies documented the movements of wandering albatross *Diomedea exulans*, shy albatross *Thalassarche cauta*, short-tailed albatross *Phoebastria albatrus,* Northern royal albatross *Diomedea sanfordi*, Amsterdam albatross *Diomedea amsterdamensis* and Antipodean albatross *Diomedea antipodensis* for periods of 10 days to one full year. Fledgling short-tailed, Antipodean, Amsterdam, and Northern royal albatrosses were found to range widely throughout the entire at-sea region exploited by older age-classes (Walker & Elliott 2006, Thomas & Holland 2010, Deguchi et al. 2013, Thiebot et al. 2014). For wandering and shy albatross, juvenile core areas did not overlap spatially with adults; however, the nature of this segregation differed between species. Wandering albatross fledglings appear to concentrate into much less productive regions but overlap more with fishing operations compared with adults (Weimerskirch et al. 2006, Riotte-Lambert & Weimerskirch 2013), whereas young shy albatrosses exhibit the opposite pattern, exploiting more productive oceanic areas than adults (Alderman et al. 2010). Investigating differential movements and habitat use has important implications for population ecology and conservation biology due to the potential consequences of niche width and differential mortality pressures faced by different age-classes (Weimerskirch et al. 1997a, 2006).

Black-footed albatross *Phoebastria nigripes* in the North Pacific Ocean are thought to exhibit some age-related differences in distribution at sea (Hyrenbach et al. 2002). Although the at-sea movements of adults from some colonies have been studied previously (Fernández et al. 2001, Hyrenbach et al. 2002, Shaffer et al. 2005, Fischer et al. 2009, Kappes et al. 2010), nothing is known about patterns of juvenile dispersal from the natal colony. The IUCN listed black-footed albatrosses as Near Threatened in 2014, based on projected declines over the next three generations due primarily to incidental fisheries mortality (Lewison & Crowder 2003, IUCN 2015). Therefore, it is critical to assess whether differential mortality of juveniles due to distribution at sea may be contributing to this decline. Unfortunately, because the distribution of juveniles has not been directly studied, little can be said about the influence of at-sea habitat use on the mortality of juvenile albatrosses in the North Pacific. In the present study, I identify for the first time the initial dispersal movements, at-sea distributions and habitat associations of tracked black-footed albatross fledglings. By combining concurrent fledgling and adult biologging data (from satellite transmitters and light-based data loggers) during the first months of post-fledging life out to sea, I assess how black-footed albatross fledglings and adults from the same colony may segregate at sea over large spatial scales.

Methods

Study Site And Device Deployment

I followed 22 fledgling black-footed albatross departing from Sand Island, Midway Atoll National Wildlife Refuge (28.21°N, 177.36°W; herein 'Midway') between 2006 and 2008 (2006 n = 10, 2007 n = 4, 2008 n = 8). Roughly 96% of the world population of this species breed at colonies in the Northwestern Hawaiian Islands, with over one-third nesting at Midway (Arata et al. 2009). This species has a well-defined breeding cycle with little documented inter-annual or inter-colony variation. The majority of eggs are laid before mid-December, followed by an average incubation period of 66 days and hatching occurs by late-January. The chick provisioning period averages 150 days, during which the adults spend most of their time foraging at sea, returning to the colony only to briefly feed chicks until fledging from mid-June to mid-July (Arata et al. 2009). All albatross fledglings in this study were captured near their nests or on the beach adjacent to their colony during the months of June and July, when adults have completed provisioning. All birds were nearly (99%) free of down and were considered near fledging age and in good body condition when captured. Each bird was equipped with a *c.* 20-35 gram satellite Platform Terminal Transmitter (PTT, SPOT4/SPOT5; Wildlife Computers, Redmond, WA, USA). The mass of these devices was approximately 1% of bird body mass, well below the suggested maximum (Phillips et al. 2003). Satellite transmitters were attached to dorsal feathers with Tesa® tape (Weimerskirch et al. 1994) and were programmed to transmit a signal every 90 seconds, for eight hours a day, operating for 33% of the total time they were deployed. Due to the tag duty cycle encompassing a 24-hour period and the spatiotemporal scale of factors considered in this study, the duty cycle of the tags did not limit broad-scale characterization of post-natal dispersal and distribution. Tag transmissions were localized by orbiting satellites of the Argos System (Fancy et al. 1988). We received an average of 6 ± 2.3 (standard deviation) locations per transmitter per day and a total of 6,577 locations during the tracking durations across all three years. All transmitters were expected to last 8-14 months (given the manufacturer's battery power specifications) and were intended to be lost at sea when fledglings underwent the first moult, some time between 16 and 21 months after fledging (Awkerman et al. 2008).

For macro-scale comparison of distributions and habitat associations between age-classes, I followed adults from the same colony at Midway using Global Location Sensing (GLS) tags that allow estimates of latitude and longitude based on ambient light levels, providing location estimates at lower accuracy than satellite-derived estimates (mean error ± standard deviation of 186 ± 114 km versus 41 ± 30 km, respectively; Phillips et al. 2004a, Shaffer et al. 2005). GLS were deployed and successfully retrieved on 16 breeding adults in 2008 (n = 7) and 2009 (n = 9). Each year, adults were captured on the nest during the incubation period (mid-December to early January) and equipped with a *c.* 6 gram Lotek LTD 2500 geolocation archival data logger (Lotek Wireless, St. John's, Newfoundland) mounted on a plastic identification leg band using UV-resistant cable ties and quick-setting epoxy, resulting in a total package <10 grams. GLS use light sensors autonomously to log maximum ambient light levels at 10-minute intervals to on-board memory. During the incubation period of the following breeding season (November to January), birds were recaptured and devices retrieved. Equinox periods do not overlap with the time period of interest for this study and did not pose a problem. Light data were processed with automated template fitting software, producing a single location estimate per day using sunrise and sunset times to estimate latitude from day length and longitude from the time of local noon/midnight (Ekstrom 2004).

Positional Data Processing And Analysis

Positional data obtained from PTT and GLS tags were filtered and interpolated using software written in Matlab (MathWorks Inc, USA; IKNOS Toolbox, Y. Tremblay unpublished). Unrealistic GLS location estimates can occur due to major interference to the light sensor (e.g. feather shading, water immersion or cloud cover) or broad daily movements, while unrealistic PTT location estimates can occur due to issues with device power output, antenna efficiency, temperature changes or rapid movements. Unrealistic locations in the datasets were removed in cases of extreme flight speeds and track spikes by applying the following filters: 1) flight speeds, calculated as transit rates between successive locations, of >80 km/h were filtered out, and 2) successive locations with an azimuth change of >170° were removed. To avoid simultaneous locations fixes from overlapping satellite transmissions, successive points <10 minutes apart were removed. All fledgling satellite tracks were interpolated at hourly intervals using a piecewise cubic Bézier curve with $\mu = 0.3$ (the parameter μ controls curve elasticity and a value of 0.3 allows high curvature, Tremblay et al. 2006) to create even sampling in time between all birds, which aids in generating reasonable Kernel Density Estimation (KDE) distributions for visualization of space use by age-class.

Visual inspection of interpolated tracks of fledglings revealed that each undertook a consistent post-tagging dispersal pattern, delineated into three distinct phases: 1) the resident pre-departure phase, 2) the directed northward transit phase, and 3) the at-sea phase (Figure 2.1). Each phase was identified by rapid shifts in travel rate and bearing between consecutive locations, along with total distance reached from the colony. For the purposes of this study, a series of rules was applied to delimit each track into these three phases for later analyses. Phase 1 was marked by low travel rates (<10 km/h) without directed travel within a 50 km radius of the colony. I defined the beginning of Phase 2 as the location at which travel rates began to increase to >10 km/h in one direction (most commonly due north) consistently for a minimum of five consecutive hourly locations. I defined Phase 3 as the point in the track where both travel rate slowed markedly (determined relative to an individual's average Phase 2 travel rate but generally <15 km/h) and where consistent northward directionality dissipated, occurring for all fledglings between 750 and 900 km from the colony (Figure 2.1).

All fledglings entered Phase 3 of post-tagging dispersal by 28 July, and all adults began the post-breeding period, when they were no longer tied to the colony, by the same date. Fledgling PTT tags ceased transmission between 7 July and 14 November, with most terminating in late August or early September. Thus, for comparative analyses of distributions and habitat between fledglings and adults, only locations during the month of August were used. This ensured that adult at-sea locations represented those of post-breeding adults at maximum temporal overlap with Phase 3 fledglings, while avoiding errors in GLS location estimates resulting from the September equinox period. Four fledgling tracks failed to enter Phase 2 due to early loss of tag transmission and were therefore not included in any analyses. To assess behaviour, descriptive track characteristics for each of the remaining 18 fledglings and 16 adults were calculated from filtered and interpolated data. Approximate travel rates (km/day) and maximum range reached from the colony (km) were calculated for all birds. In addition, I tabulated for fledglings the number of days spent in each post-tagging phase and track duration (Table 2.1).

To examine patterns of space use within and between age-classes, I employed KDE (Worton 1989) to both pooled and individual fledgling and adult August locations. Small sample sizes in terms of the number of individuals tracked within each year for both fledglings and adults necessitated pooling data within age-classes across years. Thus pooled KDEs are used here as a means of visualizing space use of the tracked birds contributing to the datasets while acknowledging that the kernel contours are likely sensitive to sampling effects, particularly for adults (Chapter Four). The geographic coordinates of each bird location was transformed to Cartesian coordinates using a Lambert Cylindrical Equal Area projection (Wood et al. 2000) and 2D (bivariate) Gaussian kernel densities were computed on a 1° x 2° grid (accounting for the approximate error of the least accurate geolocation estimation method, Shaffer et al. 2005). KDE were conducted using the IKNOS Matlab toolbox (following Shaffer et al. 2009, Kappes et al. 2010). The smoothing parameter (h) was estimated using an adaptive method to produce optimal fixed values for each dataset (Wood et al. 2000). The density surface was divided into concentric polygons to calculate utilization distribution kernel density contours of 95%, 75%, 50% and 25%.

Habitat Characterization

To examine the oceanographic characteristics of the areas used by tracked fledglings and adults, I used remotely sensed data based on location estimates for each individual and for group-level estimates of each age-class. Oceanographic variables were selected based on demonstrated biological relevance to the species and study area, as factors previously documented to influence foraging conditions and movement (e.g. Hyrenbach et al. 2006, Kappes et al. 2010). Remotely sensed data were obtained from publicly available time series of environmental data (http://coastwatch.pfel.noaa.gov/, see website for metadata on satellite sensors and parameters). These datasets included science quality products for chlorophyll *a* concentrations (Chl *a*, mg/m^3) with resolution 0.1°; multiple-satellite blended sea surface temperature (SST, °C, resolution 0.1°, for details on specific SST datasets and use of Chl *a* and SST as proxies for local biochemical regimes influencing presence of prey see Powell et al. 2008); and 3-day average surface wind vectors (0.25° resolution, likely to influence both flight conditions and local prey aggregation from surface water convergence/divergence) measured from the QuickSCAT spacecraft (Freilich 2000). Data for each environmental parameter were extracted from the global time series within a 1° by 2° grid centered on the location and date of each PTT or GLS location estimate. The mean ± standard deviation of the data for individual locations for each age-class are reported to characterize the general oceanographic conditions encountered by tracked fledglings and adults during the month of August, when all fledglings had reached Phase 3 of post-tagging dispersal and all adults had begun the post-breeding period.

Statistical Analyses

Statistical comparisons were performed using R 2.15.1 (R Development Core Team 2012). To investigate differential oceanographic conditions experienced by tracked birds of each age-class during August, mixed-effects ANOVAs were used to test for differences between environmental parameters for locations using individual bird as a random factor. Restricted maximum likelihood (REML) estimations were used, and Type 3 sums of squares were compared to account for the unbalanced design (unequal number of observations for oceanographic parameters from each bird and age-class; Shaffer et al. 2009).

Results

Fledgling Dispersal

The 22 fledglings were tracked for 46.8 ± 28.4 days (mean ± standard deviation, Table 2.1). The tracks of four individuals ceased transmission before 15 days and did not enter post-tagging Phase 2. These four birds were not included in subsequent calculations or analyses. Dispersal behaviour was highly consistent among individuals (Figure 2.1). Fledglings traveled at an average rate of 137.4 ± 54.7 km/day over the entire duration of tracking, but travel rates and bearings consistently shifted post-tagging, corresponding to each of the three post-tagging phases of dispersal. The birds remained relatively stationary (31.5 ± 15.1 km/day) for the first 8.6 ± 5.7 days after tag attachment, remaining either on shore or near the protected area of the atoll (Figure. 2.1 inset) before beginning a northerly migration. This shift marked the beginning of post-tagging dispersal Phase 2, initiated on 9 July ± 9 days. Directed transit lasted an average 5.2 ± 2.4 days, with travel rates of 199.0 ± 46.7 km/day, in a consistently northward, north-northeast or north-northwest bearing (Figure 2.1). Upon entering Phase 3, travel rates initially decreased and the sinuosity of movements increased, while maintaining an overall average travel rate of 197.7 ± 57.1 km/day. The number of days spent in Phase 3 differed between individuals due to varying transmission failure dates, with an average of 42.5 ± 28.2 days (Table 2.1).

Fledgling Movements At-Sea

Fledglings travelled quickly in Phase 2 to reach deep pelagic waters in a band between 35-40° N, before dispersing zonally across the central North Pacific in Phase 3. There was high consistency among fledglings in that they generally remained within *c.* 1,500 km north of the colony (based on the 95% kernel contour), with maximum distances from the colony for individual birds varying between 820-4,343 km (Table 2.1). The 95% kernel contour generated from pooled KDE (Figure 2.2) appears to be a reasonable representation of the group-level range and distribution given the low variability in north-south movements among fledglings during Phase 3 in August (Figure 2.1). The individual-based 95% kernel contours fell within the pooled 95% contour, thus only the pooled KDE results are shown. Most fledglings remained within 15° on either side of the dateline in August; however, later in Phase 3 five individuals did travel beyond the approximate east and west limits delineated by the pooled 95% kernel contour (*c*. 150° E and 160° W) which covered an area of *c.* 4,200,000 km^2.

Fledglings And Adults At Sea In August

Tracked non-breeding adults dispersed widely in comparison to fledglings, traveling in both study years to the shelf regions along the periphery of the North Pacific Ocean basin around Japan, the Aleutian Islands, and the Gulf of Alaska, as well as pelagic regions (Figure 2.2). The area encompassed by the pooled 95% kernel contour was *c.* 15,500,000 km^2, owing to the high individual variation in areas used among the 16 tracked adults (Figure 2.3). Throughout the month of August, non-breeding adults maintained average daily travel rates of 269 ± 92 km/day while reaching maximum distances from the colony between 2,189-5,524 km (Table 2.1). The 95% kernel contours of tracked fledglings and adults showed near complete spatial segregation in August, overlapping just at the far edges of the distributions (Figure 2.3).

Oceanographic conditions experienced by tracked fledglings and non-breeding adults in August differed significantly between age-classes in both SST and Chl *a* density ($F_{1,32} = 93$ and $F_{1,30} = 18.4$, respectively, $P<0.001$). Fledglings encountered average SST of 21.8 ± 2.2 °C whereas adults experienced much lower temperatures on average of 12.6 ± 4.7 °C. Fledgling locations were characterized by Chl *a* of 0.12 ± 0.059 mg/m^3, and adult locations of 0.67 ± 0.67 mg/m^3 (Figure 2.3). Wind vectors did not differ significantly between age-classes; fledglings encountered winds of 5.9 ± 2.1 m/s while adults encountered similar winds of 6.2 ± 1.9 m/s. No significant differences were detected among individuals within age-classes in oceanographic conditions, except for adult SST. The average SST encountered by tracked adults varied by >10 °C; average individual SST ranged from 8.25 °C (± 3.05) to 20.01 °C (± 3.29).

Discussion

Past biologging studies of marine animals have primarily targeted adults, biasing our understanding of at-sea habitat use and movement ecology toward older life stages (Hazen et al. 2012). Although tracking durations were short and sample sizes small, my results identify for the first time a striking dichotomy in basin-scale patterns of distribution and habitat between fledgling and post-breeding adult black-footed albatross tracked concurrently from the same colony. This ontogenetic niche divergence is possibly the product of juvenile naïvety, differential energetic demands and direct or historical competitive interactions between age-classes.

Fledgling Tracking Success

The duration of fledgling tracking fell short of expectations given the history of satellite tagging efforts with this and other albatross species, and this may be attributed to several possible causes. First, some fledglings could have perished at sea. Estimates of juvenile survival in black-footed albatross from Midway Atoll suggest that only 57% of fledglings survive during the first 1-3 years (Cousins & Cooper 2000). This low survival rate could be influenced by fisheries-related mortality (Cousins et al. 2000) but incidental by-catch is not the only source of mortality for fledglings. The initial days (Alderman et al. 2010) or months (Weimerskirch et al. 2006, Riotte-Lambert & Weimerskirch 2013) are thought to be the point at which juvenile mortality is at its greatest for naïve birds. Many fledglings become waterlogged and drown on ill-fated flight attempts, and others succumb to dehydration or starvation before successfully departing the colony to begin foraging for themselves. Unique to the Northwestern Hawaiian Island colonies, fledglings also face tiger shark *Galeocerdo cuvieri* predation during this already vulnerable period, as these predators are known to aggregate in the atoll waters during the fledging season awaiting naïve birds' first incursions to sea (Arata et al. 2009). It is also possible that tracking duration was limited by the failure of satellite tags to transmit before dropping off during moult, where faulty software of hardware could have resulted in transmission loss. Because we did not observe unusual transmission patterns (e.g. weak or loss of signal strength) prior to loss in signal, it is unlikely that tags failed during deployments. It is more likely that some short tracks were due to premature loss of the tag itself. Satellite tagging using leg-loop harness attachments on Laysan albatross fledglings from Midway Atoll lasted considerably longer (J. Klavitter, *pers. comm.*). Although black-footed albatross fledglings departed with freshly grown plumage, attachment of the tag itself may have weakened feathers, causing early tag loss (R. Suryan, *pers. comm.*).

Age-Based Drivers Of Movement

It has long been suggested that younger life stages have different energetic and resource allocation needs than adult stages, as well as different proficiencies in locating and exploiting food resources (Lack 1954). In albatrosses, adults are faced with energetically demanding and lengthy breeding periods, where provisioning both themselves and their growing chicks is made challenging by central-place foraging constraints and results in an unavoidable loss of adult body condition (Jouventin & Dobson 2002). The post-breeding period of only four months leaves limited time to recover, while also allocating resources to feather growth for moult and compensating for reduced flight and subsequent foraging performance due to flight feather gaps (Rohwer et al. 2011, Chapter Three). In contrast, fledglings during their first year at sea must learn to navigate, fly, forage and survive but lack the resource demands of breeding and feather replacement, as they will not undergo flight feather moult until between 16 and 21 months old (replacing only their distal three or four primaries in a pre-basic I moult; Awkerman et al. 2008).

Fledgling Dispersal Travel Rates

Daily travel rates during dispersal support the suggestion that fledglings have differing energetic demands and flight proficiencies relative to adults. The success of rapid long-distance travel in albatrosses is attributed to their remarkable adaptations for strategically exploiting wind and wave conditions through dynamic soaring (Suryan et al. 2008). Prior to attaining the sustained northward flight of true fledging, the initial stationary post-tagging phase (Phase 1) represents a period where fledglings spend time practising skills and developing flight muscles in the protected waters of the fringing reef at Midway Atoll (Figure 2.1, inset). Winds likely influence fledgling movement decisions during Phase 1, where young birds may be waiting on favourable winds for departure (Weimerskirch et al. 2006). To test this idea, future efforts could look to more localized analyses of wind effects, including both strength and direction, on fledgling movements in the vicinity of the colony. Once fledglings departed the colony (Phase 2), they travelled relatively slowly at *c.* 200 km/day. Incubating (Kappes et al. 2010), brooding and rearing (Hyrenbach et al. 2002) adults commuting to the NPTZ from Tern Island, French Frigate Shoals (approximately 1,200 km southeast of Midway), can cover *c.* 670

km/day. Fledglings on their maiden voyage lack the urgency of temporal and spatial constraints of returning to the colony to relieve a nest-bound partner or provision young, and also lack the learned efficiency of travelling rapidly with prevailing winds to productive foraging areas.

Habitat Associations At Sea

Once beyond 50 km of the atoll, each fledgling travelled north towards the oceanic region generally known as the North Pacific Transition Zone (NPTZ). Breeding black-footed albatross are known to exploit the NPTZ (Hyrenbach et al. 2002, Kappes et al. 2010) along with many other meso- and apex predators (e.g. seal, sharks, tuna, Block et al. 2011; sea turtles, Polovina et al. 2001). At the NPTZ, well known oceanographic processes create generally high biological productivity in an area positioned between 30° and 45°N, biochemically positioned at Chl *a* concentrations of >0.25 mg/m^3, and thermally positioned around the 18°C isotherm (Polovina et al. 2001). Large-scale frontal systems and meso-scale dynamic features create large gradients of horizontal oceanographic variability that heavily influence the NPTZ, enhancing productivity and concentrating food resources such as flying fish (*Exocotidae*) eggs, floating carrion, and other buoyant prey items (Hyrenbach et al. 2002, Seki et al. 2004).

Fledglings headed toward the NPTZ but stopped short of oceanographic conditions frequented by tracked adults. Kappes et al. (2010) found that SST and to a lesser extent Chl *a* were consistently the best predictors of foraging effort in breeding black-footed albatross foraging within the NPTZ despite seasonal and inter-annual variation in their core foraging areas, indicating that adults use specific environmental characteristics as foraging cues to track preferred oceanographic habitat. In contrast, fledglings head to the same broad geographical area but do not appear to encounter equally forage-rich waters. Tracked fledglings congregated too far south within the subtropical gyre (characterized by Chl *a* ≤0.15 mg/m^3) to intersect the enhanced productivity and cooler SST beyond the North Pacific Transition Zone Chlorophyll Front (TZCF): an area over 8,000 km long at the southern edge of the NPTZ that seasonally migrates north and south by *c.* 1,000 km (Figure 2.3, Polovina et al. 2001). During the breeding period, this zone of surface convergence is typically located at *c.* 30-35°N, and during the fledgling at-sea period, can meander to about *c.* 40-45°N. The majority of fledgling locations in post-tagging Phase 3 of dispersal were located below this boundary, and the spatial mismatch is responsible for low Chl *a* and high SST experienced by fledglings (*c.* 0.12 mg/m^3 and 22 °C, Figure 2.3).

Tracked adults from Midway ranged widely throughout the far northern reaches of the North Pacific Ocean basin, probably taking advantage of productive shelf break and NPTZ regions (Figure 2.3). Adult birds of unknown colonial origin captured at sea in Alaskan waters during the post-breeding period (July and August) and tagged with PTT devices were shown to forage among the Aleutian Islands, Gulf of Alaska, and extensively south of 45°N within the NPTZ but not further west than 170°W (Fischer et al. 2009). Adult birds tracked from colonies other than Midway are also known to visit the productive areas of the California Current system during breeding (Fernández et al. 2001, Hyrenbach et al. 2006, Kappes et al. 2010) and non-breeding (Chapter Four), but this behaviour was not observed for any of the fledglings or post-breeding adults tracked from Midway. The observed differences in adult distributions between this and other work could be due in part to the restricted time period investigated in this study; if adults had been tracked beyond the month of August during the non-breeding period it is possible they would be observed to use the NPTZ more heavily. The differences are also likely due in part to sampling effects, whereby the random sub-sample of birds tracked from the population did not capture a complete representation of at-sea non-breeding movements for adult birds from the Midway colony (Chapter Four).

Despite the high variability in areas used by tracked adults from Midway, and that non-breeding adults from this colony likely use regions not identified from the birds tracked in this study, there was high consistency across tracked adults in Chl *a* densities encountered (Figure 2.3). This suggests that adults have a tendency to seek out productive areas dispersed widely throughout the North Pacific, at least during the month of August. The fledgling tracking results presented here support past reports of immature birds at sea being more commonly observed further south and west than adults (Tickell 2000). Fledglings probably spend their first year at sea in the less productive and warmer south-western North Pacific, possibly shifting toward adult distributions with age and development in what is referred to as an ‘ontogenetic niche shift’ (Werner & Gilliam 1984).

The comparatively restricted oceanic distribution of fledglings relative to post-breeding adults likely reflects differing energetic demands and experience. Despite the absence of physical boundaries and central-place foraging impeding their dispersal across the entire North Pacific Ocean basin, tracked fledglings demonstrated a surprisingly consistent tendency among individuals to remain mostly within forage-poor waters in the subtropical gyre. While young birds are honing flight and foraging skills during this early life stage, experienced adults spread out widely while recovering from the breeding season and replacing plumage, mostly in productive waters. It has been suggested that direct or historical competitive exclusion by experienced adults may be responsible for wandering albatross fledglings concentrating in significantly less productive waters (Weimerskirch et al. 2006). Adults from Midway and other breeding colonies, as well as other congeners, are likely to range within the productive NPTZ during the non-breeding period and thus historical or direct interactions may competitively exclude hatch-year juveniles. Differing resource needs due to body condition and moult status, flight and foraging experience and competence, and innate evolved behaviours are all mechanisms likely to shape the divergent ontogenetic niches between age-classes.

Conclusions

Previous work has documented dispersal movements for other fledgling albatross species but those studies covered only the first 10-389 days at sea, with most tags ceasing to transmit after the first three months (Walker & Elliott 2006, Weimerskirch et al. 2006, Thomas & Holland 2010, Alderman et al. 2010, Deguchi et al. 2013, Riotte-Lambert & Weimerskirch 2013, Thiebot et al. 2014). Further investigations into at-sea distributions and habitat characteristics across age-classes, seasons and colonies should attempt to resolve the mechanisms responsible for observed differential behaviour between age-classes both in this study and other species of seabirds and marine animals. It is possible that the spatial patterns presented here could be influenced by tag-type and inter-annual variability in at-sea habitat use among and between age-classes. Given the high consistency of areas used for fledglings across years and the distance between areas frequented by tracked adults and fledglings relative to the spatial accuracy of the different device types, it was considered acceptable to compare location data derived from PTT and GLS devices to assess spatial distributions at a broad scale. Small sample sizes precluded robust comparisons between years. Future work should investigate whether juveniles predictably follow cues and exhibit the same flexibility as adults in foraging areas based on environmental cues (Kappes et al. 2010) or are generally restricted to settling into the same geographical area, in smaller and less productive zones relative to waters favoured by adults. This information will indicate age-based sensitivity to future changes in the Earth's climate and related changes in the marine environment. Furthermore, juvenile dispersal data should be integrated into analyses of overlap with fisheries and by-catch data to assess differential vulnerability between age-classes.

Because of the inherent risks that fledgling albatrosses face during the first few years of life, the fact that they spend five or more years at sea before returning to land (Fisher 1975, Weimerskirch et al. 1997a) and the cost of tracking devices, few studies have been directed at understanding this critical early life stage. Thus many questions remain about fledgling dispersal, distribution, overall movement patterns, habitat use, diet, physiology, and temporal and spatial overlap with conspecifics or congeners and anthropogenic threats. In general, our understanding of the early life stages of albatrosses, other seabirds, and other marine animals is very poor. Yet it is crucial to study this life stage because it comprises large proportions of the populations of long-lived species with delayed maturity and is when the greatest amount of mortality occurs, and thus when natural selective forces are strongest (Fisher 1975). The information obtained from this research begins to fill a large knowledge gap in at-sea habitat use during a critical life stage for this species. The continued vulnerability of this species to interactions with commercial fisheries and the precarious state of most of their breeding habitat in light of climate change-induced sea level rise (Hatfield et al. 2012) are arguments for the timeliness of studying their at-sea behaviour across all life stages.

The work in Chapter Two also appears in: Gutowsky SE, Tremblay Y, Kappes MA, Flint EN, Klavitter J, Laniawe L, Costa DP, Naughton MB, Romano MD, Shaffer SA (2014a) Divergent post-breeding distribution and habitat associations of fledgling and adult Black-footed Albatrosses Phoebastria nigripes in the North Pacific. Ibis 156:60–72. **Statement of Contribution:** SAS, ENF, JK, LL, MBN, and MDR initiated and executed data collection. SEG conceived the study design and carried out the analyses. YT and SAS assisted SEG with Matlab programming. SEG wrote the paper with the assistance and advice of SAS, DPC, and MAK.

Tables

Table 2.1 – Descriptive track characteristics for PTT-equipped fledgling black-footed albatross through three phases of post-tagging dispersal from the natal colony at Midway Atoll (2006, 2007, 2008) and GLS-equipped adults from the same colony during non-breeding (2008, 2009) in August.

	Mean	±SD	Min	Max
Fledglings (*n* = 18)				
Maximum range from colony (km)	2,027.8	845.8	820.4	4,443.5
Average travel rate (km/day)	137.4	54.7	44.0	226.0
Phase 1 travel rate (km/day)	31.5	15.1	8.5	73.1
Phase 1 duration (days)	8.6	5.7	2.1	22.3
Phase 2 travel rate (km/day)	199.0	46.7	112.1	268.6
Phase 2 duration (days)	5.2	2.4	2.9	13.1
Phase 3 travel rate (km/day)	197.7	57.1	94.1	301.4
Phase 3 duration (days)	42.5	28.2	3.7	113.8
Tracking duration (days)	59.9	26.1	26.5	120.0
Adults (*n* = 16)				
Maximum range from colony (km)	3,699.9	893.6	2,188.8	5,524.1
Average travel rate (km/day)	268.5	92.1	57.9	431.2

Figures

Figure 2.1 – Dispersal of 22 black-footed albatross fledglings departing from Midway Atoll between 2006 and 2008 during June and July, as determined by satellite telemetry. Each individual’s track is divided into three distinct phases of post-tagging dispersal. (projection: Lambert Cylindrical Equal Area, datum: WGS1984).

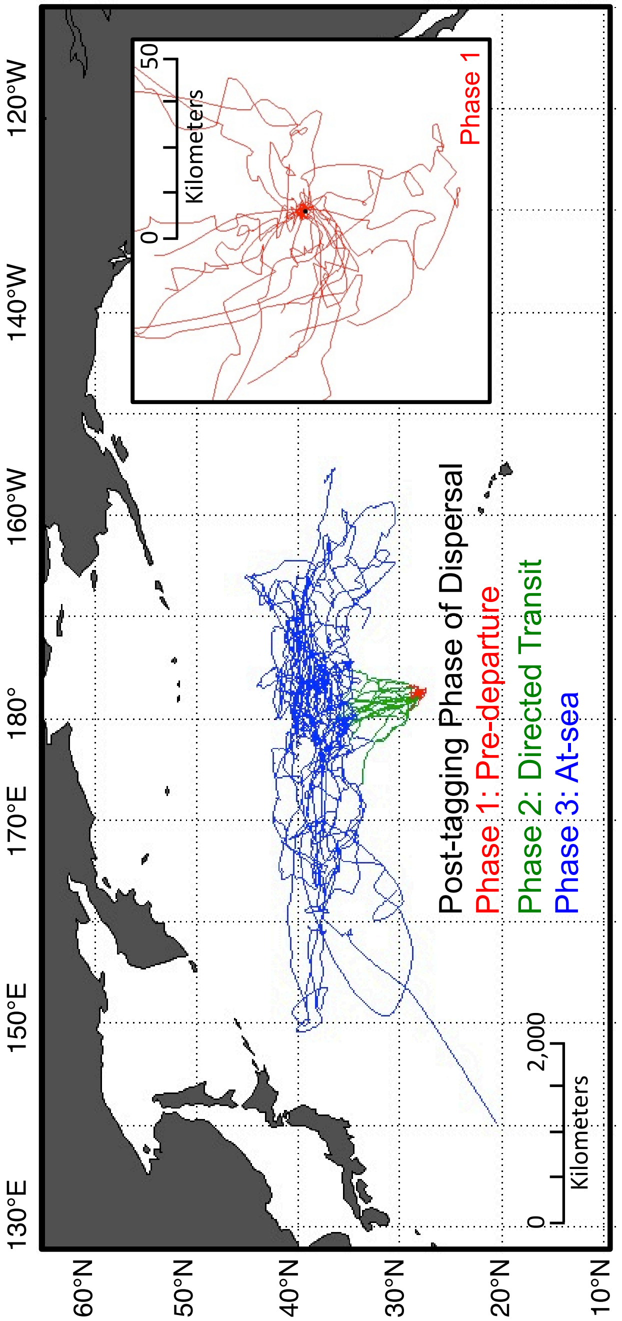


Figure 2.2 – KDE for 18 PTT-equipped fledgling black-footed albatross in Phase 3 of post-tagging dispersal (top pane) and 16 GLS-equipped non-breeding adults during the month of August. Increasingly darker shades of blue indicate the 95%, 75%, 50% and 25% kernel density contours from pooled KDE (projection: Lambert Cylindrical Equal Area, datum: WGS1984).

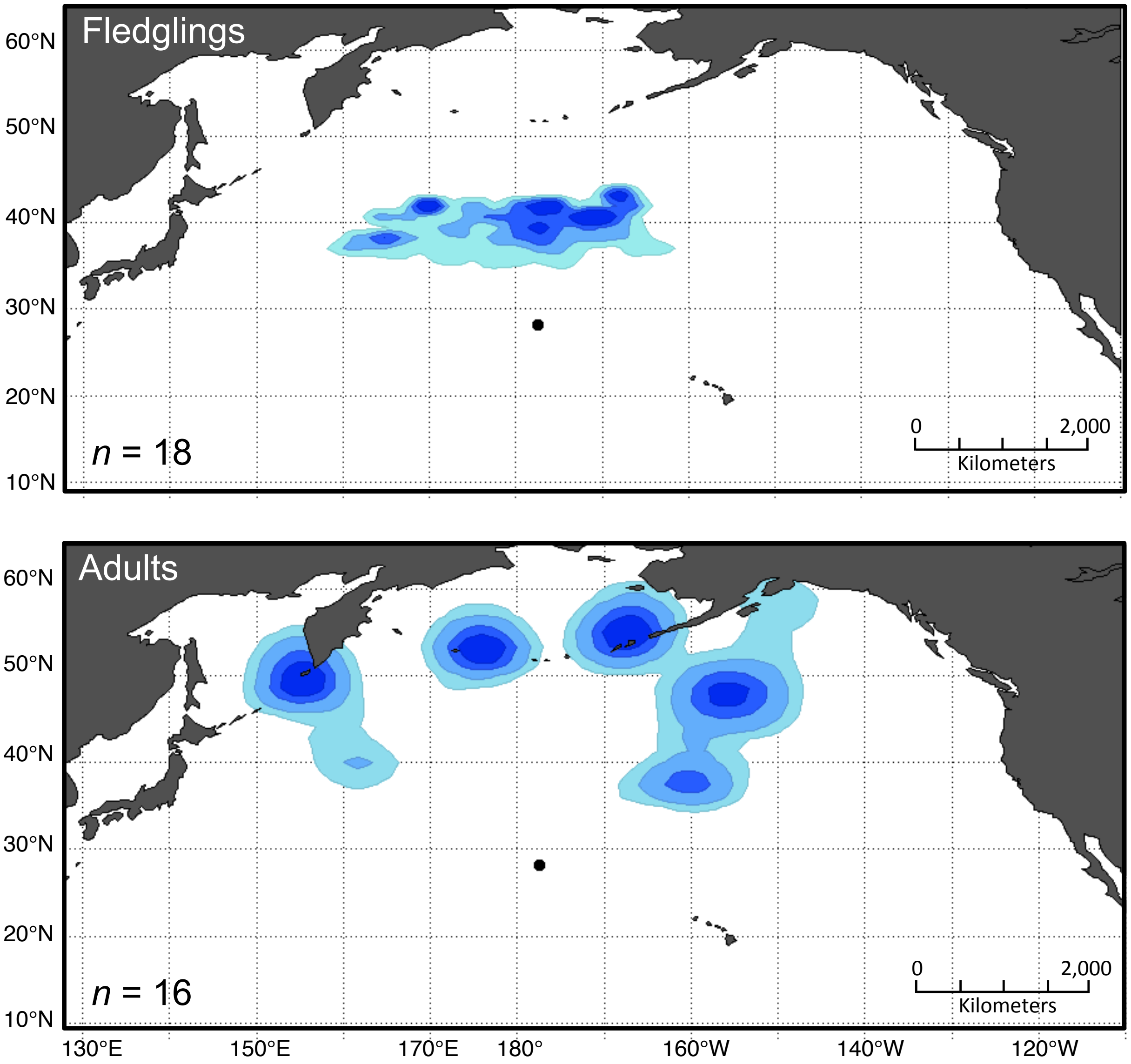
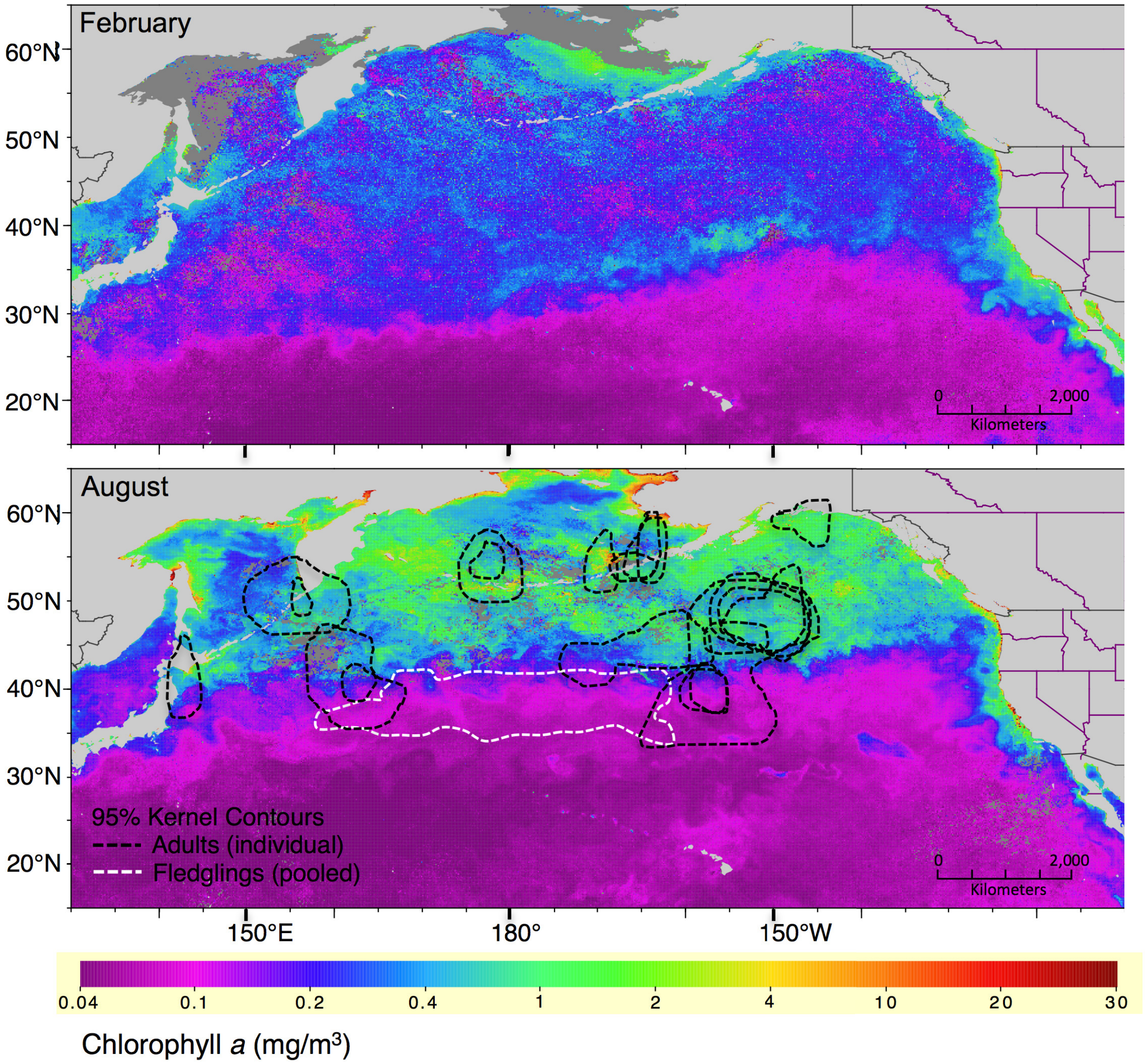


Figure 2.3 – Monthly composites of remotely sensed surface chlorophyll *a* density (mg/m^3) estimated from SeaWiFS ocean colour during February (top pane) and August (bottom pane) in 2008 (data courtesy of NOAA CoastWatch, 0.025° resolution). The north-south seasonal migration of the NPTZ chlorophyll front can be seen as the distinct purple to blue transition at 0.2 mg/m^3 (Polovina et al. 2001). The bottom panel depicts the association of PTT- (fledglings, *n* = 18, pooled KDE) and GLS- (adults, *n* = 16, individual KDE) equipped black-footed albatrosses with areas of particularly low (fledgling) and high (adult) Chl *a*. (projection: Lambert Cylindrical Equal Area, datum: WGS1984).



Chapter 3: Daily Activity Budgets Reveal A Quasi-Flightless Stage During Non-Breeding In Hawaiian Albatrosses

Abstract

Animals adjust activity budgets as competing demands for limited time and energy shift across life history phases. For far-ranging migrants and especially pelagic seabirds, activity during breeding and migration are generally well studied but the overwinter phase of non-breeding has received less attention. Yet this is a critical time for recovery from breeding, plumage replacement and gaining energy stores for return migration and the next breeding attempt. I aimed to identify patterns in daily activity budgets (i.e. time in flight, floating on the water's surface and active foraging) and associated spatial distributions during overwinter for tracked Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses using state-space models and generalized additive mixed models (GAMMs). I applied these models to time-series of positional and immersion-state data from small light- and conductivity-based data biologgers. During overwinter, both species exhibited a consistent 'quasi-flightless' stage beginning *c.* 30 days after initiating outbound migration and lasting *c.* 40 days, characterized by frequent long bouts of floating, very little sustained flight, and infrequent active foraging. Minimal daily movements were made within localized areas during this time; individual Laysan albatross concentrated into the northwest corner of the Pacific while black-footed albatross spread widely across the North Pacific Ocean basin. Activity gradually shifted toward increased time in flight and active foraging, less time floating, and greater daily travel distances until colony return *c.* 155 days after initial departure. My results demonstrate that these species make parallel adjustments to activity budgets at a daily time-scale within the overwinter phase of non-breeding despite different at-sea distributions and phenologies. The 'quasi-flightless' stage likely reflects compromised flight from active wing moult while the subsequent increase in activity may occur as priorities shift toward mass gain for breeding. The novel application of a GAMM-based approach used in this study offers the possibility of identifying consistent group-level patterns in shifting activity budgets over extended periods while allowing for individual-level variation in the timing of events. The information gained can also help to

elucidate the whereabouts of areas important at different times across life history phases for far-ranging migrants.

Introduction

As resource needs and availability change across life history phases, animals must adjust activity budgets to spend proportionally more or less time engaged in different activities with varying potential for net energy gain. Far-ranging migrants in particular make drastic adjustments to daily activity budgets as they move between vastly separated areas important at different phases in the annual cycle (Stearns 1992, Dingle 1996). Marine species can present a challenge in that comprehensively understanding activity budgets requires knowledge of behaviour and distributions for regions that may be separated by thousands of kilometres, often in inaccessible pelagic locations. For species that rely on land to breed, the breeding period is typically well studied while much less is known of activities during the non-breeding period, despite the important influence of this time on population dynamics (Calvert et al. 2009). Seabirds, for example, need the non-breeding period to recover from the demands of raising offspring, replace plumage and prepare for the next migratory journey and breeding attempt (Lack 1968, Alerstam et al. 2003, Calvert et al. 2009).

Among the world's most impressive migrants, larger members of the 'tube-nosed seabirds' (shearwaters and albatrosses of the O. *Procellariiformes*) are relatively well studied throughout breeding, as well as certain aspects of non-breeding. Some of the swiftest and most far-reaching migrations known are accomplished by tubenoses (but see (Egevang et al. 2010). For example, sooty shearwaters *Puffinus griseus* spend extended periods engaged in flight and little time resting while in migratory transit across transequatorial routes around the Pacific (Shaffer et al. 2006). These birds travel at rates of up to 1,000 km/day, accomplishing round-trip journeys of over 70,000 km between breeding and non-breeding overwintering grounds (Shaffer et al. 2006). However, as for most seabirds, daily activity and potential energetic needs or constraints within the "overwinter" phase of non-breeding have been examined in comparatively little detail relative to their often spectacular outbound and inbound migrations.

Constant advancements in biologging technology and data analysis are allowing increasingly detailed investigations into the at-sea activity of seabirds during different phases of breeding and non-breeding (e.g. Wilson et al. 1995, Weimerskirch et al. 1997b, Fernández & Anderson 2000, Catry et al. 2004a, 2011, Phalan et al. 2007, Guilford et al. 2009, Mackley et al. 2010, Gaston et al. 2011, Dean et al. 2012, Dias et al. 2012, Hedd et al. 2012, Freeman et al. 2013). Many shearwater and albatross species are ideal for deployment and retrieval of biologging devices because of their ties to a predictable 'central place' (Orians & Pearson 1979) at convenient densities for study when nesting. External temperature or wet/dry immersion loggers allow estimation of the allocation of time toward different activities. For example, prolonged warm/dry periods can indicate bouts of sustained flight, prolonged cold/wet periods indicate time on the water's surface (e.g. Wilson et al. 1995, Fernández & Anderson 2000), and brief and continuous wet/dry transitions indicate 'active foraging' (e.g. Dias et al. 2012). In combination with internal stomach temperature logger data, it is possible to estimate the relative potential net energy gained when engaged in each activity. For example, while active foraging bouts have been found to account for the majority of prey ingestion, some prey can still be captured when floating (a 'sit-and-wait' foraging strategy) and also occasionally during sustained flight bouts (a 'fly-and-forage' strategy; Weimerskirch et al. 1997b, Catry et al. 2004a).

Using these techniques, the overwinter phase has been broadly characterized for some species by reduced flight activity and frequent long bouts on the water relative to all other life history phases (e.g Guilford et al. 2009, Mackley et al. 2010, Freeman et al. 2013). This may be due to a combination of lower energetic demands from the lack of a central place constraint to the nest and locally productive foraging conditions (e.g. four albatross *spp.*; Mackley et al. 2010), along with possible constraints to mobility from moulting (e.g. sooty shearwater; Hedd et al. 2012). However, the non-breeding period can be lengthy (e.g. *c.* 200 days for sooty shearwaters (Shaffer et al. 2006) or *c.* 16 months for grey-headed albatross *Thalassarche chrysostoma* (Croxall et al. 2005)). For many species, the vast majority of this time is spent in overwintering areas between swift migratory phases. Because energetic priorities and constraints inevitably shift within this long timespan, it could be expected that average overwinter activity budgets likely mask major short-term changes in activity during this important time. Generalizations may conceal fine-scale modifications to activity, and may make identification of more sensitive time periods or important at-sea areas challenging.

Here I aimed to objectively identify patterns in activity and associated at-sea distributions across the overwinter phase of non-breeding using two North Pacific tubenoses as model species. Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses range widely across the North Pacific during non-breeding after they have vacated breeding colonies found mostly in the Northwestern Hawaiian Islands (Arata et al. 2009). These two species differ in diet and habitat preferences but breed sympatrically and are similar in size and breeding phenology (Tickell 2000, Arata et al. 2009). A number of anthropogenic threats have lead to Laysan and black-footeds' listing as 'Near Threatened' (IUCN 2015). Much is known from biologging studies of habitat use and behaviour of both species during breeding (Fernández et al. 2001, Hyrenbach et al. 2002, 2006, Young et al. 2009, Kappes et al. 2010) and of at-sea distributions during non-breeding (Hyrenbach & Dotson 2001, Young et al. 2009, Fischer et al. 2009, Block et al. 2011, Hyrenbach et al. 2012). For the largest colony of both species at Midway Atoll National Wildlife Refuge, (70% of worldwide Laysans and 35% of black-footeds; Arata et al. 2009), however, non-breeding activity and habitat use were mostly undocumented prior to the work of this dissertation.

Using small light- and conductivity-based archival data loggers, I examined daily activity budgets across the entire non-breeding season of Laysan and black-footed albatrosses from Midway. Specifically, I identified patterns in time allocation between sustained flight, floating and active foraging, and associated distributions, by applying state-space models (Jonsen et al. 2003, 2005) and generalized additive mixed-effects models (Wood 2006) to time-series of positional and immersion-state data. This allowed evaluation of patterns in activity not only by broad phases of non-breeding but also at a daily time-scale, elucidating new insights into population-level patterns and commonalities among species in the likely energetic constraints faced during this time.

Methods

Study Site And Device Deployment

Fieldwork was conducted over five field seasons (2008, 2009, 2010, 2011 and 2012) at Sand Island, Midway Atoll National Wildlife Refuge (28.21°N, 177.36°W; herein 'Midway'). Midway is home to roughly 408,000 breeding pairs of Laysan albatross and 22,000 pairs of black-footeds (Arata et al. 2009). Leg-mounted geolocation-immersion loggers (GLS; Lotek LAT2500, Lotek Wireless Inc, St John's, Newfoundland, CA) were deployed on equal numbers of opportunistically selected breeding adults of both species (sex unknown) during incubation or early chick rearing (between December and March), and were recovered during incubation in the subsequent breeding season (between early-December and early-January). GLS were mounted on a plastic leg band using UV resistant cable ties and quick-setting epoxy (logger + attachment ~6 g, <1% body mass; well below the recommended limit for albatrosses (Phillips et al. 2003)). While it was not possible to formally assess tag effects in this study, deployments and retrievals took no longer than 10 minutes and did not appear to interfere with nesting behaviour. Further, visible inspection upon retrieval indicated that attachments did not cause any physical harm. GLS deployments at other Laysan colonies have resulted in no detectable short-term effects on reproductive success (Young et al. 2009). Of 119 GLS deployed over five seasons, 77% were recovered. Upon download, 62% of those recovered revealed technological failures causing appreciably spurious or missing light or immersion data, yielding 35 GLS with complete concurrent time series of both location and immersion data for this study. All tags recovered from the 2010 deployment season ($n = 20$) failed to produce reliable immersion data and were not used in subsequent analyses.

All recovered and functional GLS recorded light levels at 10-minute intervals to estimate daily locations and saltwater immersion to estimate on/off water activity patterns (determined by conductivity between two external pins). GLS recorded instantaneous immersion state (wet or dry) at a programmed interval and produced time series of states with resolutions between 32 and 100 seconds depending on tag programming in the year of deployment (2008: 100-sec, Laysan $n = 3$, black-footed $n = 4$; 2009: 90-sec, Laysan n

= 8, black-footed *n* = 6; 2011/2012: 32-sec, Laysan *n* = 9, black-footed *n* = 5). Immersion state changes occurring in <90 seconds were excluded, ensuring all time series reflect similar behavioural changes (Dias et al. 2012). Light data were processed with automated template fitting software, producing a single location per day using sunrise and sunset times and estimate latitude from day length and longitude from the time of local noon/midnight (Ekstrom 2004). The accuracy of latitude estimates during equinox periods is unavoidably compromised, as day length depends only weakly on latitude at this time (Ekstrom 2004). For this study, locations on 15 days of either side of the fall equinox were excluded based on consistently suspect latitude estimates.

Positional Data Processing

Cloud cover, feather shading or large daily travel distances can further compromise light signals causing short periods of spurious or missing locations (Shaffer et al. 2005). Unrealistic location estimates are often discarded from a dataset based on subjective criteria (Thiebot & Pinaud 2010, Chapter Two). Here I used recently developed time-series state-space models (SSMs) estimated with Bayesian techniques to avoid unnecessary data loss (implemented in R, R Core Team 2014, through a remote cluster server). This approach comprises two probabilistic components: a process model of the biological mechanisms influencing locations and an observation model of how the location estimates were obtained. SSMs correct observed locations for tag error and biological realism to make inferences about the true ‘hidden state’ or locations (Jonsen et al. 2003, 2005). Estimates of tag error have been derived elsewhere by ‘double-tagging’ experiments in which Laysans and black-footeds carried both GLS and higher-accuracy satellite Platform Terminal Transmitter (PTT) tags (Laysan longitude error SD = 1.9° and latitude error SD = 1.2°, black-footed longitude error SD = 3.8° and latitude error SD = 1.9°; Shaffer et al. 2005 further refined in Block et al. 2011). Latitude estimates in these studies were derived using an algorithm that matches remotely-sensed SST-gradients to SST data recorded on-board the GLS. I did not have reliable SST data for all GLS in this study and therefore observed latitudes are more likely to have errors similar to those estimated for longitude. I took a conservative approach by fixing the SSM tag error parameter estimates for both latitude and longitude of both species equal to the maximum estimated error for longitude in Block et al. (2011). Positions falling over continental landmasses were constrained toward the marine environment in the SSM by a land mask. The SSM was fitted using Markov Chain Monte Carlo (MCMC) sampling. For each bird, two independent and parallel MCMC chains each of length 100,000 were run and a sample of 2,000 from the joint posterior probability distribution was obtained by discarding the first 80,000 iterations and retaining every 20th of the remaining iterations. MCMC algorithm convergence was assessed using the ratio of variances for parameters between the retained MCMC chains (the potential scale reduction factor or *R*-hat statistic); when models are well converged, the values are near 1. The final SSM-processed once-daily true-position estimates were obtained from the mean of appropriately converged posterior distributions (Jonsen et al. 2005).

Individual Seasonal Phenology

I estimated the timing of non-breeding departure and return based on known travel rates using patterns in positional data and great circle distance to the colony. Both species are known to travel >30 km/h on foraging trips from the colony with an unlikely but not impossible maximum daily distance travelled of 720 km (Young et al. 2009). The date of initiation of the non-breeding season (i.e. definitively no longer visiting the colony) was determined as the first day an individual was estimated >720 km from the colony with all subsequent locations increasingly distant without return. Similarly, I determined the final day of the non-breeding season as the first day with distance to the colony <720 km with a clear pattern of decreasing distance to the colony before this date and locations indicating potential colony visits after this date.

I delineated the three phases of non-breeding for each bird through visual inspection of daily movement patterns and individual non-breeding phenology: outbound transit (series of consecutive movements following departure directed away from the colony with daily travel rates >100 km/day), overwinter (beginning with the first prolonged series of days with decreased travel rate and directed movements), and inbound transit (series of travel days terminating on the probable colony return date as determined above, Table 3.1). For two Laysans, initiation of the inbound transit phase overlapped the end of the equinox window; therefore daily activity parameters for these birds are only used to describe the full non-breeding period.

I examined patterns of at-sea distribution among individuals within species with Kernel Density Estimation (KDE; Worton 1989) applied to SSM-processed locations using software written in Matlab (MathWorks Inc, USA; IKNOS Toolbox). KDEs were conducted independently for each individual and as pooled KDEs by species, where all Laysan or black-footed locations are pooled together for the analysis. The geographic coordinates of each bird location were transformed to Cartesian coordinates using a Lambert Cylindrical Equal Area projection and 2D Gaussian kernel densities computed on a 0.25° x 0.25° grid. I estimated the smoothing parameter (h) using an adaptive method to estimate an optimal fixed value for each dataset (Sheather & Jones 1991, Wood et al. 2000). The density surface was divided into concentric polygons to calculate 50% and 95% kernel density contours. I used plots of stacked, partially-transparent individual 50% kernel contours to visualize both inter-individual variation in space use, as well as the areas of most intense overlap among individual high-use areas. I also plotted the 95% pooled kernel contour as a means of visualizing the group-level range of the equipped birds of each species, while acknowledging that the size and location of pooled kernel contours are sensitive to sampling effects (Chapter Four).

Immersion State Data Processing

I used immersion state time series (wet/dry) to calculate the following parameters related to daily at-sea activity: 1) the number and duration of sustained bouts of flight, floating and active foraging each day (details below) and 2) the proportion of each day spent in sustained flight, floating on the water and actively foraging. Wet or dry intervals that overlapped the cut-off transition between days at midnight were excluded (McKnight et al. 2011, Hedd et al. 2012).

To identify different bout types, I assessed patterns in the immersion state time series. A period of relatively brief and continuous wet-dry transitions resulting from an episode of frequent landing and take-off events from the ocean's surface can be used as an indicator of 'active foraging' in non-diving seabirds (e.g. Weimerskirch et al. 1997b, Dias et al. 2012). A small number of these episodes could also indicate other activities including conspecific interactions, but at least reflect periods of active movements and increased energy expenditure (Weimerskirch et al. 2000a, Shaffer et al. 2001a, McKnight et al. 2011), given birds are alighting from and landing on the water while flying relatively short distances between landings, probably requiring at least some flapping flight. Longer periods of sustained wet or dry states are taken to indicate bouts of prolonged floating on the water's surface (wet) or flight (dry). The temporal interval breakpoint that separates periods of rapid wet-dry transitions and periods of prolonged wet or dry activity can be identified as a bout ending criteria or *BEC* using a maximum-likelihood approach (Luque & Guinet 2007). This approach has been employed widely on diving animals with time-depth recorders (e.g. Luque et al. 2008, Regular et al. 2011, Leung et al. 2013) but much less on non-diving seabirds that do not forage below the first few meters of the ocean surface. Following methods outlined in Dias et al. (2012), individual *BEC*s were calculated using the R diveMove package (Luque 2007) developed for the software R and were used to identify bouts within a bird's immersion state time series as: 1) a probable active foraging bout (a series of wet/dry event transitions lasting less than the *BEC*), 2) a sustained flight bout (any dry event lasting longer than the *BEC*) or 3) a floating bout (any wet event lasting longer than the *BEC*). I used individual *BEC*'s to delineate bout types within each bird's immersion time series due to a high degree of individual-level variation (Laysan 33.5 ± 8.6 minutes and black-footed 45.6 ± 9.5 minutes, mean ± SD). Future studies applying this approach should assess *BEC* variation before proceeding to delineate bouts using either a single value across all birds (Dias et al. 2012) or assessing individuals independently (this study). From the bout-type classifications along the time series, daily activity parameters were calculated for each bird as noted above.

Statistical Analysis For Day-To-Day Activity Patterns

Data exploration indicated potentially non-linear relationships in daily activity parameters with time, thus I implemented generalized additive mixed models (GAMMs) to assess patterns in daily activity budgets over the course of non-breeding (R mgcv package, Wood 2006). Due to a large number of zeros in the data, a two stage hurdle model was used to analyse sustained flight as either: 1) the time when birds were detected to be in sustained flight (proportion of sustained flight) or 2) whether birds were in sustained flight (flight: yes/no). As a smoothing function, this model included days since departure (DSD) from the colony. The time spent while floating on the water and actively foraging was used as the response variables for two additional models. Fixed categorical factors for all models included non-breeding phase and species. Individual bird was modelled as a random effect (intercept-only) as birds contributed repeatedly and unevenly with respect to data (Zurr et al. 2009). Adequacy of model fit was examined via autocorrelation lag plots, variograms, and the normalized residuals against independent variables including those not in the models (e.g. spatial location). Because our data consisted of a time series and were found to be autocorrelated, I included a temporal correlation structure (corExp, which also then accounted for associated spatial autocorrelation as positions close in time are also close in space, Zurr et al. 2009). Including a correlation structure and random effect allowed me to model compound correlation between observations from the same bird and the temporal correlation between all observations from the same bird and DSD (Zurr et al. 2009). Backward model selection was performed until all terms were significant, and the correlation structure and random effect improved model fit for all three response variables. Models were again validated using the techniques described by Zurr et al. (2009).

Results

Overwinter Movements And Destinations

From colony departure to return, Laysans travelled on average 22,134 ± 3,825 km (mean ± SD, range 17,000-30,000 km). Total distance travelled ranged more widely for black-footeds (17,997 ± 4,688 km, mean ± SD, range 11,000-28,000 km). Outbound and inbound transit phases were clearly identifiable for all birds, lasting 2-16 days for Laysans and 2-20 days for black-footeds (Table 3.1). Periods of limited localized movements during the *c.* 125 days of overwinter (Table 3.1) were contained within one to three distinct areas for each bird with larger movements between areas lasting 2-5 days. For Laysans, birds were found mostly within the following three main regions (Figure 3.1): (1) 75% of birds (15 of 20) ranged between the southern tip of the Kamchatka Peninsula, Russia, to the Commander Islands and the western side of the mid-to-northern Emperor Seamount, (2) 60% of birds used areas between 300–1000 km east of Honshu Island and Hokkaido Island, Japan and, (3) 30% ranged south of the southern-most islands of the Southern Aleutian Arc, Alaska. Three individuals spent 5–14 days in the pelagic mid-North Pacific to the northwest of the colony as their second or third overwinter destination, and one individual spent the first 73 days around the Aleutians before moving 1,000 km W of the Oregon coast for 33 days. For Laysans that used only a single overwinter area ($n = 4$), two spent all of their time around the Kamchatka Peninsula and two east of the Japanese continental margin.

For black-footeds, 53% (8 of 15) of birds spent at least some portion of the overwinter period centred around Unalaska Island of the Aleutians, ranging around 400 km north–south and 500 km east–west along the Alaskan Peninsula (Figure 3.1); four birds remained in this region for the entire duration of the overwinter period. Another 53% of individuals spent time ranging comparatively widely across the mid-North Pacific, mostly northwest of the colony toward the Emperor Seamounts; three birds remained in this broad area making only localized movements throughout the overwinter period. Two black-footeds used areas southeast of Honshu Island and Hokkaido Island, Japan, while one individual spent 30 days off the northwest coast of British Columbia, Canada, around Haida Gwaii, then 35 days in the Gulf of Alaska before finishing the overwinter phase in the mid-eastern North Pacific.

Seasonal Activity Patterns

For both species, sustained flight bouts comprised a high proportion of inbound and outbound transit days; 27-44% of each day was spent engaged in 1-4 flight bouts lasting roughly 2 hours each (Table 3.2, Figure 3.2). During overwinter, limited time was spent in sustained flight each day (Table 3.2, Figure 3.2). For the entire overwinter phase, Laysans spent on average 46.9 ± 16 days without engaging in any bouts of sustained flight accounting for 37 ± 10% of each individual's overwinter phase, and black-footeds 52.3 ± 14 days (43 ± 14% of overwinter). The vast majority of time during overwinter was detected as long and frequent floating bouts for both species (Table 3.2, Figure 3.2). Floating also comprised a high proportion of the day throughout both inbound and outbound transit phases but with less frequent short bouts (Table 3.2, Figure 3.2). For all phases and both species, on average 21 to 31% of each day was spent engaged in active foraging split between 2-5 individual bouts (Table 3.2, Figure 3.2).

Daily Activity Patterns

For both species, the proportion of each day spent in sustained flight followed a similar overall pattern with increasing DSD, but differed significantly in their smooth functions (Table 3.3, Figure 3.3). Both species showed an initial decrease in time spent in sustained flight over the first 30 days. Laysans exhibited a more rapid decline followed by an extended period of few daily flight bouts before increasing again. This differs slightly from the more gradual decline in daily flight time for black-footeds, which reached a low around 50 days before gradually rising once more (Figure 3.3). Neither species displayed a noticeable shift in flight activity upon initial arrival at the first overwinter area, but instead steadily decreased time in sustained flight following arrival. The same pattern held true for the initiation of colony return for black-footeds; these birds steadily increased the time spent in sustained flight bouts each day after the low-point in flight activity, gradually increasing flight time before and during their inbound transit journey. Laysans exhibited a slight rise in flight activity within ten days of the initiation of inbound transit, but overall show a less smooth but consistent pattern between species of increased flight activity following an approximately 40-day window of low flight activity from 30–70 DSD.

The temporal pattern in time spent engaged in floating bouts over the non-breeding period did not differ significantly between species (Table 3.3, Figure 3.3). An approximate 40-day window from 30–70 DSD also coincided with the highest proportion of time on the water's surface. Again, the proportion of each day spent on the water continually increased before and after arrival at the first wintering area. After 70 days, all birds began to slowly decrease the proportion of each day floating until inbound transit began; at which point the amount of time floating each day reached a low but consistent level. The pattern in time spent active foraging for both species mirrored closely that seen for time spent in sustained flight as a similar overall pattern with increasing DSD, but differing significantly in smooth functions between species (Table 3.3, Figure 3.3). Daily time spent engaged in active foraging activity gradually declined until a low around 60 DSD for Laysans and around 10 days earlier for black-footeds, before rising once again. A period of low active foraging activity is again detectable roughly between 30–70 DSD for both species.

The date of overwinter arrival and departure, and thus outbound and inbound transit phases, were determined based on spatial data, whereas the consistent pattern in activity between 30–70 DSD emerged from immersion-state activity budgets. I re-visited the spatial data within this window to examine whether the distribution of birds at-sea during this period differed from that of the *c.* 125-day overwinter phase as a whole (Figure 3.4). Indeed, the range of nearly all individuals during this time remained restricted within one of the previously identified overwintering areas; no birds made directed movements between major overwinter areas within this window. While all Laysans were confined to a small area of the northwest Pacific relative to the broader distribution of black-footeds (Figure 3.4), the average daily distance travelled by individual Laysans was 77 ± 18 km/day, and by black-footeds was 61 ± 26 km/day.

The number of days between 30–70 DSD with complete absence of sustained flight bouts detected was 21 ± 5 days for Laysans (ranging from 13–30 days) and 25 ± 6 days for black-footeds (ranging from 14–33 days). All birds of both species spent at least one full day during this time entirely floating on the water. Further, Laysans on average spent 7 ± 5 days floating on the water's surface for >90% of the day and 16 ± 7 days floating for >80% of the day. Similarly, black-footeds on average spent 10 ± 7 days floating for >90% of the day and 18 ± 7 days floating for >80% of the day. In the time following this 40-day window until the birds initiated return inbound transit, Laysans travelled on average 50 km further each day, and black-footeds 23 km each day (Laysan, 127 ± 27 km/day over 64 ± 19 days; black-footed, 84 ± 45 km/day over 66 ± 18 days) but this average value represents highly variable daily travel distances which generally increased following 70 DSD until colony return for both species (Figure 3.5).

Discussion

This study is the first I know of to examine seabird behaviour over the course of non-breeding at a detailed daily time-scale, allowing new insights into the modification of daily activity budgets as constraints on time and energy shift through this demanding life history phase. I also document associated movements and habitat use across the North Pacific Ocean basin, revealing distinct areas important throughout overwinter for both Laysan and black-footed albatross. Over two-thirds of worldwide Laysan and one-third of black-footeds return to the Midway Atoll colony to breed each year (Arata et al. 2009). My work, while restricted in sample size, adds to a limited body of research explicitly examining at-sea habitat use and behaviour of these 'Near Threatened' residents (IUCN 2015) at any time in the breeding or life cycle.

Overwinter Destinations

During overwinter, Laysan and black-footed albatross tracked from Midway revealed discrete patterns in distributions throughout the North Pacific Ocean (Figure 3.1). Not surprisingly, these movements are associated with areas of known localized current convergence and upwelling that promote high primary and secondary productivity thus attracting and aggregating fish, squid, and ultimately Laysan and black-footed albatross (Shuntov 1972). Differences in habitat use among species were also expected and mostly follow that known from tracking studies of birds captured at-sea and from other smaller colonies throughout the annual cycle (Hyrenbach & Dotson 2001, Fernández et al. 2001, Hyrenbach et al. 2002, 2006, 2012, Young et al. 2009, Fischer et al. 2009, Kappes et al. 2010, Block et al. 2011, Chapter Four). There were however some notable exceptions in the use of the Russian Kamchatka Peninsula region (Young et al. 2009, Fischer et al. 2009, Hyrenbach et al. 2012), California Current System (Hyrenbach & Dotson 2001, Hyrenbach et al. 2012) and more pelagic areas (Young et al. 2009, Fischer et al. 2009). Together, the known distributions of tracked non-breeding Laysan and black-footed albatross indicate that these species range widely across the North Pacific during the four months when not tied to the colonies, crossing through multiple national and international jurisdictions and well into the high seas, with high individual- and colony-level variation in the use of broad overwinter areas. Future work should investigate variation within and between breeding colonies spanning the entire annual cycle of these species as necessary next-steps in the complete assessment of movement ecology and population dynamics (Arata et al. 2009, Calvert et al. 2009).

Activity During Transit Phases Of Non-Breeding

Outbound and inbound transit lasted *c.* 9-12 days, although this ranged predictably between individuals depending on colony proximity to the first and last overwinter areas. Non-breeding Laysans and black-footeds spent less time in flight than breeding birds on foraging trips from Tern Island during the brooding period (Fernández & Anderson 2000). Although Fernández & Anderson (2000) simply summed the number of 3-second intervals where immersion loggers registered as dry (thereby including time in sustained flight and flights within active foraging bouts), the average daily proportion of time off the water's surface (90%) still far exceeds the combined time in flight and active foraging at any point in the non-breeding season (Figure 3.2). Brooding birds likely spent most of their time in flight searching out widely dispersed prey within close proximity to the colony. Migrating birds can rest more frequently and avoid areas of low productivity by adopting an opportunistic 'fly-and-forage' strategy similar to that reported for other migrating tubenoses (e.g. cory's shearwater, Dias et al. 2012) and migratory birds of prey (e.g. osprey *Pandion haliaetus*, Strandberg & Alerstam 2007).

Daily Activity Patterns During Overwinter

It has been suggested that floating may comprise the vast majority of time during overwinter due to relatively low energetic requirements that are readily met while free from central-place constraints and chick-provisioning demands (Mackley et al. 2010). For example, comparable maximum flight bout durations during breeding and non-breeding in four species of southern hemisphere albatrosses could indicate that movement is not restricted but that birds are exercising the freedom afforded by low energetic demands to rest after directed movements between profitable foraging areas (Mackley et al. 2010). My results suggest that while infrequent but long flight bouts during non-breeding may be similar in duration to those taken during breeding, the proportion of each day spent engaged in different activity types and the daily distances travelled are still likely to differ, especially if non-linear day-to-day temporal shifts in activity are considered. Differences in average activity budgets between overwinter and transit phase days did not reflect immediate modifications to daily activity budgets upon arrival to overwintering areas, but instead masked a gradual shift in activity toward a 'quasi-flightless' stage (where birds appear to be flight-limited though not completely) followed by an increasing trend in flight and active foraging until colony return (Figure 3.3).

The 'quasi-flightless' stage is matched by highly restricted ranges and daily movements of individual birds (Figures 3.4 & 3.5) and coincides with a known period of intensive flight feather moult and loss of body fat stores (Edwards 2008). The sandy breeding habitat of Laysan and black-footed albatross causes severe abrasion to the outermost primary flight feathers, leading to P8-P10 replacement annually overwinter, and an overall complex moult strategy (Edwards & Rohwer 2005). Birds accomplish complete flight feather moult by splitting the replacement of feathers between two consecutive winters with either two consecutive medium moult series or a small moult series followed by a large moult series. The latter strategy, where a large and intensive moult series is necessary, causes up to 35% of Laysans and black-footeds to skip breeding in the following season; time and energy are too limiting to accomplish both (Rohwer et al. 2011). All of the birds in this study returned to Midway and were captured on the nest with an egg or chick, so I assume none of these birds underwent an intensive moult series but that all replaced at least their first three primaries along with initiating one or two other small or medium moult series during the 'quasi-flightless' stage of overwinter.

Approximately 40–60 days are required to complete moult during which at least one to three feathers within each series of each wing are missing or growing at any time (Edwards & Rohwer 2005, Edwards 2008). Albatross have highly specialized anatomy for exceptionally efficient gliding flight, where rigid feather "sails" on long, slender, pointed wings are supported by specially adapted wing muscles and joints (Tickell 2000, Meyers & Stakebake 2005). Worn, missing and growing feathers can compromise the wing's airfoil through fluttering, creating asymmetries in wing shape and aspect ratio, and increasing wing loading from decreased wing surface area (Langston & Rohwer 1996, Hedenstrom & Sunada 1999, Bridge 2006, Suryan et al. 2008). Lower body mass during moult may partially compensate for changes in flight dynamics (Edwards 2008), but this likely does not optimize wing loading and increased flight costs given the high sensitivity of albatrosses to even small reductions in flight dynamics (Langston & Rohwer 1996). Added flight and feather synthesis costs likely constrain birds from relying heavily on 'active foraging' or 'fly-and-forage' strategies and from engaging in long bouts of soaring flight. Occasional larger movements may occur when the benefit of travelling from a crowded or poor foraging area outweighs the cost of flight, when small moult extents are accomplished more quickly for some individuals, or when strong currents simply carry floating birds away from a particular region (Figure 3.4 & 3.5). Effectively, both Laysan and black-footed albatross likely experience *c.* 40 days of facultative quasi-flightlessness where foraging strategies shift to predominantly 'sit-and-wait' tactics.

Similar U-shaped temporal patterns in overwinter foraging activity have been documented in other tubenoses (e.g. manx shearwater *Puffinus puffinus*, Freeman et al. 2013). Birds may be intensely foraging after initial arrival to the overwintering grounds, possibly to replace body condition lost during breeding and to build up energy and nutrients needed for upcoming feather replacement (Catry et al. 2011). Following the 'quasi-flightless' stage, Laysans and black-footeds may begin a 'post-moult rush' to gain mass in preparation for breeding. Moult status and fat scores of drowned birds salvaged from drift-net fisheries showed a marked increase in body condition from relatively low fat stores during active moult to significantly higher following moult termination (10-20% gain in body mass, Edwards 2008). Further, other albatrosses initiate egg formation *c.* 30 days before colony arrival (Astheimer et al. 1985), and both sexes of Laysan and black-footed albatross are known to arrive to the Midway colony with extensive fat deposits and females with eggs in the oviducts (Frings & Frings 1961). The period of rapid fat accumulation and probable initiation of egg formation coincides with the gradual increase in sustained flight and active foraging along with less time floating on the water as colony return approaches (Figure 3.3). This 'pre-migratory hyperphagia' suggested for some other tubenoses (e.g. cory's shearwater, Dias et al. 2012) appears to progress steadily following the 'quasi-flightless' stage (Figures 3.3 & 3.5) and is likely a crucial 'post-moult rush' for breeding preparation as birds become increasingly mobile and actively seek out fruitful foraging areas before departing on their inbound transit journey.

Conclusions

Importantly, the shift in activity budgets and habitat use within the overwinter period would have gone undetected if patterns were not assessed at a daily time-step relative to individual-level DSD from the colony. Other tubenose species may also exhibit identifiable stages during non-breeding if patterns in daily activity are examined at a daily temporal resolution. Because colony departure dates varied (across 54 days for Laysans and 39 days for black-footeds), the calendar days when individuals at sea are undergoing these drastic adjustments to activity budgets span half the year, from June to November. The oceanic areas important during overwinter spread across nearly the entire North Pacific Ocean basin for birds from the large Midway colony, and likely further still into the California Current for birds from other colonies (Hyrenbach & Dotson 2001, Hyrenbach et al. 2012, Chapter Four).

If the space use and behaviour of the Laysans equipped with devices in this study are representative of the Midway colony, the Northwest corner of the Pacific Ocean may be a critical area for the potentially vulnerable 'quasi-flightless' stage (Figure 3.4) and for many birds at some point during non-breeding (75% of Laysans in this study used this region for at least one of three overwinter areas). These waters must offer immense productivity to support birds mostly feeding opportunistically while floating on the water's surface. Many other non-breeding tube-nosed seabirds also target this area including the 'Vulnerable' short-tailed albatross *Phoebastria albatrus* (Suryan et al. 2007, IUCN 2015) and several trans-equatorial migratory shearwater species (Shaffer et al. 2006, Rayner et al. 2011, Carey et al. 2014). The productive Russian Far East is also the focus of an industrial demersal long-line fishery estimated to kill an average 6,500 seabirds/year, making the Russian Exclusive Economic Zone a prime candidate for marine protective measures (Anderson et al. 2011). In contrast, black-footeds tracked from Midway in this study spread out widely across the North Pacific during this time, but individuals tended to remain in relatively localized areas, likely with sufficient resources for meeting the nutritional demands of feather replacement and days spent mostly on the water (Figure 3.4). Again, if the space use and behaviour of the black-footeds equipped with devices in this study are representative of the Midway colony, their wide distribution may buffer against potential threats during this vulnerable time, but would pose a challenge to targeted protected areas or fisheries management.

It is well accepted that events occurring outside of breeding critically influence the demography of migratory populations (Calvert et al. 2009). The restricted distributions and modifications to activity during the non-breeding period for Laysan and black-footed albatross are likely at least in part due to energetic constraints imposed by the necessity of plumage replacement. This may be even more pronounced in birds that skip breeding to undergo the largest and most intensive moult extents (Rohwer et al. 2011). For at least a 40-day window of each year, these birds are relegated mostly to the ocean's surface. This is probably to recover from and prepare for the taxing demands of an extreme life history strategy leaving little time to refresh flight feathers critical to their long-distance oceanic travels. Clearly, far-ranging migrants must carefully manage trade-offs in the allocation of limited time and energy toward shifting energetic demands as primacies shift throughout distinct life history phases and also at a finer day-to-day scale within these periods.

The work in Chapter Three also appears in: Gutowsky SE, Gutowsky LFG, Jonsen ID, Leonard ML, Naughton MB, Romano MD, Shaffer SA (2014b) Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses. Mov Ecol 2:23. **Statement of Contribution:** SAS, MBN, and MDR initiated and executed data collection. SEG partipicated in fieldwork in 2010, and conceived the study design. IDJ assisted SEG with SSM analyses, and LFGG assisted SEG with GAMM analyses. SEG wrote the paper with the assistance and advice of LFGG, IDJ, MLL and SAS.

Tables

Table 3.1 – Phenology of non-breeding season phases for Laysan (*n* = 20, or if *, *n* = 18) and black-footed (*n* = 15) albatrosses from Midway Atoll (mean ± SD), 2008-2012.

	Laysan	black-footed
Colony departure	29 Jun ± 16 days	25 Jun ± 14 days
Duration of outbound transit	10 ± 6 days	12 ± 8 days
Overwinter arrival	10 Jul ± 16 days	02 Jul ± 11 days
Duration of overwinter	125 ± 18 days *	126 ± 21 days
Overwinter departure	12 Nov ± 5 days *	05 Nov ± 8 days
Duration of inbound transit	9 ± 4 days *	10 ± 8 days
Colony return	18 Nov ± 13 days	16 Nov ± 14 days

Table 3.2 - Summary of daily activity among three phases of non-breeding for Laysan (*n* = 18) and black-footed albatrosses (*n* = 15) from Midway Atoll (mean ± SD). (Out = outbound transit, OW = overwinter, In = inbound transit).

	Laysan			black-footed		
	Out	OW	In	Out	OW	In
Sustained flight bouts (/day)	2.8 ± 1.0	1.2 ± 0.3	3.4 ± 1.3	2.3 ± 1.0	1.2 ± 0.5	2.8 ± 1.1
Floating bouts (/day)	2.9 ± 1.4	3.4 ± 0.8	2.3 ± 1.0	2.0 ± 0.7	2.5 ± 0.5	1.5 ± 0.6
Active foraging bouts (/day)	4.3 ± 1.1	3.4 ± 0.7	4.3 ± 1.5	3.9 ± 1.1	2.8 ± 0.7	3.0 ± 1.2
Flight bout length (mins)	105 ± 32	67 ± 18	114 ± 27	114 ± 36	77 ± 20	120 ± 37
Float bout length (mins)	169 ± 65	264 ± 56	133 ± 55	270 ± 123	315 ± 63	175 ± 87
Forage bout length (mins)	77 ± 20	65 ± 16	75 ± 30	103 ± 18	84 ± 20	95 ± 35
Distance travelled (km/day)	285 ± 19	105 ± 4	433 ± 19	273 ± 22	76 ± 9	305 ± 48

Table 3.3 - Results from the generalized additive and linear mixed-effects components of the GAMM output (colons ":" indicate interaction terms, "s" refers to the smoothing factor, "sp" indicates species (LAAL= Laysan Albatross, BFAL= black-footed albatross)).

Model #	**Response**	**Model Term**	***df***	***F***
1.	Sustained Flight, > 0	s(DSD):sp(LAAL)	6.78	12.82
		s(DSD):sp(BFAL)	3.88	39.97
		Non-breeding Phase	2	9.86
		Species	2	15.98
		Phase:Species	2	4.01
2.	Sustained Flight (0,1)	s(DSD)	4.50	23.73
		Non-breeding Phase	2	10.07
3.	Floating	s(DSD)	5.78	16.83
		Non-breeding Phase	2	11.26
4.	Foraging	s(DSD):sp(LAAL)	3.12	7.67
		s(DSD):sp(BFAL)	3.58	6.19
		Non-breeding Phase	2	6.55

Degrees of freedom for the smoothers are taken from the model hat matrix. Proportion of time spent daily in sustained flight was zero-inflated (>35% zeros) and thus was modeled in two parts as a hurdle model with both quasi-binomial and binary distributions (Models 1 and 2).

Figures

Figure 3.1 – Stacked individual 50% kernel density contours for GLS-equipped Laysan albatross (*n* = 18, top panel, blue) and black-footed albatross (*n* = 15, bottom panel, grey) during the overwinter phase of non-breeding in 2008, 2009, 2011 and 2012. The lightest shade indicates areas used by a single individual, and the darkest indicates areas of most intense overlap among individuals. The thick polygon outlines depict the group-level range of equipped birds of each species based on the 95% kernel contours from pooled KDE. The solid black circle indicates the colony at Midway Atoll National Wildlife Refuge (projection: Lambert Cylindrical Equal Area, datum: WGS1984).

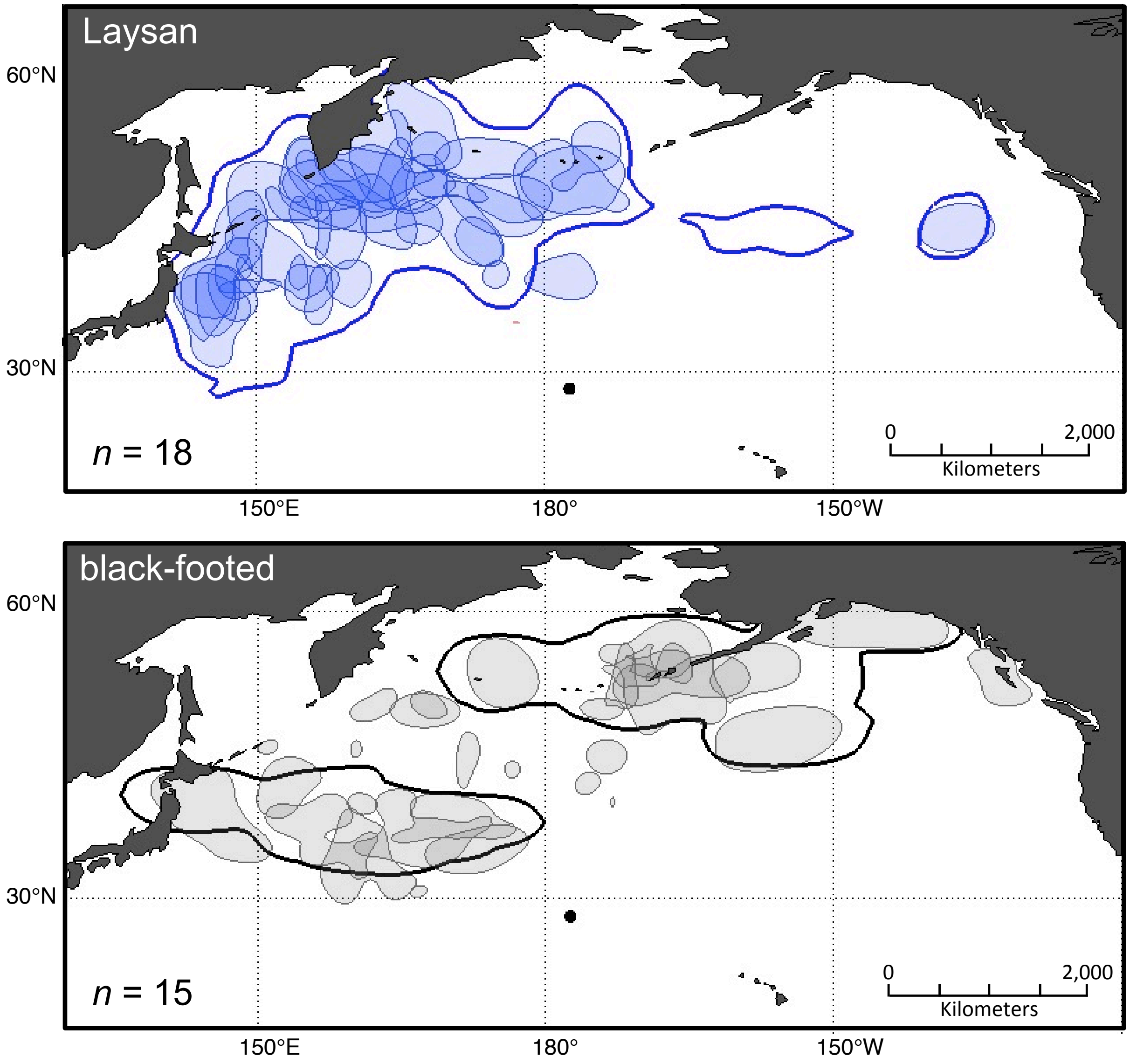


Figure 3.2 – Activity budgets derived from immersion-logger data for Laysan albatross (*n* = 18, top panel) and black-footed albatross (*n* = 15, bottom panel) during the non-breeding period. The proportion of each day within each phase of non-breeding spent engaged in three different activity bout types are reported as mean ± SE.

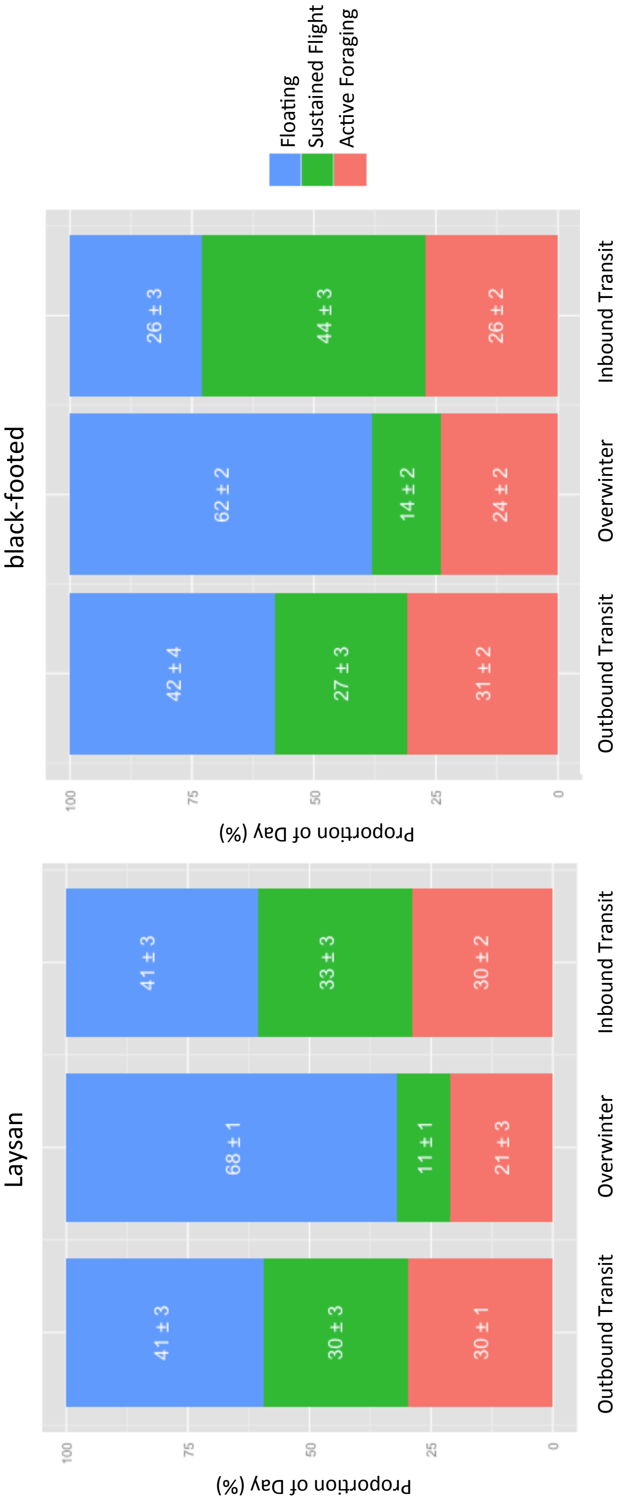
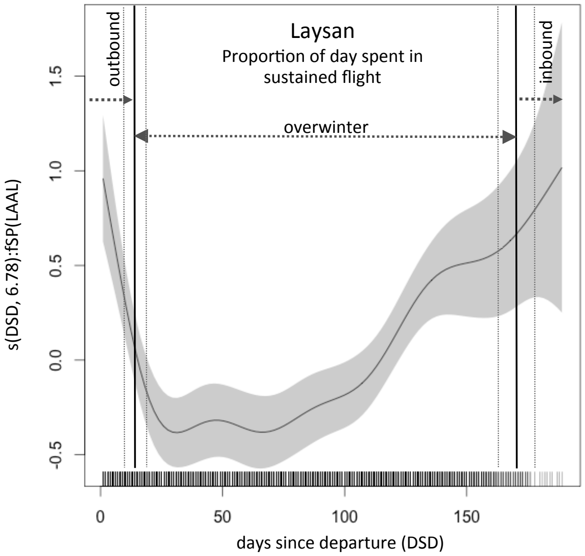
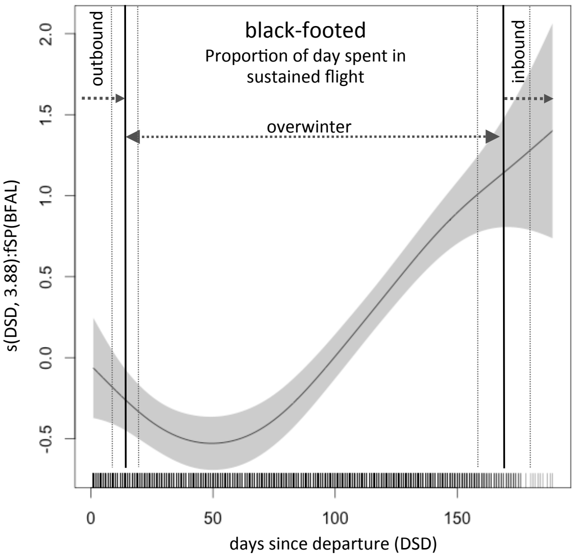
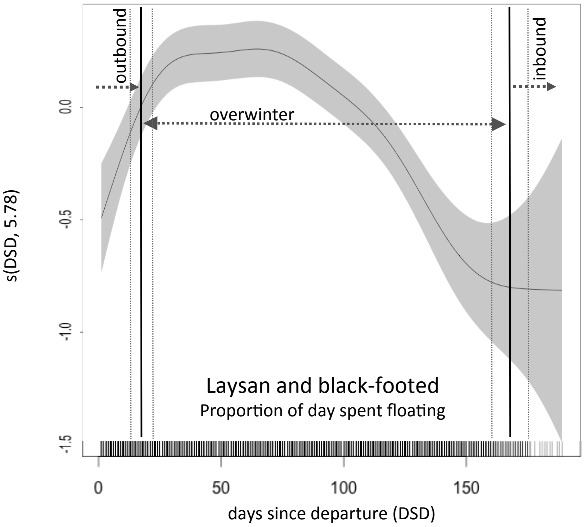
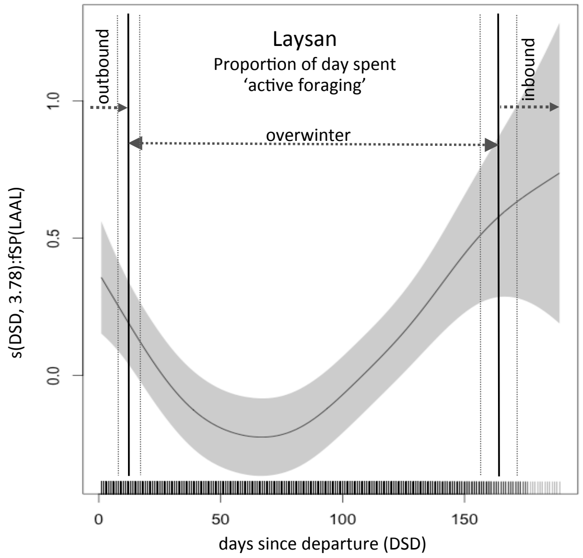


Figure 3.3 – Partial residual plots of daily patterns in non-breeding activity for Laysan and black-footed albatrosses. Estimated smoothing functions (solid lines) with 95% point-wise confidence intervals (delineated by the grey shaded area) estimated from the proportion of daily time spent engaged in sustained flight (top panels), floating on the water's surface (middle panel), and actively foraging (bottom panels) smoothed by the days since colony departure (DSD). The relationship differed significantly between species for sustained flight and active foraging bouts although the general pattern over time is similar. Vertical lines depict the average duration of each non-breeding phase, with outbound transit followed by arrival day at the first overwinter area, and then inbound transit initiation (mean ± SD).


Laysan
Proportion of day spent in sustained flight
outbound
inbound
overwinter
s(DSD, 6.78):fSP(LAAL)
1.5
1.0
0.5
0.0
-0.5
0
50
100
150
days since departure (DSD)


black-footed
Proportion of day spent in sustained flight
outbound
inbound
overwinter
s(DSD, 3.88):fSP(BFAL)
2.0
1.5
1.0
0.5
0.0
-0.5
0
50
100
150
days since departure (DSD)


Laysan and black-footed
Proportion of day spent floating
outbound
inbound
overwinter
s(DSD, 5.78)
0.0
-0.5
-1.0
-1.5
0
50
100
150
days since departure (DSD)


Laysan
Proportion of day spent 'active foraging'
outbound
inbound
overwinter
s(DSD, 3.78):fSP(LAAL)
1.0
0.5
0.0
0
50
100
150
days since departure (DSD)

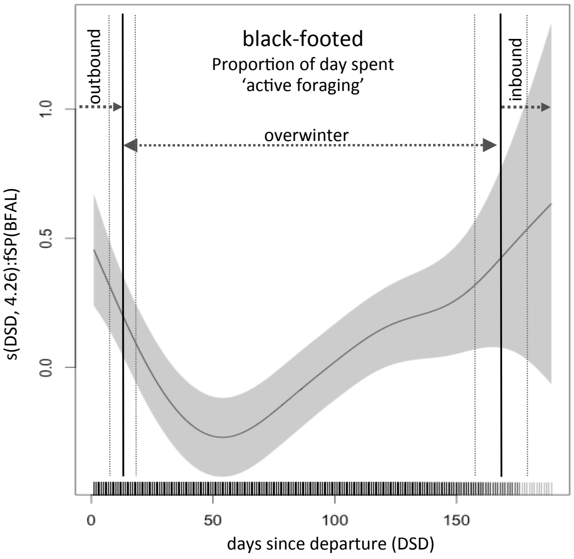

black-footed
Proportion of day spent 'active foraging'
outbound
inbound
overwinter
s(DSD, 4.26):fSP(BFAL)
1.0
0.5
0.0
0
50
100
150
days since departure (DSD)

Figure 3.4 – Individual GLS-equipped Laysan albatross (*n* = 20, top panel) and black-footed albatross (*n* = 15, bottom panel) during the 'quasi-flightless' stage of the overwinter phase (40-day window between 30–70 days since colony departure) in 2008, 2009, 2011 and 2012. Individual birds are indicated with unique colours (projection: Lambert Cylindrical Equal Area, datum: WGS1984).

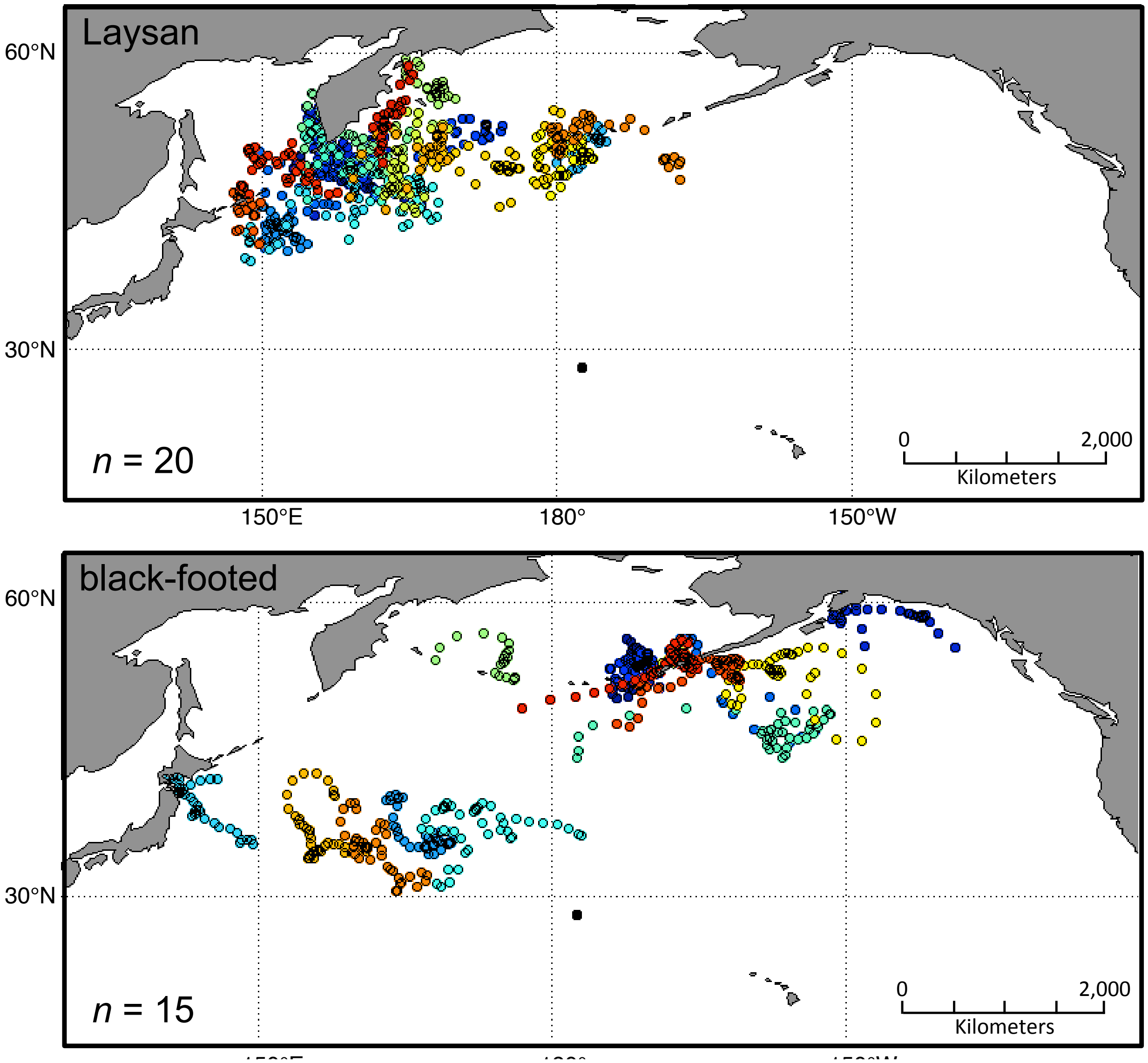
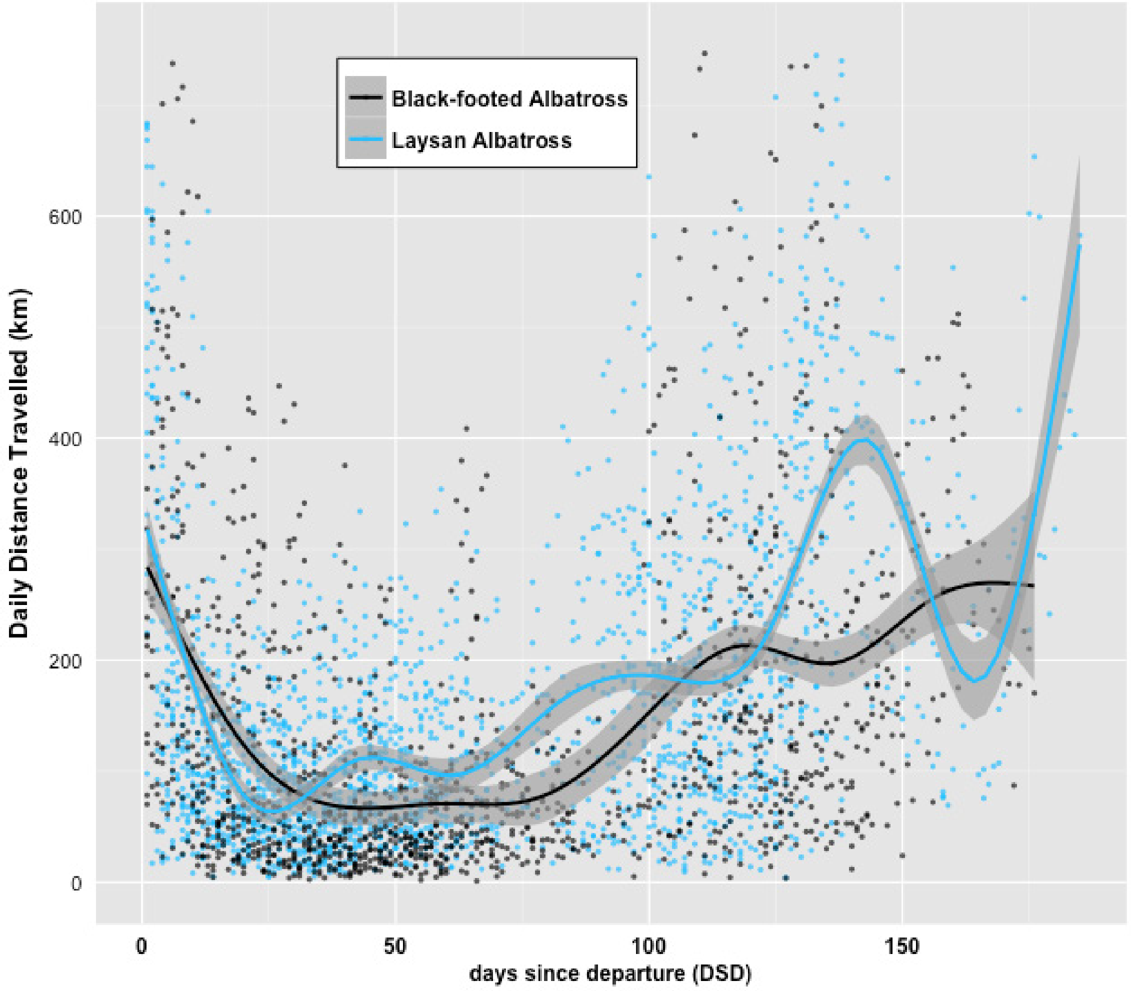


Figure 3.5 – All raw data of daily distance travelled (km) from colony departure (DSD = 0) to return (varies by individual) from GLS-equipped Laysan albatross (*n* = 20) and black-footed albatross (*n* = 15) during the non-breeding season. A LOESS smoother was added to add visual interpretation.



Chapter 4: Individual-Level Variation And Higher-Level Interpretations Of Space Use In Wide-Ranging Species: An Albatross Case Study Of Sampling Effects

Abstract

Marine ecologists and managers need to know the spatial extent of at-sea areas most frequented by the groups of wildlife they study or manage. Defining group-specific ranges and distributions (i.e. space use at the level of species, population, age-class, etc.) can help to identify the source or severity of common or distinct constraints or threats among different at-risk groups. In biologging studies, this is accomplished by estimating the space use of a group based on a sample of tracked individuals. A major assumption of these studies is consistency in individual movements among members of a group. The implications of scaling up individual-level tracking data to infer higher-level spatial patterns for groups (i.e. size and extent of areas used, overlap or segregation among groups) is not well documented for wide-ranging pelagic species with high potential for individual variation in space use. I present a case study exploring the effects of sampling (i.e. number and identity of individuals contributing to an analysis) on defining group-specific space use with year-round multi-colony tracking data from two highly vagile species, Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatrosses. The results clearly demonstrate that caution is warranted when defining space use for a specific species-colony-period group based on datasets of small, intermediate, or relatively large sample sizes (ranging from n=3-42 tracked individuals) due to a high degree of individual-level variation in movements. Overall, I provide further support to the recommendation that biologging studies aiming to define higher-level patterns in space use exercise restraint in the scope of inference, particularly when pooled Kernel Density Estimation techniques are applied to small datasets for wide-ranging species. Transparent reporting in respect to the potential limitations of the data can in turn better inform both biological interpretations and science-based management decisions.

Introduction

A common goal in spatial ecology research or conservation planning is to identify the areas most frequented by a target group of free-ranging animals. In marine systems, this often involves identifying important areas beyond the shoreline, creating unique challenges for species that range widely across the open sea. Groups of interest for marine spatial planning could include for example specific community-level functional groups (e.g. apex predators, Block et al. 2011), taxonomic groups (e.g. seabirds, Ronconi et al. 2012), species-at-risk (e.g. African penguins *Spheniscus demersus*, Ludynia et al. 2012), sub-populations (e.g. seabird colonies, Louzao et al. 2011; sea turtle breeding areas, Schofield et al. 2013) or specific life history phases, often divided further by sex (e.g. pupping female white sharks *Carcharodon carcharias*, Domeier & Nasby-Lucas 2013). Our ability to study the space use of marine animals belonging to a specific group of-concern continues to expand with innovations in animal-attached biologging devices that record location and other ancillary data (Cooke 2008, Hussey et al. 2015, Wilson et al. 2015). Importantly, how we use these individual-based data to define space use more broadly for the higher-level group to which the tracked animals belong, influences how we interpret the biological and management implications of the findings.

For seabirds, individual-based tracking data are commonly used to inform higher-level interpretations of space use. The distant separation between terrestrial breeding and marine foraging areas requires the use of biologging devices to gain insights into habitat use at sea. Because extinction now threatens over 30% of extant seabird species (IUCN 2015), a priority in conservation planning is to assess the variability and extent of the at-sea areas most frequented by birds (Ronconi et al. 2012, Croxall et al. 2012). Seabirds are generally seasonally colonial and migratory, thus specific regions are more heavily visited during different periods of their annual cycle. Defining period-specific space use can help to identify the source or severity of common or distinct threats posed at different periods in the annual cycle for a species, and for further sub-groups divided by for example age-class (e.g. Riotte-Lambert & Weimerskirch 2013, Péron & Grémillet 2013, Chapter Two), or sex (e.g. Phillips et al. 2004b, Hedd et al. 2014). At the colony level, individual-based tracking data have been used to discern period- and colony-specific space use and potential associated impacts for population dynamics for a variety of seabird species (e.g. Young et al. 2009, Catry et al. 2011, Wakefield et al. 2011, Gaston et al. 2011, Frederiksen et al. 2012, McFarlane Tranquilla et al. 2013).

Various analytical approaches are available to estimate home ranges (i.e. full extent of the area used) and utilization distributions (i.e. areas of concentrated space use within the range) from biologger-derived location data (Fieberg & Börger 2012). Kernel Density Estimation (KDE) remains one of the most common tools for visualizing and quantifying animal ranges and distributions since its inception in ecological studies (Worton 1989). KDE is a non-parametric statistical method for estimating probability densities. When applied to tracking data, the result of a KDE analysis is the creation of contours representing densities or intensities of space use, often called a Kernel Density Estimate (herein I use 'KDE' interchangeably to refer to both the analytical approach and output of the analysis). There has been much discussion over best practises in implementing and reporting for KDE and other similar approaches, and these have been thoroughly reviewed elsewhere (e.g. Nicholls et al. 2005, Laver & Kelly 2008, Kie et al. 2010, Fieberg & Börger 2012, Fleming et al. 2015, Signer et al. 2015). Despite shifting baselines in execution, KDE continues to endure among ecologists as a relatively simple and accessible tool for describing space use.

Generally, the results of independent KDE for each tracked individual in a dataset are reported, thus facilitating comparisons among individuals in the extent and locations of home ranges and areas of high use. Generalizations are often made for the higher-level group to which the tracked individuals belong by reporting results across individuals (Laver & Kelly 2008). However, within the seabird literature, location data from multiple individuals are often combined into a single pooled KDE analysis to describe space use without discriminating among individuals. The results are then used to extrapolate space use to the higher-level group to which the tracked individuals belong (e.g. species-colony-period specific). Wood et al. (2000) were among the first to recommend pooled KDE as a tool to define and compare space use between groups of seabirds based on group-level sets of KDE contours (two albatross *spp*. from the same colony during breeding), and the practise has since become commonplace. Some recent examples include the use of pooled KDE to compare space use between different annual periods for a species and colony (e.g. Robertson et al. 2014) or for different sexes (e.g. Burke et al. 2015), different species from the same colony (e.g. Linnebjerg et al. 2013), different colonies of the same species (e.g. Thiebot et al. 2011, Young et al. 2009), and different species and colonies (e.g. McFarlane Tranquilla et al. 2013, 2015).

Scaling up individual-level location data in a pooled analysis to infer higher-level group spatial patterns has two related consequences: 1) the output masks the degree of variation in movements among the individuals in the dataset contributing to the analysis, and 2) it assumes tracked individuals reasonably represent the larger group as a whole. Individual-level space use is rarely reported together with group-level pooled analyses, unintentionally inhibiting assessment of the contribution of individuals to the observed higher-level spatial patterns. The assumption of representativeness is sometimes briefly conceded, but implications for the biological interpretations of the results generally are not formally evaluated. A number of marine vertebrate studies have illustrated an asymptotic saturation effect of increasing the number of tracked individuals or number of foraging trips per individual on estimates of the size of the area occupied by a sample of tracked animals in a pooled analysis (e.g. Wood et al. 2000, Hindell et al. 2003, Taylor et al. 2004, Breed et al. 2006, Soanes et al. 2013, Orben et al. 2015). These studies suggest that a sample of individuals may be representative of their respective group if the estimated occupied areas reach an asymptote before the maximum sample size is included in the analysis. In addition to the estimated size of the area occupied by a group, it has also been demonstrated that the geographic locations of contours resulting from pooled analyses of different individuals can vary depending on the degree of individual variation within the sample (Taylor et al. 2004, Breed et al. 2006, Orben et al. 2015). Beyond these few examples which directly address assumptions of group-level representativeness of a sample, consistencies in movements among individuals comprising a dataset and among members of the higher-level group they represent remain un-tested assumptions, especially in seabird studies with small sample sizes (Soanes et al. 2013).

Importantly, this oversight persists despite a number of published works recommending that biologists using biologging technologies exercise restraint in the inferential scope of the findings (Lindberg & Walker 2007, Hebblewhite & Haydon 2010, Torres et al. 2013). Here, I explicitly demonstrate the impacts of individual variation and sample size on inter-colony comparisons of space use (i.e. differences in the size of areas used, overlap or segregation in distributions) in relation to the stage of the annual cycle in two highly vagile seabirds, the Laysan *Phoebastria immutabilis* and black-footed *P. nigripes* albatross. Past work has used sub-sampling routines to identify the presence of an area asymptote as justification for pooled analyses. I use a similar approach but focus rather on the range in output at different sample sizes to assess the potential for sampling effects from individual-level variation on higher-level interpretations of space use. When not at the breeding colonies, Laysan and black-footed albatross inhabit the vast open waters of the North Pacific Ocean basin. Like many seabirds, a variety of anthropogenic threats have resulted in both species being listed as 'Near Threatened' (IUCN 2015), thus identifying at-sea habitat and spatial overlap with risks has been a management priority (Naughton et al. 2007, Arata et al. 2009). I expect this practical demonstration of the consequences of sampling effects to provide further insights into the importance of considering the inferential limitations of small datasets, for these and other wide-ranging species, especially when informing science-based conservation planning strategies and management decisions.

Methods

Study Sites and Device Deployment

Fieldwork was conducted between 2008-2013 at two colonies in the Northwestern Hawaiian Islands: Sand Island, Midway Atoll National Wildlife Refuge (28.21°N, 177.36°W; herein 'Midway') and Tern Island, French Frigate Shoals (23.87°N, 166.28°W; herein 'Tern'). These breeding sites are located 1,200 km apart with population sizes (including all islands within the atolls) for Laysan albatross (herein 'Laysans') of 408,130 breeding pairs at Midway and 3,230 pairs at Tern, and for black-footed albatross (herein 'black-footeds') of 21,830 pairs at Midway and 4,260 pairs at Tern (Arata et al. 2009). Two types of leg-mounted global location sensing (GLS) biologgers were deployed and recovered, using similar approaches across device types, colonies and species (Table 4.1). Breeding birds (generally of unknown sex and only one member of a pair) were selected and captured opportunistically at the nest during incubation or chick brooding for device deployment and recaptured for device retrieval in a subsequent breeding season. All devices were mounted to a plastic leg band using cable ties and marine grade quick-setting epoxy and attached to the tarsus (logger+attachment *c.* 5-9g, <1% body mass; well below the recommended limit for albatrosses, Phillips et al., 2003). GLS recovery rates varied among years but were on average 77% at Midway (2008-2013) and 91% at Tern (2008-2010). While it was not possible to formally assess tag effects, deployments at a Laysan albatross colony on Oahu, Hawaii resulted in no detectable short-term effects on reproductive success (Young et al. 2009).

Positional Data Processing

GLS were programmed to record ambient light level data sub-sampled to maximums at 10-minute intervals. Time of sunrise and sunset, estimated from thresholds of light level intensity, allowed for daily estimation of latitude from day length and longitude from the time of local noon/midnight. Light data from BAS GLS were processed manually using *BASTrak* software and light data from Lotek GLS were processed internally by automated template fitting software. The accuracy of latitude estimates during equinox periods is unavoidably compromised, as day length depends only weakly on latitude at this time (Ekstrom 2004). For this study, locations on 15 days of either side of the equinoxes were excluded based on consistently suspect latitude estimates. All remaining locations were then processed using state-space models (SSMs) estimated with Bayesian techniques (Jonsen et al. 2005, Block et al. 2011, Winship et al. 2012) to improve estimate accuracy and consistency across colonies and device types and to avoid unnecessary data loss (for SSM details see Chapter Three).

I divided daily locations into four periods of the annual cycle approximately overlapping different life history phases (phenology can vary between species and colonies by *c.* 1-2 weeks) for subsequent analyses (Figure 4.1). Each period is 60 days in length thus avoiding overlap with the equinoxes (01-Mar to 15-Apr and 01-Sep to 15-Oct) and avoiding intervals of most intensive logger deployment and recovery wherein each individual bird's deployment length varied most (15-Dec to 01-Jan). Locations within each period for each bird were included only if an individual contributed >30 days of data within that period to ensure each individual exhibited a range of natural behaviours for each life history phase (i.e. capturing time spent both at the colony and foraging at sea during the breeding season periods).

I examined patterns of at-sea distribution within species between colonies for each annual period with KDE (Worton 1989, Wood et al. 2000, Laver & Kelly 2008, Kie et al. 2010), using purpose-built software written in Matlab (MathWorks Inc, USA; IKNOS Toolbox, Y. Tremblay unpublished). Limited sample sizes within years inhibited inter-annual comparisons due to the inability to differentiate among individual variation and true annual effects. Therefore, data were pooled across years within each period by colony and species. KDEs were conducted independently for each individual and as pooled KDEs where all locations from individuals within a species-colony-period dataset are pooled together for the analysis.

A KDE for bivariate data is defined as:

$$f(x) = [1/(nh^2)] \sum_{i=1}^{n} K\left\{\frac{(x - X_i)}{h}\right\}$$

where $X_i(i = 1, 2, \ldots, n)$ is the sample of n observed locations (i.e. a coordinate vector of longitude and latitude) from a distribution with unknown density f, x is the location where the function is evaluated, $h > 0$ is the smoothing parameter (or bandwidth; details below), and K is a kernel density (I use a biweight kernel, as described in Seaman & Powell 1996). The KDE method essentially places a kernel over each observed location in the dataset of sample size n, where X_i is the ith observation. A grid is superimposed over the data and the function is evaluated at each grid intersection, or x (KDEs were computed on a 0.25° x 0.25° grid), providing a two-dimensional (bivariate) Gaussian density estimate for each x. The density estimated for each grid intersection represents an average density of all the kernels that overlap that location. Observations closer to the intersection contribute more to the estimate than those further away. The density surface can then be converted into contours of concentric polygons by connecting areas of equal density. Following the standard for most KDE studies (Laver & Kelly 2008), I took the 50% kernel contour to represent regions of high use for each sample of individuals or individual, and the 95% kernel contour to represent the outermost limits of the range. The contours can then be visualized as distribution maps.

The most important decision in computing KDEs is the selection of the smoothing parameter, *h* (Kie 2013). The value of *h* influences both the outermost limits of an estimated range, and the shape and distribution of the regions of high use (Kie et al. 2010); high values of *h* can lead to over-smoothing the kernel contours (i.e. contours contain fewer more contiguous polygons, considered lower precision with higher bias toward larger areas) while low values of *h* can under-smooth the kernel contours (i.e. contours break into smaller disjointed polygons, considered higher precision with bias toward smaller areas). The influence of *h* changes with the sample size of a dataset, where a higher number of locations contributing to an analysis will have lower optimal values of *h* for minimizing under- and over-smoothing (Kie et al. 2010). Because each species-colony-period dataset differed in sample size (including locations from six to 42 individuals in pooled KDEs), I selected *h* independently for each dataset using an automated data-based selection method to estimate optimal values for *h* (Sheather & Jones 1991, Sheather 2004). A second decision in calculating kernel contours is whether to hold *h* constant for all evaluated points (fixed kernels) or to allow *h* to vary as a function of local densities (local kernels, Kie 2013). Local kernels increase *h* at points with lower location densities allowing for greater smoothing in areas with more uncertainty (Worton 1989). With local kernels, smaller datasets comprised of fewer location estimates are subject to increased smoothing and less reliable contours overall relative to larger datasets, especially at the peripheries of the range (>80% kernel contours; Seaman et al., 1999). Because I am interested in comparing both the 50% and 95% kernel contours of KDEs generated from datasets of different size, I used a fixed kernel approach for analyses. KDE iterations in the analyses resulted in optimized fixed *h* values for each dataset ranging from 0.0043°-0.0738° latitude and 0.0038°-0.119° longitude (mean ± standard deviation 0.0282° ± 0.01° latitude and 0.0385° ± 0.02° longitude).

Sampling Effects

I performed four period-specific independent KDEs for each individual, as well as a pooled KDE for each complete species-colony-period dataset. As a first assessment of the potential influence of individual-level variation on perceived higher-level space use from pooled KDE, I consider the effect of excluding a single individual on KDE output from each full species-colony-period dataset. I performed a pooled KDE (as outlined above) for iterations of max *n*-1 individuals (sequentially excluding each individual once, for a total number of iterations equal to max *n*), and recorded the area and geographic location of the resulting kernel contours. To represent the geographic location of pooled KDE kernel contours, I assessed the maximum and minimum latitudes and longitudes of the 95% and 50% contours. Because each set of kernel contour polygons can comprise multiple variably shaped polygons, it was not practical to compare the location of polygon centroids between pooled KDE iterations. The peripheral limits of the contours provide a generalization of the location of each group of polygons.

I also used a simple sub-sampling approach to assess the influences of different *n* and identity of the individuals comprising the sample on the output of pooled KDE for each species-colony-period dataset. My approach is similar to previous studies (Wood et al. 2000, Hindell et al. 2003, Taylor et al. 2004, Breed et al. 2006, Soanes et al. 2013, Orben et al. 2015) but my focus is not identifying the presence of an asymptote but rather the range in output at each sample size. For each dataset, I randomly sub-sampled *n* individuals (without replacement) beginning with *n* = 3 and increasing in increments of two, up to three less than the maximum number available. For each value of *n,* I repeated the random selection process 100 times, resulting in 100 unique sub-samples of individuals for each *n*. I then carried out a pooled KDE generated from the daily locations of each sub-sample of individuals. The value of *h* for each KDE was again determined based on the data within each sub-sample. This approach most accurately simulates having only the data in the sub-sample from which to estimate the range and distribution of the represented group (i.e. the species and colony in a given period of the annual cycle). This differs from past studies, where a pre-determined fixed value of *h* was applied to all KDE iterations (e.g. Breed et al. 2006, Orben et al. 2015). Here I am interested in the degree of variation among KDE outputs given the "available" data set, and therefore a data-based selection method for each independent KDE is most appropriate. For each KDE, I recorded the total area of the resulting 95% and 50% kernel contours. I visualized the influence of *n* on the kernel contour areas by plotting the results of each set of 100 KDE iterations for a given value of *n* [as median, interquartile range

(IQR, 50% of iterations around the median), whiskers to 1.5xIQR, and outlying data points indicating the maximum and minimum estimates for each n].

Results

Assessing Individual-Level Variation Within A Dataset

The results of independent KDE for each bird show differing degrees of variation in space use among the individuals tracked, depending on the species-colony-period dataset (Table 4.2, Figure 4.2 & 4.3). Stacked individual 50% kernel contours visualize variation in geographic locations used by all individuals in a dataset, as well as the areas of most intense overlap among individuals. As one example, while independent 50% kernel contours for Laysans from Midway overlap most north and northwest of the colony during PBE, nine (of 42) tracked birds also exhibit 50% contours to the east and northeast of the colony (Figure 4.2). During this period, individual Laysans from Midway occupied a mean 50% kernel contour area of 532,000 km^2, but this varied greatly among individual birds (±341,000 km^2 standard deviation, Table 4.2). The 95% kernel contour areas also varied greatly among individuals (6,624,000 ± 3,228,000 km^2, mean ± standard deviation; Table 4.2). Similarly, 50% kernel contours for black-footeds from Tern during OW occurred mostly along the coasts and offshore from British Columbia and Alaska, but four (of 24) tracked birds also occupied 50% kernel contours north and northwest of the colony over the open North Pacific (Figure 4.3). During this period, 50% kernel contours occupied a mean 149,000 km^2 (±149,000 km^2) and 95% contours occupied a mean 2,001,000 km^2 (±1,526,000 km^2).

The results of layering pooled KDE generated from the maximum *n* for each dataset with independent stacked KDE indicate differing potential for misrepresentation of individual spatial diversity depending on the species-colony-period (Figure 4.2 & 4.3). Generally, the 50% kernel contours resulting from pooled KDE including all locations in a dataset together fail to represent the extent of variability among individuals, both in geographic locations (Figure 4.2 & 4.3) and size of areas used (Table 4.2). As one example, for black-footeds from Tern during LCR, 11 (of 23) individuals occupied 50% kernel contours along the northeast perimeter of the North Pacific ranging throughout offshore waters of Alaska to California, yet a pooled KDE identifies a group-level 50%

kernel contour occupying a relatively small area near Vancouver Island, British Columbia (Figure 4.3). During this period, individual black-footeds used 50% kernel contour areas of 815,000 ± 471,000 km^2, while a pooled KDE indicates an overall area used of 2,710,000 km^2, masking the variation among individuals in the dataset (Table 4.2).

KDE outputs generated from iterations where single individuals are sequentially excluded from the analysis show variable sensitivity of pooled KDE to individual-level variation depending on the species-colony-period dataset (Table 4.3 & 4.4). For example, max n-1 sampling sensitivity during OW for both colonies was low for Laysans but high for black-footeds. For Laysans during OW, outputs from pooled max n-1 KDE were generally consistent in area and geographic location, suggesting that variation in movements among the individuals comprising the datasets from each colony during this period is relatively low (Table 4.3 & 4.4). Areas occupied by OW 50% contour estimates varied by 129,000 km^2 and 158,000 km^2, for Midway (max n = 42) and Tern (max n = 26), respectively (Table 4.3). For Midway Laysans, the locations of OW 50% contour estimates among max n-1 iterations were consistent (northern-most limits varying by only 0.66°N, western-most limits varying by 1.04°W; Table 4.4). Tern Laysans differed more in their east-west movements during OW, resulting in variable estimates of the western 50% contour limits (up to 5.93°W), while the northern limits were more consistent (ranging 0.38°N). For both colonies, estimates of the areas and geographic locations of the 95% contours followed similar patterns (Table 4.3 & 4.4). In contrast, black-footeds tracked from both colonies exhibited higher individual-level variation during OW than Laysans. 50% contour area estimates from max n-1 pooled KDE iterations for both colonies varied ≥ 500,000 km^2 and 95% contour estimates varied >2,500,000 km^2 (Table 4.3). The northern limits of both 50% and 95% contour estimates varied by ≤2°N, but the western limits varied widely (Table 4.4). Western 50% contour limits were estimated across 5°W and 2.64°W and 95% contour limits across 14.18°W and 32.1°W (Midway and Tern, respectively; Table 4.4). The high individual-level variation in space use among black-footeds for both colonies during OW illustrated by independent KDEs (Figure 4.2 & 4.3, Table 4.1) results in high variability in max n-1 pooled KDE outputs (Table 4.3 & 4.4).

Sampling Sensitivity Of Pooled KDE At Intermediate Sample Sizes

Pooled KDE iterations generated from the daily locations of 15 randomly selected individuals showed varying sensitivity of KDE output at intermediate values of *n*. The difference between the largest and smallest 50% contour estimated from KDE iterations of *n*=15 ranged from 595,000 km^2 (Laysans from Midway during ECR) to 4,861,000 km^2 (black-footeds from Midway during OW; Table 4.3). The area of the 95% contour was similarly variable at *n*=15; the difference between the largest and smallest estimated 95% contour was least for Laysans from Tern during PBE (2,200,000 km^2) but this dataset had a small total number of individuals (max *n*=18) from which to draw sub-samples. KDE iterations of *n*=15 produced 95% contours varying in area generally between 3,000,000 and 9,000,000 km^2, but varied by as much as 13,115,000 km^2 for black-footeds from Midway during the OW period (Table 4.3).

The geographic location of the 50% contour was highly sensitive to sampling effects at *n*=15. The outermost limits of 50% contours resultant from 100 unique KDEs of 15 randomly sub-sampled individuals varied widely depending on the species-colony-period considered (Figure 4.4). 50% contours varied least in location during ECR, however this could only be assessed for Midway. During the remaining three annual periods, the limits of the 50% contour estimated from KDE iterations for both colonies of Laysans and black-footeds varied least in the southernmost extents (Figure 4.4). The high degree of variation in the northern-, eastern- and western-most limits resulted in 50% contours spread widely across the North Pacific, yielding either high overlap or complete segregation among colony-specific ranges depending on the 15 individuals contributing to the KDE (Figure 4.4).

Sampling Sensitivity Of Pooled KDE At Small Sample Sizes

Small values of *n* comprised of only a few individuals resulted in highly variable pooled KDE output (Figure 4.5 & 4.6). Sub-samples of three to five random individuals consistently produced areas of 50% and 95% kernel contours that varied by a factor of three to four. For example, three randomly selected Laysans or black-footeds from Midway during PBE can produce a 95% contour encompassing an area anywhere from 5,000,000 to 20,000,000 km^2 (Figure 4.5 & 4.6). Similarly, five randomly selected

Laysans from Tern during OW can produce a 50% contour encompassing areas from 600,000 to 2,300,000 km^2 (Figure 4.6). The highest degree of spatial diversity among individuals occurred among black-footeds tracked from Tern during OW, where pooled KDE based on location data from five (of 24) individuals can result in 50% contours encompassing areas differing by a factor of eight (ranging from 400,000 to 3,200,000 km^2, Figure 4.6).

The locations of contours were also highly sensitive to the sample of individuals at small values of *n*. Generally for both species and colonies during all annual periods, sub-samples of three to five random individuals produced 50% and 95% kernel contours that varied in their northern limit by at least 10° of latitude. Contours often varied in the northern limit by 20°, and up to 30° of latitude for the 95% contour representing black-footeds from Tern during LCR. The amount of variation among iterations at small *n* was generally similar regardless of the size of the full dataset from which sub-samples were drawn.

Sampling Effects With Increasing Sample Size

For species-colony-period datasets where the maximum *n* was >30 individuals, the sensitivity of pooled KDE in the resultant areas of 50% and 95% contours appears to stabilize with increasing *n*. The median areas of the contours roughly approach an asymptote between *n*=17-21 (both species from Midway, Figure 4.5 & 4.6). Around the same *n*, the area estimates resulting from each set of iterations encompass similar IQRs and maximum/minimum values. At this *n*, increasing the number of individuals contributing to a KDE does not appear to increase the probability of obtaining a more refined estimate of the amount of area occupied by a pooled estimate of the 50% or 95% kernel contour. However, the range in pooled KDE outputs for some species-colony-period datasets remains large even when sampling effects appear to reach saturation. For example, sub-samples of *n*=31 individual Laysans from Midway during PBE result in 95% contour areas varying by 7,250,000 km^2 and 50% contour areas varying by 1,000,000 km^2, despite an apparent stabilization of median outputs around *n*=17. As *n* approaches within five individuals of the max *n*, the variability among KDE area outputs predictably decreases, as the sub-samples are drawn from a finite pool of individuals and the results will inevitably become increasingly similar. Species-colony-period datasets with maximum *n* less than 30 individuals exhibited less consistently identifiable values of *n* at which sampling sensitivity for KDE area estimates stabilized (both species from Tern, Figure 4.5 & 4.6). For these datasets, the estimated areas occupied by the 50% and 95% contours continue to increase or remain highly variable until *n* reaches within five individuals of max *n*.

Discussion

From my exploratory assessment of sampling effects, the number and selection of individual Laysan or black-footed albatrosses contributing location data to a pooled KDE had a marked effect on perceived spatial usage at the colony level for both species. Where an asymptotic saturation effect was detectable (datasets with maximum *n*>30), a minimum of 17-21 individuals was required to minimize the variability among mean KDE outputs generated from sub-samples of individuals representing a higher-level group. Even when this minimum sample size is satisfied, the influence of inconsistencies among individual space use on higher-level interpretations is apparent when the full range in outputs at the saturation sample size is considered, along with independent individual-level KDE. My analysis highlights some of the major limitations for biological interpretations based on different sample sizes that are not apparent from pooled KDE analyses alone. I discuss some examples of common individual-to-colony level extrapolations in seabird biologging research that could benefit from reporting and discussing the potential influence of individual variation.

Commonly in multi-colony biologging studies, the size of the areas used and the degree of at-sea spatial segregation among seabird colonies are delineated by a pooled KDE from a sample of biologger-equipped individuals from each group. The size of pooled KDE 50% or 95% contours are quantified and compared, and the degree of overlap between groups is calculated (e.g. Young et al. 2009, Thiebot et al. 2012, Frederiksen et al. 2012, McFarlane Tranquilla et al. 2013, Burke et al. 2015). However, without consideration of individual variation within an available dataset, these higher-level inferences can be inadvertently misleading. With a small number of sampled individuals (*n* = 3-15) of Laysans or black-footeds, my analysis shows that the calculated degree of overlap between contours taken to represent colony-specific ranges can vary between complete segregation and extensive overlap, dependent on the identity and number of individuals sampled. Predictably, sampling effects are strongest outside of the early chick rearing period (Figure 4.5 & 4.6), a time when central place constraints are most limiting on the degree of individual variation in movements (Orians & Pearson 1979).

Biologger-equipped individuals are sometimes used to estimate the proportional use or potential presence within specified regions and periods for birds from different colonies based on colony population size estimates. For black-legged kittiwakes (Frederiksen et al. 2011) and murres (*Uria* spp., McFarlane-Tranquilla et al. 2013), the overwinter movements of equipped individuals have been taken to represent all of their colony members proportional to the colony's breeding population, thereby 'distributing' members among specified regions of interest. Pooled KDE 50% contours generated from fifteen or fewer individuals were taken to represent 11 of 16 kittiwake study colonies, and three of those colonies were represented by 5-7 tracked birds (Frederiksen et al. 2011). For example, seven birds from one colony represented the spatial distributions of *c.* 150,000 pairs nesting in the Newfoundland-Labrador Shelf Large Marine Ecosystem. Similarly for murres, pooled KDE 50% contours were generated from 5-29 individuals tracked from each of seven colonies (McFarlane-Tranquilla et al. 2013). For example, thirteen individual murres from one colony were taken to represent the potential presence within defined regions for >400,000 breeding pairs. From my case study, it is clear that colony-level inferences of space use based on pooled KDE generated from <15 individual Laysans and black-footeds from Midway and Tern would result in considerably different estimates of potential presence of birds from these colonies throughout the North Pacific depending on the identity of the individuals tracked. Further, if fifteen individual black-footeds were taken to represent the overwinter range and distribution of the Midway colony, the area within which >21,000 pairs (>35% of the total breeding population, Arata et al. 2009) would be 'distributed' could differ by as much as 13,000,000 km^2 (Table 4.3) and vary greatly in geographic location (Figure 4.4), depending on the individuals sampled.

Even a reasonably large sample size can result in a biased depiction of space use based on pooled KDE 50% kernel contours. Presenting the results of independent KDE for each of the 42 Laysans tracked from Midway during PBE illustrates how pooled KDE vastly under-represents the potential presence of the >400,000 pairs of Laysans nesting at Midway (*c.* 70% of the total breeding population, Arata et al. 2009) over the pelagic eastern North Pacific during this time (Figure 4.2). Similarly, pooled KDE for 18 Laysans tracked from Tern during PBE under-estimates the potential importance of the western North Pacific for birds from this small colony (Figure 4.2). The size of the pooled KDE 50% contour areas would be estimated around 3,000,000 km^2 for both colonies, but would differ greatly among the individuals tracked (Table 4.2). If pooled analyses from both colonies were used to 'spatially distribute' Laysans throughout the North Pacific Ocean during PBE, an assessment of proportional use between the colonies based on my complete biologging datasets would be misguided. In past studies, authors have often acknowledged the assumption that the movements of sub-sampled birds are representative of all birds from each colony but the potential implications for the conclusions are not made explicit. Addressing sampling effects with a clear representation of individual variation within the datasets would help to ensure that management recommendations made are as reliable and useful as possible.

A straightforward approach to reporting individual variation in movement within a biologging dataset is to conduct and report individual-level analyses, for example, as illustrated by Phillips et al. (2006), Ceia et al. (2014), Young et al. (2015) and in the present study (Table 4.2, Figure 4.2 & 4.3). While identifying the locations and areas of high use regions is more challenging to describe quantitatively from stacked individual contours, the degree of variation among individuals in the sample is clear. If group-level pooled analyses are still desirable, asking the simple question, "If we tracked one less individual, how different could the results of the pooled analysis be?" can be an effective means of considering whether a pooled analysis is appropriate for higher group-level inferences. As illustrated with my max *n*-1 analyses, exclusion of a single individual in some cases can have a significant influence on the group-level range and distributions estimated from a pooled KDE (Table 4.3 & 4.4), sending up a 'red flag' for pooled analysis alone. For example, the east-west variation among the movements of Laysans tracked from both Midway (*n*=42) and Tern (*n*=26) during late chick rearing has a sizeable effect on the western-most limits of max *n*-1 pooled KDE 95% contours (Table 4.4). Taking the space use of these birds as representative of all members of their respective colony during this period would be ill advised. The convenience of a single pooled analysis to represent the space use of a group of individuals can come at the loss of important information on individual movements that can greatly impact higher-level biological inferences.

Importantly, the shape of area saturation curves alone do not fully disclose the influence of individuals on the output of pooled analyses, especially when the outputs are used to draw comparisons in space use among groups of interest. The variability among sub-samples should be assessed including maximum and minimum estimates in area occupied, along with the range in geographic locations of those areas. Increasingly, studies are including significance tests for overlap analyses; the proportional area of overlap between specified contours estimated for groups of interest from full datasets are compared with those estimated from randomized iterative sub-samples as a test of whether enough individuals were tracked to make reasonable higher-level inferences of significant spatial segregation (e.g. Breed et al. 2006, Kappes et al. 2011, Cleasby et al. 2015, Orben et al. 2015). This approach, coupled with area saturation curves, can improve confidence in the appropriateness of higher-level extrapolations. However, it is important these assessments are conducted for smaller contours (i.e. 50%) where individual variation has a much higher influence on pooled outputs (Figure 4.5 & 4.6), and should be accompanied by reporting of individual-level analyses, especially where the size of datasets are limited.

Here I focus on KDE, but there are a variety of approaches for estimating group-specific ranges and the distribution of locations within that range (Kie et al. 2010). Grid cell methods offer a simple alternative, where the cumulative time spent within cells of a predefined grid size is used to identify the extent of a group’s range and areas of most intense use (e.g. Soanes et al. 2013). Other methods take a habitat preference modelling approach, which takes into account environmental factors that shape patterns of space use (e.g. Aarts et al. 2008, Wakefield et al. 2011, Raymond et al. 2015). There have been a number of recent advances in approaches for estimating space use at the individual level which incorporate both the spatial and temporal nature of tracking data to estimate distribution contours, but most have not been expanded to generate group-level estimates of space use (e.g. Time Local Convex Hull, Lyons et al. 2013, Baker et al. 2015; movement-based KDE, Benhamou 2011). Regardless of the approach selected as the best method to scale up individual location data to infer higher-level patterns in space use, the number and identity of the individuals contributing to the analysis has some effect on the output. The biases introduced from individual variation and sample size can be accounted for in part by methods that use mixed-effects modelling (e.g. Aarts et al. 2008). For other methods, like KDE or grid cells, the output of pooled analyses should be interpreted with careful consideration of the sensitivity to sampling effects, especially for wide-ranging species with high potential for individual-level variation in movements.

Location data can be obtained from a variety of biologging device types, varying in location uncertainty (Wakefield et al. 2009a). Devices with higher uncertainty, such as GLS deployed on animals capable of travelling large daily distances, will inherently introduce more error in defining group-specific ranges and distributions. SSM approaches offer a considerable advancement in refining location estimate uncertainty by incorporating device-specific error and movement dynamics into estimates of true daily positions (Jonsen et al. 2005, Winship et al. 2012). Still, the remaining uncertainty in my SSM-estimated locations was not accounted for in KDE (estimated as Bayesian 95% credible limits from the posterior distributions of individual location estimates, mean ± standard error, 0.89 ± 0.08° latitude and 0.92 ± 0.06° longitude). While small differences in geographic locations of contours may be attributable in part to underlying location estimate uncertainty, the large differences observed among sub-sampled KDE iterations for many species-colony-period KDEs likely reflect individual-level differences. Given the vast spatial scale at which my study species are acting and the magnitude of differences among KDE outputs, the effect of location uncertainty is not likely greater than the effect of true individual-level spatial diversity on the observed variation among pooled KDE output (particularly KDE of n=15 random individuals; Table 4.3, Figure 4.4).

Conclusions

I am certainly not the first to caution that small sample sizes of biologger-tracked individuals increase the probability of erroneous higher-level conclusions (e.g. Lindberg & Walker 2007, Hebblewhite & Haydon 2010, Schofield et al. 2013, Soanes et al. 2013). Further, the examination of intra-population variation among individual movements is presently a burgeoning field in biologging studies of marine vertebrate behaviour (reviewed by Patrick et al. 2014). Yet a major gap remains where inferences continue to be drawn from individual-based tracking data with insufficient consideration of the influence of sampling effects. Consistency among individuals in their movements will vary depending on a given species' biology, and the representativeness of a sample will also be a function of the total size of the represented group (Lindberg & Walker 2007, Hebblewhite & Haydon 2010). Sampling effects should be evaluated on a case-by-case basis. Many seabirds do not range widely from small colonies during the breeding season, for example, and colony-level interpretations of space-use may be entirely justified (e.g. Wakefield et al. 2013). During non-breeding, many migrate far from the colonies where colony members may or may not be consistent in their movements and overwinter areas most frequented (e.g. Phillips et al. 2005, Dias et al. 2011). In some cases, it may simply be unreasonable to delineate the boundaries of group-specific distributions due to an inability to confidently infer higher-level patterns with the available sample of individuals. As albatrosses may be an extreme example of wide-ranging pelagic seabirds, a comparative analysis similar to that presented here could be undertaken for species with differing degrees of individual variation and extent in movements throughout the annual cycle. In light of my results, I caution against drawing lines around group-specific ranges based on a sample of individuals without assessing and reporting potential sampling effects. This is especially true in calculating proportional areas of overlap and estimating 'potential presence' between groups of interest (i.e. species, colonies, periods, age classes, sexes) based on substantial extrapolations from few tracked individuals.

Biologging data have a key role to play in developing management and recovery plans for seabird species-at-risk, and in the designation and monitoring of Marine Protected Areas, especially when integrated with a variety of different approaches

(Ronconi et al. 2012, Croxall et al. 2012, Young et al. 2015). The effectiveness of advising conservation decisions based on the movements of individuals ultimately depends on the clarity with which we concede the limitations of the data and subsequent analyses. This is especially important for wide-ranging pelagic seabirds, as these families have experienced the largest documented population declines (Paleczny et al. 2015) and have high potential for individual variability in movements across the oceans they inhabit relative to shorter-ranging and coastal species. For most marine wildlife biologging studies, the number of individuals successfully tracked falls short of an 'ideal' (i.e. statistically robust and biologically relevant) sample size. Rather, the ultimate sample size is governed by ethics, time, costs and recovery rates, where the final dataset can often unavoidably be comprised of location data from few individuals. As such, assessment and acknowledgement of the sensitivity of a chosen analytical approach to sampling effects at the available sample size need to become the norm, especially for higher-level interpretations of space use for wide-ranging marine species.

The work in Chapter Four also appears in: Gutowsky SE, Leonard ML, Conners M, Shaffer SA, Jonsen ID (2015) Individual-level variation and higher-level interpretions of space use in wide-ranging species: An albatross case study of sampling effects. Front Mar Sci 2:93. **Statement of Contribution:** SAS and MC initiated and executed data collection. SEG partipicated in fieldwork in 2010, and conceived the study design. IDJ assisted with SEG with SSM analyses. SEG wrote the paper with the assistance and advice of IDJ, MLL, MC, and SAS.

Tables

Table 4.1 – Number of individual GLS datasets used in analyses by species-colony-year. Recoveries of GLS biologgers from Laysan and black-footed albatross from Midway Atoll National Wildlife Refuge and Tern Island, French Frigate Shoals. Year refers to the hatch-year during deployment (i.e. GLS deployed in Dec 2010 and recovered in Jan 2012 is considered a 2011 deployment). All GLS were Model LAT2500 and LAT2900 (Lotek Wireless, Inc., St. John's, Newfoundland, Canada) except 8 deployments of Model MK3 and MK7 (British Antarctic Survey (BAS), Cambridge, UK) in 2013.

	Hatch-year of deployment					
Species Colony	2008	2009	2010	2011	2012	2013
Laysans						
Midway	10	9	8	7	5	3
Laysans						
Tern	9	11	6			
Black-footeds						
Midway	6	7	3	6	3	5
Black-footeds						
Tern	10	9	5			

Table 4.2 – Kernel contour areas from pooled and individual KDE analyses. Total area (km^2) of 50 and 95% kernel contours from pooled KDE including the maximum available number of individuals, and mean ± standard deviation KDEs from each species-colony-period dataset (Laysan and black-footed albatross from Midway Atoll National Wildlife Refuge and Tern Island, French Frigate Shoals). The four periods (ECR, LCR, OW, PBE) correspond to phases of the annual cycle (see Figure 4.1).

			Area (x10^3 km^2)			
Species Colony	Annual Period	max *n*	Pooled 50% Kernel Contour	Pooled 95% Kernel Contour	Individual 50% Kernel Contour	Individual 95% Kernel Contour
Laysans						
Midway	PBE	42	3270	15400	532 ± 341	6624 ± 3228
	ECR	34	1520	11000	377 ± 140	4743 ± 2292
	LCR	42	2580	11700	575 ± 370	5409 ± 2737
	OW	42	2040	9200	157 ± 104	2204 ± 1558
Laysans						
Tern	PBE	18	2920	11000	516 ± 281	6107 ± 2704
	ECR	6	2610	10000	449 ± 202	2928 ± 2615
	LCR	26	2500	11300	646 ± 423	6128 ± 3533
	OW	26	1750	7700	178 ± 89	2547 ± 1479
Black-footeds						
Midway	PBE	29	3050	15000	690 ± 613	7046 ± 4944
	ECR	23	2010	14500	531 ± 404	6284 ± 4510
	LCR	30	2910	19600	714 ± 548	7732 ± 5657
	OW	30	3720	20600	179 ± 203	2508 ± 2497
Black-footeds						
Tern	PBE	16	3200	12900	539 ± 327	6455 ± 2787
	ECR	6	2340	11500	724 ± 584	2434 ± 2737
	LCR	24	2710	16900	815 ± 471	9161 ± 4176
	OW	24	2490	13500	149 ± 149	2001 ± 1526

Table 4.3 – Range in areas of 50 and 95% contours from pooled KDE with sample sizes of maximum *n* less one and *n*=15. Kernel contour areas (km^2) were calculated from pooled KDE iterations including all tracked individuals successively excluding one from each iteration (max *n*-1) and 100 KDE iterations including 15 randomly sub-sampled individuals. The difference between the maximum and minimum estimated areas (max-min) from each set of iterations for each species-colony-period dataset are presented (Laysan and black-footed albatross from Midway Atoll National Wildlife Refuge and Tern Island, French Frigate Shoals during four periods of the annual cycle (ECR, LCR, OW, PBE; see Figure 4.1)).

			50% kernel contour max-min Area (x10^3 km^2)		**95% kernel contour max-min Area (x10^3 km^2)**	
Species Colony	Annual Period	max *n*	max *n*-1	*n* = 15	max *n*-1	*n* = 15
Laysans						
Midway	PBE	42	287	2008	937	8700
	ECR	34	100	595	1154	6592
	LCR	42	202	1553	791	6301
	OW	42	129	1400	906	5426
Laysans						
Tern	PBE	18	458	1037	1514	2200
	ECR	6	--	--	--	--
	LCR	26	289	1551	608	3743
	OW	26	158	1120	851	3099
Black-footeds						
Midway	PBE	29	260	1949	1394	8791
	ECR	23	209	1009	2166	8571
	LCR	30	380	2782	1312	8273
	OW	30	678	4861	2811	13115
Black-footeds						
Tern	PBE	16	400	--	1178	--
	ECR	6	--	--	--	--
	LCR	24	309	1449	2238	6968
	OW	24	497	1929	2641	7397

Table 4.4 – Range in 50 and 95% contour locations from KDE successively removing one individual. Kernel contour locations were determined from pooled KDE iterations including all tracked individuals successively excluding one from each iteration (max *n*-1). The difference between the maximum and minimum estimated locations (max-min, in degrees of latitude or longitude) from each set of iterations for each species-colony-period dataset are presented (Laysan and black-footed albatross from Midway Atoll National Wildlife Refuge and Tern Island, French Frigate Shoals during four periods of the annual cycle (ECR, LCR, OW, PBE; see Figure 4.1).

			50% kernel contour		**95% kernel contour**	
Species Colony	Annual Period	max *n*	northern limit (max-min, °N)	western limit (max-min, °W)	northern limit (max-min, °N)	western limit (max-min, °W)
Laysans						
Midway	PBE	42	2.98	0.4	1.52	0.53
	ECR	34	0.34	1.5	0.63	1.48
	LCR	42	0.52	1.32	1.9	22.2
	OW	42	0.66	1.04	1.17	0.66
Laysans						
Tern	PBE	18	0.51	3.53	1.49	9.9
	ECR	6	--	--	--	--
	LCR	26	2.8	3	3.14	25
	OW	26	0.38	5.93	0.57	6.3
Black-footeds						
Midway	PBE	29	1.23	2.06	4.53	2.22
	ECR	23	2.7	2.2	2.06	1.35
	LCR	30	3.68	4.92	0.54	1.3
	OW	30	1.23	5	2	14.18
Black-footeds						
Tern	PBE	16	0.36	7.93	3.26	3.26
	ECR	6	--	--	--	--
	LCR	24	0.97	20.64	16.8	0.6
	OW	24	1.11	2.64	0.43	32.1

Figures

Figure 4.1 – The four periods of the annual cycle considered in analyses. Daily GLS locations of Laysan and black-footed albatross were divided into four 60-day periods (vertical light gray blocks) associated with different life history phases (horizontal dark gray bars). Early chick rearing (ECR) coincides with late incubation, peak hatch, and early chick rearing (01-Jan to 01-Mar). Late chick rearing (LCR) coincides with the end of chick rearing (05-Apr to 15-Jun). Overwinter (OW) occurs during the non-breeding season, when all birds have departed the colonies and are at overwintering areas at sea (01-Jul to 01-Sep). Pre-breeding and eggs (PBE) encompasses the end of non-breeding, the return of birds to the colonies for courtship, and the transition into egg laying and incubation (15-Oct to 15-Dec). The timing of reproductive events were derived from Arata et al. (2009) and Chapters Two and Three and typically varies little among colonies or between species (at most by *c*. 2 weeks). Each period avoids overlap with the equinoxes and intervals of most intensive biologger deployment and recovery (15-Dec to 01-Jan).

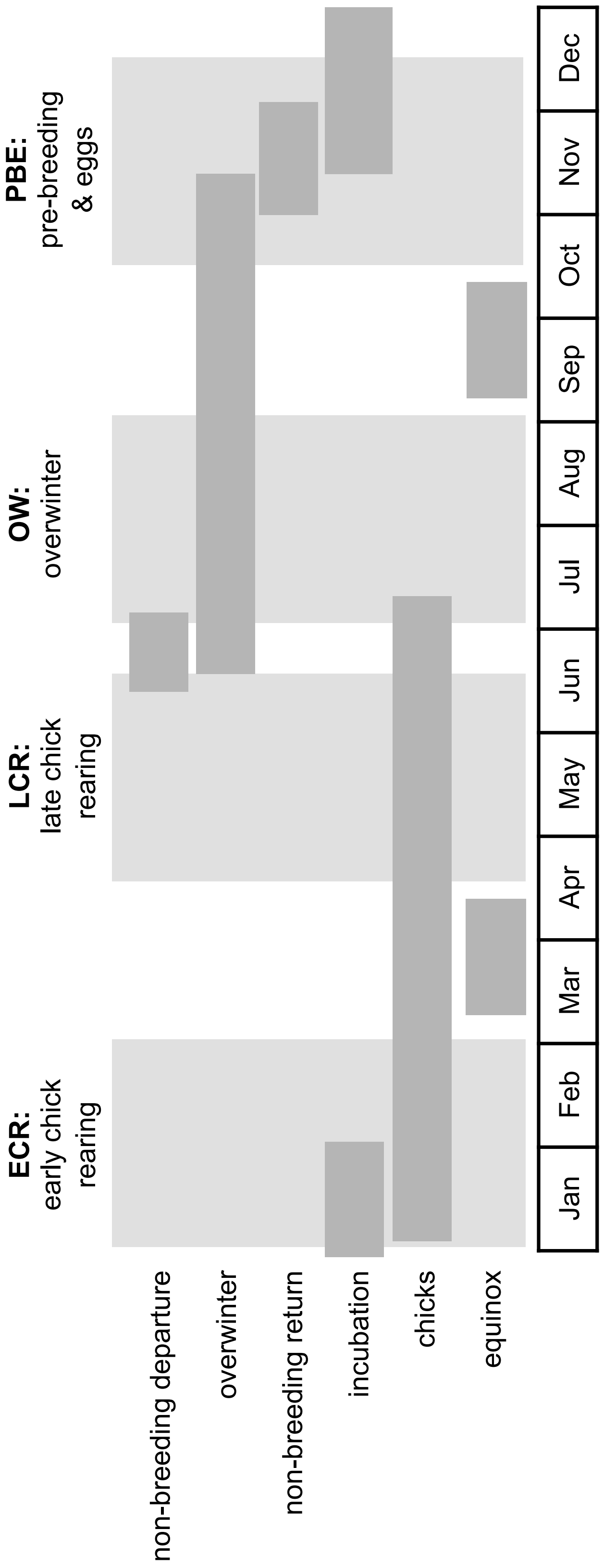

ECR:
early chick
rearing
LCR:
late chick
rearing
OW:
overwinter
PBE:
pre-breeding
& eggs
non-breeding departure
overwinter
non-breeding return
incubation
chicks
equinox
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec

Figure 4.2 – Pooled and stacked 50% kernel contours for two colonies of Laysan albatross during four periods of the annual cycle. Dashed polygons show 50% kernel contours from pooled KDE including GLS location data from all individual Laysan albatross tracked from Midway (left panes in grey) and Tern (right panes in blue) during four periods of the annual cycle: (A) ECR, (B) LCR, (C) OW, and (D) PBE (see Figure 4.1). Shaded polygons show 50% contours from individual KDE including data from each bird independently. The lightest shade indicates areas used by a single individual, and the darkest indicates areas of most intense overlap among individuals. Colonies are indicated in panels (C) by solid circles in their respective colours (projection: Lambert Cylindrical Equal Area, datum: WGS1984).

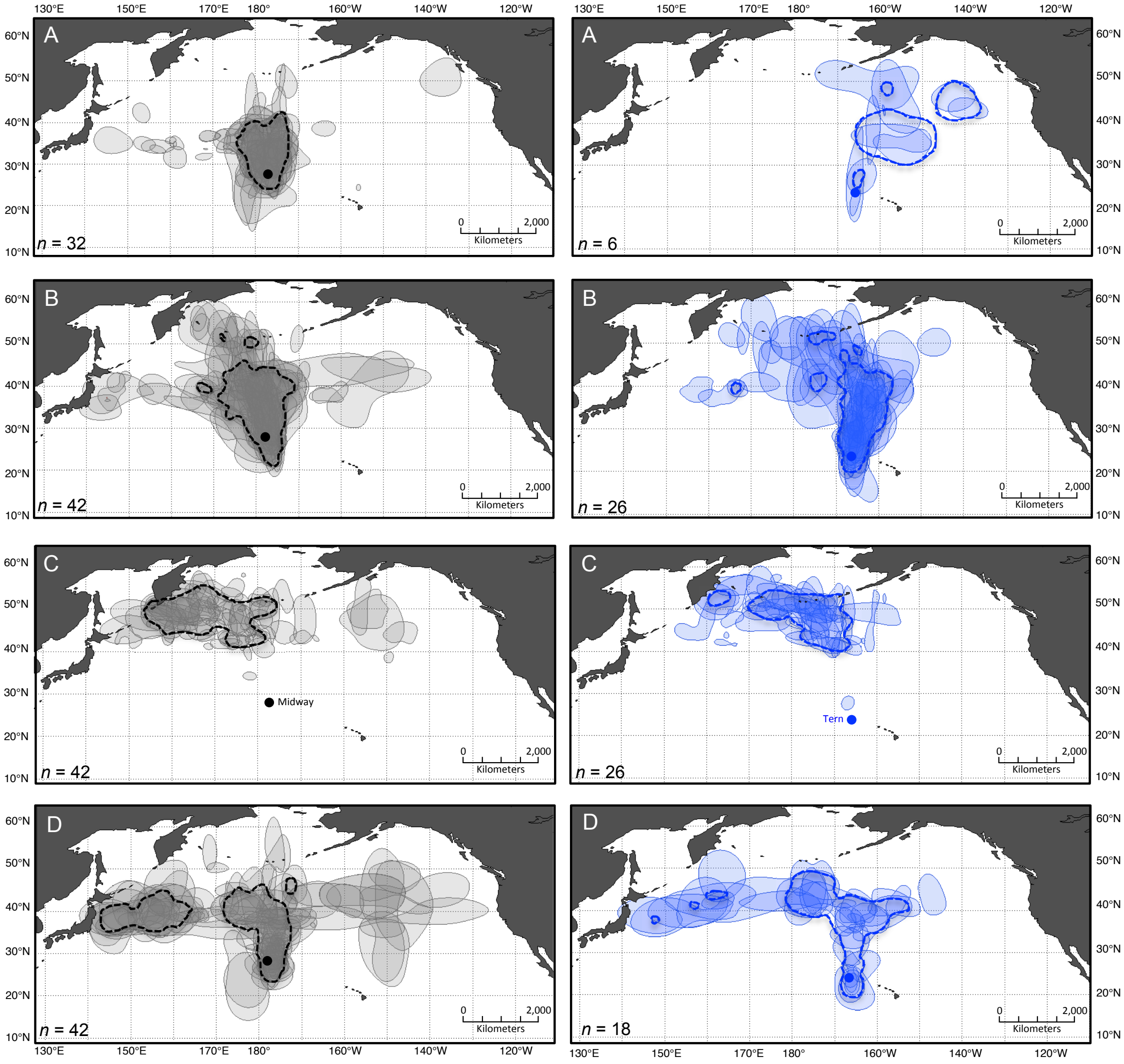
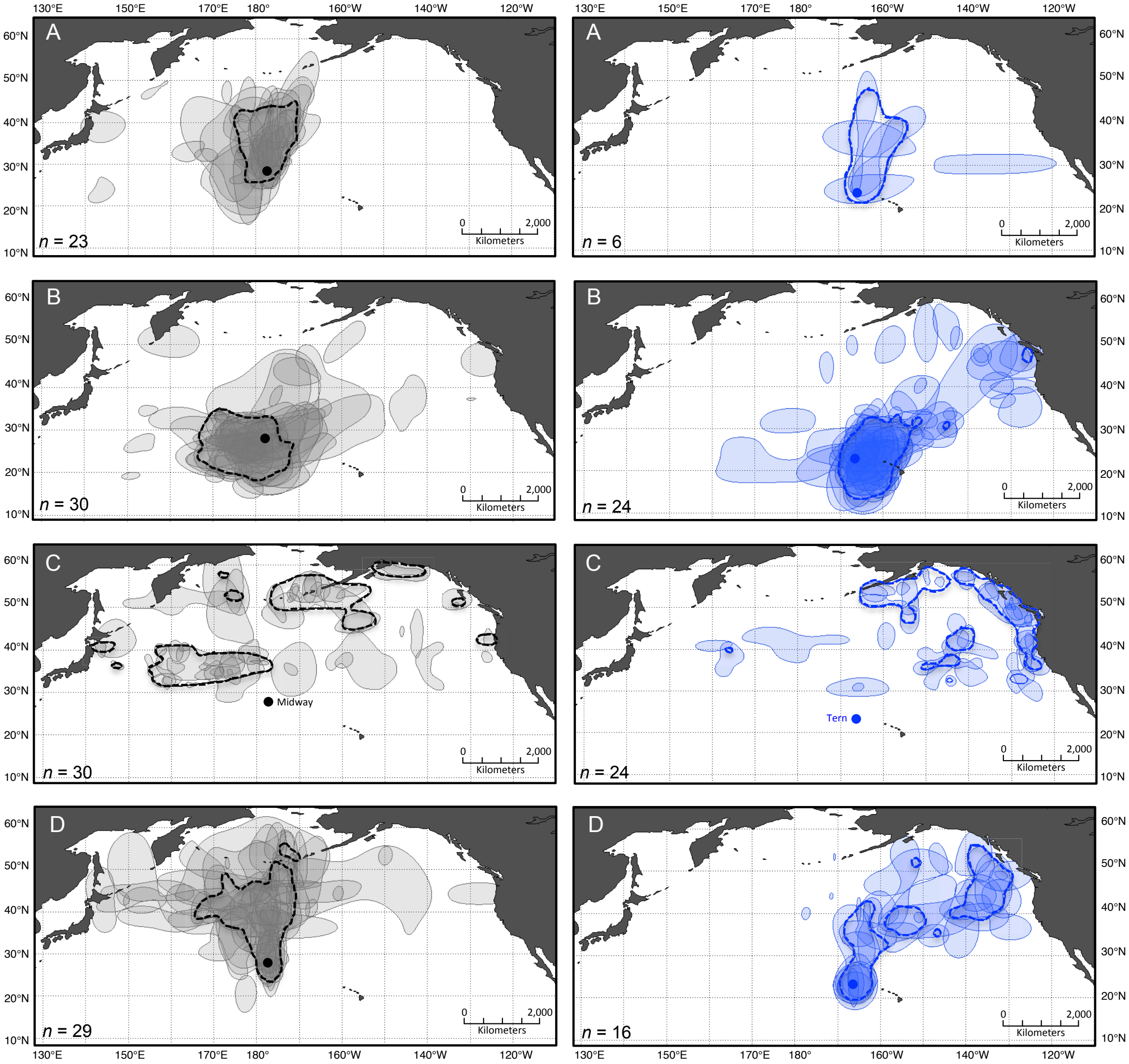
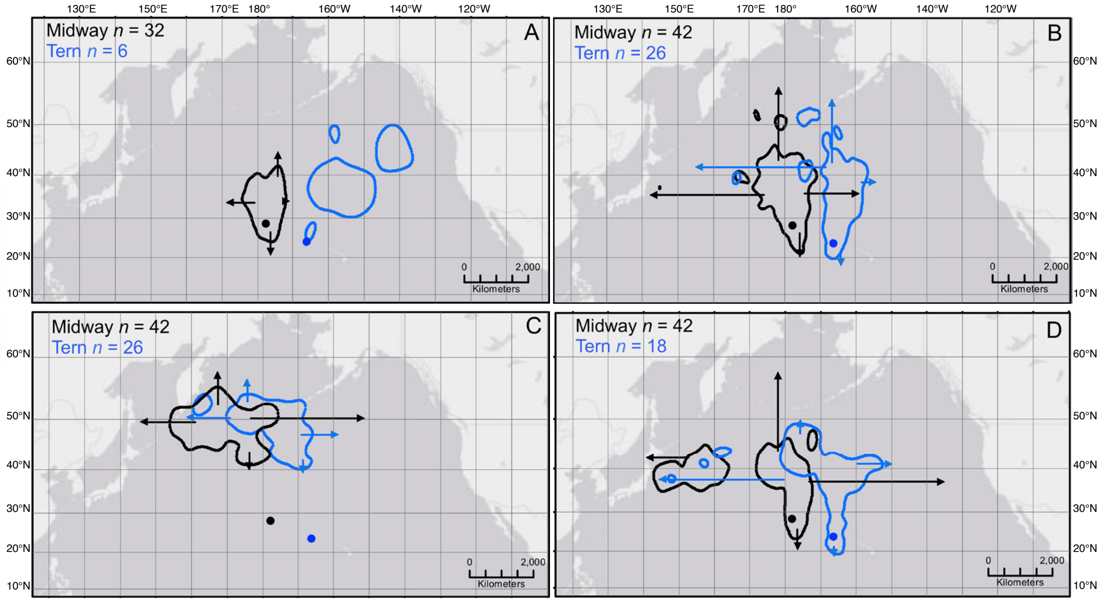

130°E
150°E
170°E
180°
160°W
140°W
120°W
60°N
50°N
40°N
30°N
20°N
10°N
A
n = 32
A
n = 6
B
n = 42
B
n = 26
C
Midway
n = 42
C
Tern
n = 26
D
n = 42
D
n = 18
0
2,000
Kilometers

Figure 4.3 – Pooled and stacked 50% kernel contours for two colonies of black-footed albatross during four periods of the annual cycle. Dashed polygons show 50% kernel contours from pooled KDE including GLS location data from all individual black-footed albatross tracked from Midway (left in grey) and Tern (right in blue) during four periods of the annual cycle: (A) ECR, (B) LCR, (C) OW, and (D) PBE (see Figure 4.1). Shaded polygons show 50% contours from individual KDE including data from each bird independently. The lightest shade indicates areas used by a single individual, and the darkest indicates areas of most intense overlap among individuals. Colonies are indicated in panels (C) by solid circles in their respective colours (projection: Lambert Cylindrical Equal Area, datum: WGS1984).



130°E
150°E
170°E
180°
160°W
140°W
120°W
60°N
50°N
40°N
30°N
20°N
10°N
A
n = 23
A
n = 6
B
n = 30
B
n = 24
C
Midway
n = 30
C
Tern
n = 24
D
n = 29
D
n = 16
0
2,000
Kilometers

Figure 4.4 – Sampling effects on the location of 50% kernel contours from pooled KDE for two colonies of Laysan and black-footed albatrosses during four periods of the annual cycle. Polygons show 50% kernel contour results from pooled KDE including GLS location data from all individual Laysan albatross (top four panes) and black-footed albatross (bottom four panes) from Midway and Tern (*n* shown in each pane). Arrows depict the outermost extents of 50% kernel contours (northern, eastern, southern and western limits for each set of polygons) resulting from 100 KDE generated from the daily locations of 15 randomly selected individuals from the full dataset for each colony. The outermost perimeter of the 50% kernel contour from KDEs ranged between the beginning and end of each arrow in the four cardinal directions as shown. Each set of four panes represent the four periods of the annual cycle: (A) ECR, (B) LCR, (C) OW, and (D) PBE (see Figure 4.1). Colonies are indicated by solid circles in their respective colours (projection: World Azimuthal Equidistant, datum: WGS1984).


130°E
150°E
170°E
180°
160°W
140°W
120°W
60°N
50°N
40°N
30°N
20°N
10°N
Midway n = 32
Tern n = 6
A
Midway n = 42
Tern n = 26
B
Midway n = 42
Tern n = 26
C
Midway n = 42
Tern n = 18
D
0
2,000
Kilometers

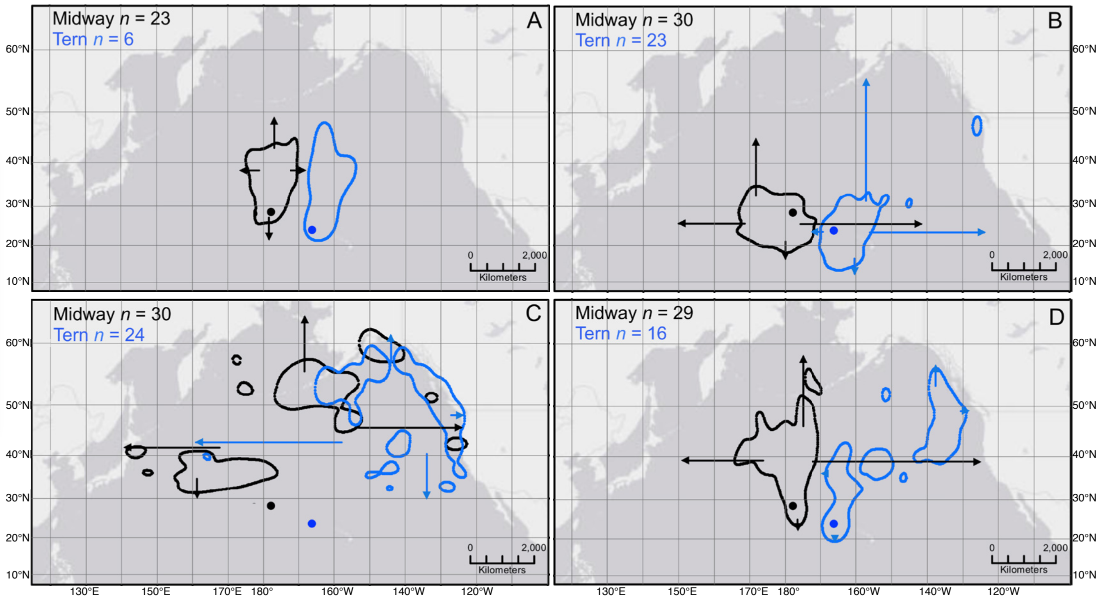
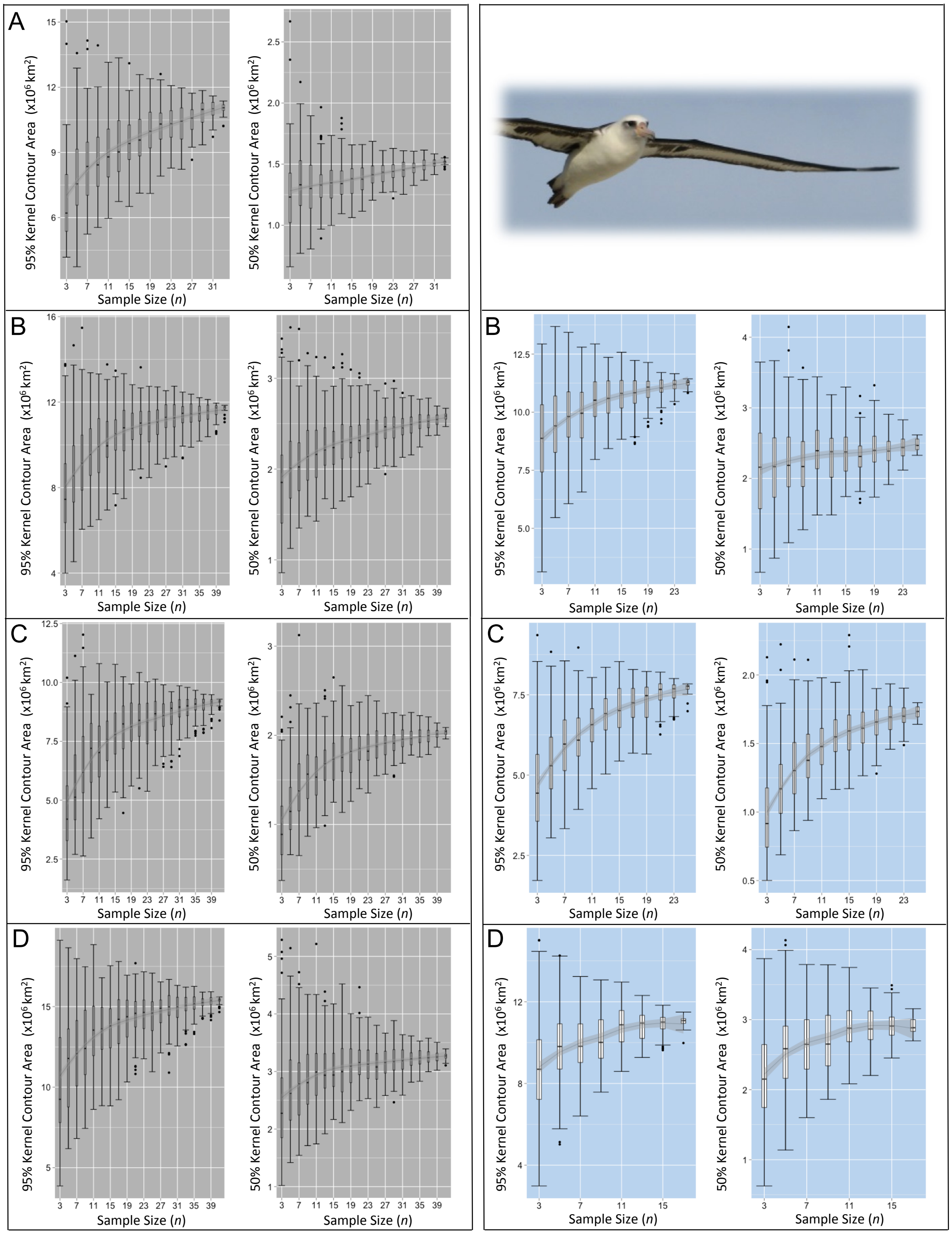

Midway n = 23
Tern n = 6
A
Midway n = 30
Tern n = 23
B
Midway n = 30
Tern n = 24
C
Midway n = 29
Tern n = 16
D
60°N
50°N
40°N
30°N
20°N
10°N
0
2,000
Kilometers
130°E
150°E
170°E
180°
160°W
140°W
120°W

Figure 4.5 – Pooled KDE contour areas for Laysan albatross from two colonies during four periods of the annual cycle. Pooled KDE contour area (km2) outputs for Laysan albatross from colonies at Midway (left panes in gray) and Tern (right panes in blue). Boxplots for each sample size (from n = 3 to n = max n–3) represent the 95 and 50% kernel contour areas of 100 iterations of KDE generated from the daily locations of n randomly selected individuals' GLS tracks. The final boxplot in each panel depicts the results of KDE iterations of max n–1 (i.e., removing one individual from the dataset for each KDE), resulting in max n number of total iterations. Each set of four panes represent the four periods of the annual cycle: (A) ECR (insufficient data for Tern), (B) LCR, (C) OW, and (D) PBE (see Figure 4.1). LOESS smoothers are for visual interpretation and should be used only as a guide.


A
15
12
9
6
95% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31
Sample Size (*n*)
2.5
2.0
1.5
1.0
50% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31
Sample Size (*n*)
B
16
12
8
4
95% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31 35 39
Sample Size (*n*)
3
2
1
50% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31 35 39
Sample Size (*n*)
B
12.5
10.0
7.5
5.0
95% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23
Sample Size (*n*)
4
3
2
1
50% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23
Sample Size (*n*)
C
12.5
10.0
7.5
5.0
2.5
95% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31 35 39
Sample Size (*n*)
3
2
1
50% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31 35 39
Sample Size (*n*)
C
7.5
5.0
2.5
95% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23
Sample Size (*n*)
2.0
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50% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23
Sample Size (*n*)
D
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95% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31 35 39
Sample Size (*n*)
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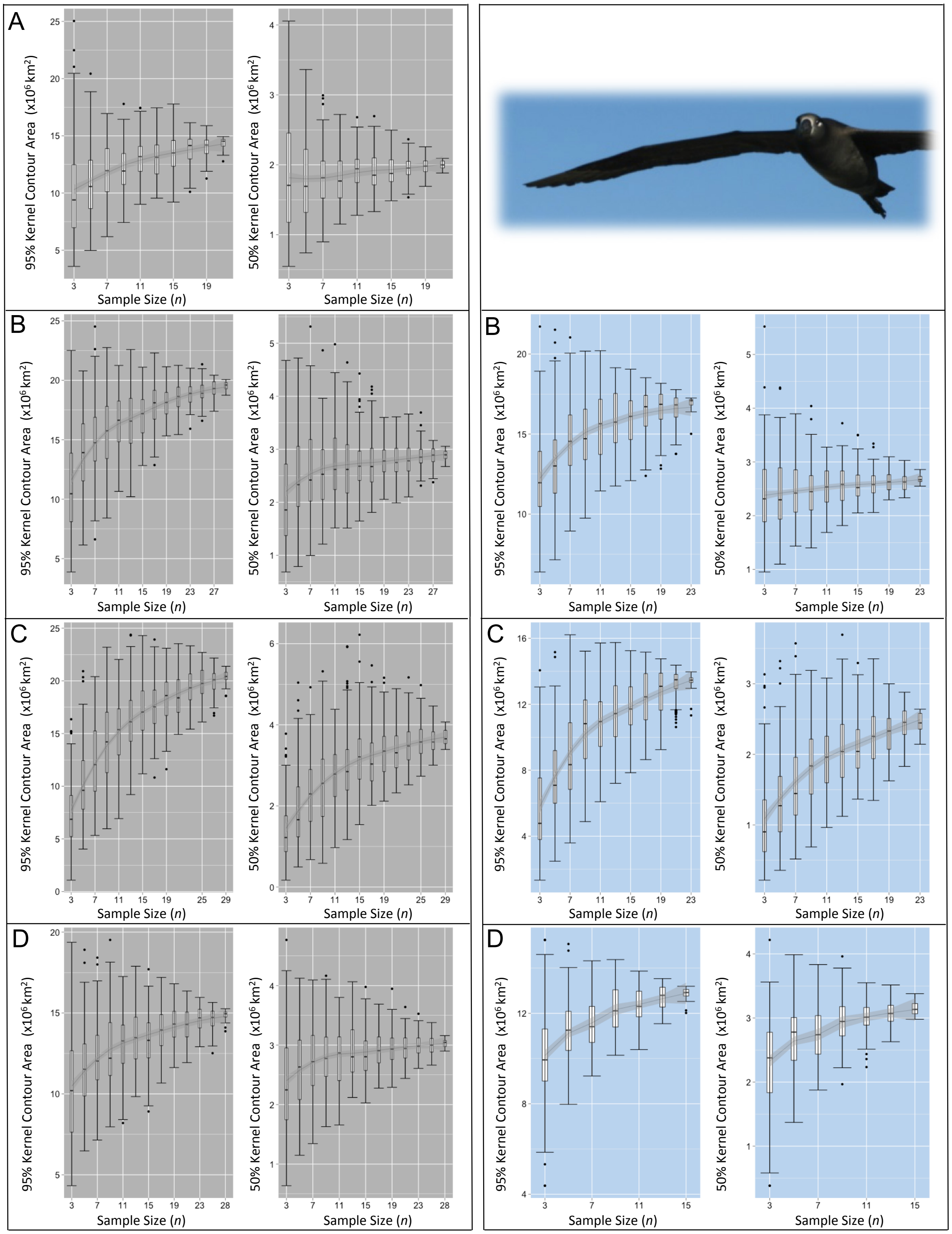
4
3
2
1
50% Kernel Contour Area (x10^6 km^2)
3 7 11 15 19 23 27 31 35 39
Sample Size (*n*)
D
12
8
4
95% Kernel Contour Area (x10^6 km^2)
3 7 11 15
Sample Size (*n*)
4
3
2
1
50% Kernel Contour Area (x10^6 km^2)
3 7 11 15
Sample Size (*n*)

Figure 4.6 – Pooled KDE contour areas for black-footed albatross from two colonies during four periods of the annual cycle. Pooled KDE contour area (km2) outputs for black-footed albatross from colonies at Midway (left panes in gray) and Tern (right panes in blue). Boxplots for each sample size (from n = 3 to n = max n–3) represent the 95 and 50% kernel contour areas of 100 iterations of KDE generated from the daily locations of n randomly selected individuals' GLS tracks. The final boxplot in each panel depicts the results of KDE iterations of max n–1 (i.e., removing one individual from the dataset for each KDE), resulting in max n number of total iterations. Each set of four panes represent the four periods of the annual cycle: (A) ECR (insufficient data for Tern), (B) LCR, (C) OW, and (D) PBE (see Figure 4.1). LOESS smoothers are for visual interpretation and should be used only as a guide.


A
95% Kernel Contour Area (x10⁶ km²)
5
10
15
20
25
Sample Size (n)
3
7
11
15
19
50% Kernel Contour Area (x10⁶ km²)
1
2
3
4
Sample Size (n)
3
7
11
15
19
B
95% Kernel Contour Area (x10⁶ km²)
5
10
15
20
25
Sample Size (n)
3
7
11
15
19
23
27
50% Kernel Contour Area (x10⁶ km²)
1
2
3
4
5
Sample Size (n)
3
7
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15
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27
B
95% Kernel Contour Area (x10⁶ km²)
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Sample Size (n)
3
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15
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23
50% Kernel Contour Area (x10⁶ km²)
1
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5
Sample Size (n)
3
7
11
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19
23
C
95% Kernel Contour Area (x10⁶ km²)
0
5
10
15
20
25
Sample Size (n)
3
7
11
15
19
25
29
50% Kernel Contour Area (x10⁶ km²)
0
2
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6
Sample Size (n)
3
7
11
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19
25
29
C
95% Kernel Contour Area (x10⁶ km²)
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12
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Sample Size (n)
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19
23
50% Kernel Contour Area (x10⁶ km²)
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3
Sample Size (n)
3
7
11
15
19
23
D
95% Kernel Contour Area (x10⁶ km²)
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15
20
Sample Size (n)
3
7
11
15
19
23
28
50% Kernel Contour Area (x10⁶ km²)
1
2
3
4
Sample Size (n)
3
7
11
15
19
23
28
D
95% Kernel Contour Area (x10⁶ km²)
4
8
12
Sample Size (n)
3
7
11
15
50% Kernel Contour Area (x10⁶ km²)
1
2
3
4
Sample Size (n)
3
7
11
15

Chapter 5: Building A Framework For Conceptualizing The Drivers Of Albatross Movement

Abstract

The collective objective of movement ecology (ME) research is to understand the connections among the multitude of factors that drive *why, when, where and how* individual organisms move. The basic conceptual ME framework envisions how four major components (internal state, navigation capacity, motion capacity, and external elements) interact to generate a focal individual's movement path. Empirical studies of the drivers of individual movements have become increasingly sophisticated with major advancements in animal-attached biologging technologies that provide estimates of individual movements paths. These tools have been applied extensively in the study of movement for a group of highly mobile ocean-going birds known as the albatrosses (Order: *Procellariiformes*, Family: *Diomedeidae*). Despite the considerable volume of published albatross-biologging movement research, the complex factors and processes that govern the movements of these birds have not before been unified into a comprehensive framework. This paper has two main objectives: 1) to integrate ideas from across disciplines to build a custom conceptual ME framework for albatrosses, and 2) to use this framework to critically evaluate the albatross-biologging movement literature for trends, strengths, and weaknesses in our understanding of the drivers of movement. I define each of the four major components of the basic ME framework such that discrete and comparable factors within each component can be identified, thus populating the framework with 45 unique factors. I show that the basic conceptual ME framework provides a solid foundation on which ideas from across disciplines can be integrated to build a framework tailored to a specific target taxa. I then apply my custom framework as a guide in conducting a literature review focused on the use of bird-borne biologging devices in the study of albatross movement. I survey the published literature to assess which of the 45 factors are most commonly measured or suggested as important in determining observed movement patterns. In doing so, I discuss gaps in our understanding of what drives a bird to move via a given movement path, I identify trends toward change in the drivers we explore with biologging, and I recommend future research directions. As the sophistication of analytical and biologging tools continues to grow, hopefully so too will the breadth and complexity of processes invoked and investigated to explain albatross movements. I conclude by advocating for the development of custom ME frameworks as a

conceptual guide for movement research for any target group of individual animals studied with biologging tools.

Introduction

The movements routinely achieved by individual organisms from taxa across the Animal Kingdom are striking in their diversity and magnitude. For example, a worker buff-tailed bumblebee *Bombus terrestris* will fly over 2.5 km from the hive to pollen-bearing flower patches (Hagen et al. 2011). Also impressive, a leatherback turtle *Dermochelys coriacea* will swim over 7,000 km from the nesting beach to pelagic foraging areas (Benson et al. 2011). We owe our appreciation for these two feats of individual movement to biologging technologies (micro radio and satellite telemetry in these cases, respectively), in which animal-attached devices can provide sequential location data (and other ancillary data, reviewed by Cooke et al. 2004, Cooke 2008). The location data from the bee and turtle in these examples provide insight into the role of movement in determining fitness. More broadly, location data can provide insight into how movements impact the strength and outcome of ecological interactions that drive population, community, and ecosystem dynamics, and ultimately influence evolutionary processes that shape life on Earth (Nathan et al. 2008).

The ecological and evolutionary significance of individual movement is the motivation behind a proposed field of research called Movement Ecology (herein ‘ME’; Nathan et al. 2008). The collective objective of ME research is to understand the connections among the multitude of factors that drive *why, when, where and how* individuals move (Nathan & Giuggioli 2013). By considering all aspects of individual movement together, ME offers a cross-disciplinary framework for conceptualizing the underlying mechanisms of movement patterns, and the role of movement in ecological and evolutionary processes (Nathan et al. 2008). The framework is universal to the study of movement in that it is applicable across taxa, movement phenomena and methodologies, and at any spatiotemporal scale.

The movements of organisms of all kinds can be explored in the context of the many factors that influence an individual ‘movement path’ (defined as a sequence of locations occupied by an individual during some definitive duration within its lifespan; Nathan et al. 2008). The factors simultaneously influencing a focal individual’s movements can be considered within a basic framework comprised of four interacting components (Figure 5.1 adapted from

Nathan et al. 2008): 1) The **internal state** component encompasses all factors that influence *why* an individual moves along a given movement path by considering intrinsic factors that influence an individual's motivation to move (e.g. age or body condition). 2) The **navigation capacity** component considers factors relevant to an individual's cognitive and noncognitive "decision-making" of *when and where* to move along a movement path (e.g. olfactory or geomagnetic cues). 3) The **motion capacity** component covers the biomechanical and morphological traits that allow an individual to move via different modes (e.g. soaring or flapping flight), thus influencing *how* a movement path is generated. 4) The **external environment** component comprises all abiotic and biotic elements that influence a movement path through interactions with the other three components (e.g. wind or the presence of other individuals could influence *when, where and how* a bird might move). All four components interact through a variety of processes represented in the ME framework (Figure 5.1). For example, *why* an individual moves can determine the types of information likely relevant to *when* and *where* they move (e.g. the age of a bird could determine the cues influencing its movements). This interaction is represented in the ME framework as *navigation processes* acting between the internal state and navigation capacity components. The components and processes influencing movements are inevitably over-simplified in such a framework. Still, identifying key factors within each component, and how they interact, is the primary challenge in populating the ME framework such that it is customized to a particular system or group of organisms under study (Nathan et al. 2008).

In this review, I populate the basic ME framework proposed by Nathan et al. (2008) based on the published literature for a group of highly mobile ocean-going birds known as the albatrosses (Order: *Procellariiformes*, Family: *Diomedeidae,* all 22 common and scientific species names in Table 5.1). There is a wealth of movement studies conducted on albatrosses, and this can be attributed to a number of traits in these birds, not least of which is their suitability for carrying biologging devices. Their large body size (wingspans ranging from 1.9-3.2 m and mass ranging from 1.7- 11.9 kg; Tickell 2000) was recognized 25 years ago as a robust platform for device attachment by Jouventin & Weimerskirch (1990). Since this seminal study deploying satellite-tracking devices on wandering albatross, movement paths of individuals of all 22 albatross species have been recorded using the myriad of continually advancing biologging technologies (Taylor et al. 2004, Pinaud et al. 2005, Wakefield et al. 2011; Table 5.1), and over 100 movement studies have been published in peer-reviewed journals. Further traits contributing to the high number of biologging studies for albatrosses include long lifespans with high adult survivorship and high site fidelity to their conspicuous surface nests (Warham 1990, 1996, Tickell 2000). This means that adults are generally easy to capture and re-capture at their nests as they reliably return to breed throughout their long lives, making them optimal candidates for the deployment and recovery of devices (Burger & Shaffer 2008).

In addition to being model organisms for studying movement using biologging approaches, there is considerable conservation incentive to investigate albatross ME. Fifteen species are currently considered ‘Vulnerable’ to extinction, ‘Endangered’ or ‘Critically Endangered’ by the International Union for the Conservation of Nature (the remaining seven are considered ‘Near Threatened’; Table 5.1, IUCN 2015). Understanding what drives patterns in range and distributions at sea, especially in relation to overlap with fisheries and other threats like pollution, is a key component in effective conservation planning for these species (Burger & Shaffer 2008). Conservation concerns, in combination with body size and life history traits, have lead to a significant body of research based on recording individual movement paths of biologger-equipped albatrosses.

Despite the considerable volume of published albatross-biologging movement research, the complex factors and processes that govern the movements of these birds have not before been unified into a comprehensive framework. Instead, our understanding of the multitude of factors that drive albatross movements remains scattered across disciplines, including for example spatial, behavioural, physiological, and sensory ecology, neurophysiology, biomechanics, and biological oceanography. This paper has two main objectives: 1) to integrate ideas from across disciplines to build a custom conceptual ME framework for albatrosses, and 2) to use this framework to critically evaluate the albatross-biologging movement literature for trends, strengths and weaknesses in our current understanding of the drivers of movement. In order to meet the first objective, I pull together pieces from the cross-disciplinary body of research that help in addressing the questions of *why, when, where and how* albatrosses move. I define each component such that discrete and comparable factors within each component can be identified. Throughout, I identify interactions within and among the components, and identify biotic and abiotic elements in the environment that interact with all other factors to produce a movement path. I show that the basic conceptual ME framework provides a solid foundation on which ideas from across disciplines can be integrated to build a framework tailored to a specific target taxa. For the second objective, I then apply my custom framework as a guide in conducting a literature review of published research where bird-borne biologging devices are used to record sequential location data of individual albatrosses. I survey the literature for the factors most commonly measured or suggested as important in determining the observed movement patterns. This allows for the recognition of components and factors within the framework that have received the most consideration, and those in need of attention in order to develop a more holistic understanding of albatross movement. I conclude by advocating for the development of custom ME frameworks as a conceptual guide for movement research for any target group of individual animals studied with biologging tools.

The Internal State – Intrinsic Factors That Influence *Why* Move

The internal state component of the ME framework is defined here as comprising the factors intrinsic to an individual that drive *why* it moves and thus influence an observed movement path (Nathan et al. 2008). The internal state at any given moment could be thought of as a multidimensional vector of intrinsic factors that play a role in determining *why* an individual moves. For example, a bird's movements may be influenced by the effects of age, breeding phase and body condition (i.e. intrinsic factors) on its need to both forage and rest. Below I briefly review a number of distinct intrinsic factors likely to play a role in determining an individual's movements (summarized in Figure 5.1). These factors are first presented independently with simple examples of their effects on individual movement. This is followed by discussion of the inter-relatedness of intrinsic factors (i.e. how factors interact within the internal state), how the influence of intrinsic factors depend on the external environment, and how these relationships and processes are represented in the ME framework.

Species

An individual's species is the fundamental intrinsic factor that plays a role in influencing *why* a bird moves along a particular movement path by determining the general species-specific ecological niche. An individual is considered to belong to a species based on genetically inherited traits that in part determine its physical and behavioural attributes, which influence movement. Among albatross species, these traits might include for example species-specific wing loading (e.g. Suryan et al. 2008) and foraging techniques (e.g. Fernández & Anderson

2000, Weimerskirch & Guionnet 2002). Thus, individuals of different species fill distinct ecological niches in terms of their habitats (both on land and at sea) and diet (e.g. Suryan & Fischer 2010, Kappes et al. 2010). An individual's species establishes the foundation for its unique set of intrinsic factors that influence *why* move via a given movement path. For example, the movements of a Laysan albatross in the North Pacific Ocean may be driven in part by adaptations associated with its diet of squid acquired from cool deep waters, while the movements of a black-footed albatross within the same ocean basin may be driven in part by adaptations associated with its diet of flying fish eggs found in warmer waters (Kappes et al. 2010).

Age

An individual's age can influence *why* it moves along a particular path. Generally albatrosses have delayed sexual maturity (age of first breeding attempt >5 years) with high longevity (>50 years), and experience senescence (i.e. physical deterioration and reduced reproductive success with increasing age) in later life (Warham 1990, Tickell 2000, Catry et al. 2006, Lecomte et al. 2010). The movements of an immature, pre-breeding aged bird in its first years out to sea are likely driven mostly by the need to feed itself, while the movements of a mid-aged bird could be driven in part by the need to feed itself and also by the demands of breeding such as finding a mate or feeding a chick (e.g. Alderman et al. 2010, Riotte-Lambert & Weimerskirch 2013, Chapter Two). The movements of an older bird may be driven by similar needs to that of a mid-aged bird as it continues to raise offspring, but with increased self-provisioning demands from declining faculties such as visual acuity or muscular function (e.g. Catry et al. 2006, Angelier et al. 2006, Lecomte et al. 2010, Pardo et al. 2013, Froy et al. 2015).

Breeding Phase

Once an individual has reached breeding age, its present breeding phase can influence *why* it moves along a particular path. The breeding cycle for albatrosses is divided into distinct phases including pre-breeding (courtship, nest building, laying of a single egg), incubation, chick brooding, chick rearing, and overwinter (Warham 1990, Tickell 2000). The overwinter phase can begin following fledging or during any phase of the breeding cycle if the reproductive attempt fails, and will also be extended to a sabbatical year at varying frequencies depending on the species (Warham 1990, Tickell 2000, Jouventin & Dobson 2002). The movements of an individual in the incubation phase could be driven by the need to feed itself at sea, to recover from fasting and replenish reserves for its next incubation shift, and to return to the nest to relieve its incubating mate. The movements of an individual in the chick rearing phase could be driven by the need to both feed itself and its growing chick (e.g. Salamolard & Weimerskirch 1993, Shaffer et al. 2003, Hedd & Gales 2005, Young et al. 2009).

Sex

An individual's sex can influence *why* it moves along a particular path. In albatrosses, males and females can differ in their dietary or habitat needs due to reproductive role specialization and foraging niche divergence (e.g. Salamolard & Weimerskirch 1993, Weimerskirch et al. 1997c, 2000b, Shaffer et al. 2001b, Phillips et al. 2004b, 2011). The movements of a female albatross following return from overwinter could be driven in part by the need to recover resources invested into developing an egg (e.g. Frings & Frings 1961), while the movements of a male could be driven more by the need to spend time ashore at the colony for courtship and establishing a territory in the hopes of securing a mate or to wait near the same nest site shared with a mate in the previous year (e.g. Fisher 1971a, Pickering 1989). Further, the movements of a chick rearing bird of a sexually dimorphic species could be driven by an interaction between the individual's sex and the sex of the chick; the movements of a larger male parent may be driven by its own energetic demands and the high demands of rearing a fast-growing and heavy male chick (e.g. Weimerskirch et al. 2000b).

Personality

An individual's personality (i.e. consistent behavourial tendencies) can influence *why* it moves along a particular movement path. Albatrosses have been shown to exhibit distinct personalities where individuals can be characterized along a shy-bold continuum using standardized tests (i.e. 'boldness' toward an approaching human or novel object ranging from consistently shy to aggressive; Patrick et al. 2013). The movements of a bolder individual during the incubation and chick brooding phases may be driven by a personality-related tendency to forage nearer to the colony in shallow areas where competition for abundant resources is high, while a shyer individual would be more likely to forage further from the colony over deeper, less productive waters (Patrick & Weimerskirch 2014).

Body Condition

An individual's morphological or physiological body condition can influence *why* it moves along a particular movement path. Body condition in birds is most often treated as a reflection of energy reserves (Labocha & Hayes 2012), which impact a bird's physiological functions and in turn drives it to move. Body condition can be represented by morphometric estimates of energy stores such as abdominal fat profiles, fat scoring, or body mass (Labocha & Hayes 2012). Other qualititave or quantitative variables can be taken as a proxy for body condition based on expected relationships with energy reserves, including for example the size and time of the last meal (Catry et al. 2004b), blood levels of hormones linked to mobilizing energy reserves and coping with energetic stress (Angelier et al. 2006, 2011), or parasite loads linked to decreased body fat stores (Langston & Hillgarth 1995). The movements of an individual in poor body condition, measured as any of these variables, may be driven by both the need to forage intensively to meet high immediate energetic demands and to increase energy reserves for future use such as when fasting on the nest.

Moult Status

An individual's moult status can influence *why* it moves via an observed movement path. For albatrosses, maintaining the plumage needed for efficient long-distance flight is an energetically costly process, necessitating complex multi-year or biennial flight feather moult strategies (e.g. Langston & Rohwer 1996, Edwards 2008). An individual's moult status at any point in time could consist of entirely fresh plumage, mostly old or severely worn plumage, or any combination of new and old, and could also include active replacement of some body or flight feathers. The movements of an albatross are likely driven in part by their moult status. The movements of an adult with flight feathers requiring replacement would be driven in part by a need to build energy, protein and nutrient stores sufficient for upcoming feather growth while also potentially compensating for reduced flight efficiency from worn plumage (e.g. Chapter Three).

Experience

An individual's cumulative lifetime experience can influence *why* it moves via an observed movement path. Experience is often measured relative to age or total number of breeding attempts (e.g. Angelier et al. 2007). However, experience will differ among individuals of the same age and breeding history, as it encompasses a bird's unique history of breeding failures and successes as well as social and competitive interactions, foraging, and exposure to stresses. The learning opportunities (or lack thereof) afforded by an individual's unique cumulative lifetime experiences likely influence its movements. The movements of a less experienced bird may be driven by an increased need to forage due to low foraging proficiency (i.e. poor choice of foraging areas, poor recognition of suitable prey items, poor prey handling; Riotte-Lambert & Weimerskirch 2013, Froy et al. 2015) or by the need to be present at the colony for courtship practice with other un-paired individuals (Pickering & Berrow 2001).

Colony Of Origin

An individual's colony of origin can influence *why* it moves via an observed movement path. Albatrosses have high natal philopatry (i.e. recruitment of first-time breeders to their birth colony) and near-absolute fidelity to their breeding island (i.e. once they've started breeding, an individual continues to nest at the same colony for their lifetime; Tickell 2000). Thus, an individual's colony of origin can be an important factor intrinsic to the individual that may influence its movements. The movements of a breeding bird with an egg or chick will be constrained by its ties to the colony (i.e. central place foraging constraints; Orians & Pearson 1979). The movement path of a bird during breeding will also be influenced by the level of competitive pressure for local resources around the colony, which will depend on the size and location of the colony (Ashmole 1963, Cairns 1989). The movements of an albatross originating from a large colony (or from a small colony in close proximity to a large one) may be driven in part by local competitive pressure during periods of high central place constraint, which would be the result of the bird's colony of origin (e.g. Wakefield et al. 2011).

Interactions Among Intrinsic Factors

While each intrinsic factor within the internal state has been presented here in isolation, the true impact of any one factor in determining an individual's movement path is more realistically understood when considered in concert with others. Each individual has a unique multidimensional vector of intrinsic factors that together drive *why* it moves along a particular path. The interactions among intrinsic factors are represented in the ME framework as *internal dynamics* acting within the internal state component (Figure 5.1). One example of interactions among intrinsic factors is the inter-relatedness of breeding phase, body condition and moult status. Moult status is determined in part by breeding phase, and in turn likely influences, and is influenced by, body condition. For example, an albatross will typically only actively moult flight feathers during overwinter (Bridge 2006, Rohwer et al. 2011), and an actively moulting bird is likely to have lower body condition in terms of energy stores due to the energetic demands of feather growth and reduced ability to forage from compromised flight dynamics (e.g. Edwards 2008, Chapter Three). A bird's movements are likely influenced by the combined effect of these three intrinsic factors on *why* a bird would move via a particular path.

Another example of interactions among intrinsic factors is the inter-relatedness of experience and body condition. The *internal dynamics* acting among these factors could be considered as carryover effects, defined by O'Connor et al. (2014) as "any situation where an individual's previous history and experience explains their current performance in a given situation". *Why* an individual albatross moves along a particular path is likely influenced in part by carryover effects from past experiences on their present body condition in terms of energy stores, aerobic capacity and hormonal status (e.g. Crossin et al. 2012, 2013). For example, a female albatross returning to the colony after overwinter may skip the opportunity to breed (Tickell 2000) and hence present a movement path atypical of a breeding bird. The movements of this individual will be driven in part by present body condition, which will depend on experiences during recent movements, and during the previous overwinter and breeding phases (Crossin et al. 2013).

Interactions Between The Internal State And The External Environment

All movement occurs within an environmental context (i.e. 'The environment' in Figure 5.1), and thus the effects of intrinsic factors on movement are related to the external environment in which they act. These interactions are represented in the ME framework as *internal and external dynamics* acting between the internal state and the external environment (Figure 5.1). Many of the biotic and abiotic elements in the external environment also co-vary, represented in the ME framework as *external dynamics* acting within the environmental component (Figure 5.1). For example, as demonstrated earlier, colony of origin can influence *why* an individual moves along a particular movement path. It is also, however, an important determinant of elements within the external environment that a moving bird is likely to encounter, such as the density of conspecifics at sea, the local colony topography (i.e. nest site substrate or slope), and the local species assemblage both at sea and on land (all of which are inter-related). Colony of origin will also in part determine the oceanographic and meteorological conditions likely to be encountered along a movement path, as well as likelihood of encounters with fishing vessels or anthropogenic litter. Overall, each of the intrinsic factors discussed above will interact in some way with elements in the external environment to influence an individual's movement path.

Navigation Capacity – Information That Influences *When And Where* To Move

The navigation capacity component of the ME framework is defined here as comprising the sources of navigational information that influence an individual's "decision-making" of *when and where* to move (i.e. initiation, cessation and direction of movement) and thus influence an observed movement path. Similar to an individual's internal state, an individual's navigation capacity at any given moment could be thought of as a multidimensional vector of information inputs that together impact movement decisions at various spatial scales (Bonadonna et al. 2003a, Muheim et al. 2006, Mardon et al. 2010). An individual's "decisions" in response to information inputs are both noncognitive processes (i.e. timing or direction determined by inherited traits; Åkesson & Weimerskirch 2005, Åkesson & Hedenström 2007), and true cognitive choices that reflect navigation skills (i.e. aptitude for processing information inputs and sense of current location) learned through experience (e.g. Kenyon & Rice 1958, Fisher 1971b, Riotte-lambert & Weimerskirch 2013). Albatross frequently cross vast expanses of open ocean that are devoid of physical cues detectable by the human eye, yet these birds achieve remarkable precision in navigating back to their colonies (even when experimentally displaced more than 6,000 km; Kenyon & Rice 1958). The navigation capacities of these birds must encompass a diversity of sensory abilities for varied information inputs. Below I briefly review a variety of information inputs likely to influence the movement decisions of an albatross. This is followed by a discussion of the processes that determine how factors within the internal state and elements in the environment influence the types of navigational information that might be available or relevant to an individual, and how these processes are represented in the ME framework.

Celestial Information

Celestial cues (i.e. information from the sky) are a probable source of navigational information for decisions of *when* and *where* to move. Both diurnal and nocturnal celestial information, including photoperiod, sun polarization, sun position, stellar orientation and moon position, are known cues used by long-distance songbird migrants during their large bi-annual movements (e.g. Able & Able 1996, Gould 1998, Muheim et al. 2006). Although there is no direct evidence that celestial cues are important for navigation in albatross, it has been suggested this mechanism is used (Mouritsen et al. 2003, Bonadonna et al. 2005). The distance covered during annual songbird migrations are often equivalent to the foraging commutes made by albatrosses dozens of times each breeding season. For example, a wandering albatross off-duty from incubation at the nest could travel over 13,000 km over 28 days across a vast pelagic landscape (Weimerskirch et al. 1997b). It is reasonable to suggest that individual albatross use celestial information in movement decisions in these routine large-scale movements similar to that used by migrating songbirds.

Geomagnetic Information

Geomagnetic cues (i.e. information from the magnetic field of the earth) are another probable source of navigational information for decisions of *when* and *where* to move. Magnetic field strength or inclination can act as a guide to orient movement direction (reviewed by Wiltschko & Wiltschko 1996, O'Neill 2013). While some experimental evidence suggests that albatross can navigate without geomagnetic cues (e.g. Åkesson & Alerstam 1998, Bonadonna et al. 2003b, 2005, Mouritsen et al. 2003), their general use cannot be ruled out. Geomagnetic cues may be part of a multi-modal navigation system where different sources of navigational information can be substituted based on availability, to accomplish the same movement (Åkesson & Alerstam 1998, Mouritsen et al. 2003). An individual albatross traveling thousands of kilometers across an open ocean landscape is likely to be integrating multiple sources of navigational information to orient its movements, possibly including geomagnetic cues.

Dynamic Pressure Information

Dynamic pressure cues (i.e. information from changes in air pressure) are a probable source of navigational information for decisions of *when* and *where* to move. The long-distance movements of albatrosses and many of their tube-nosed relatives rely on a method of flight called ‘dynamic soaring’ that depends on an ability to detect changes in wind speed and direction, in both the vertical and horizontal plane (Weimerskirch et al. 2000a, Pennycuick 2002), likely using an innate internal barometer or ‘baroreception’ (O’Neill 2013). The olfactory neuroanatomy of tubenoses show strong hypertrophy, occupying *c.* 37% of the total brain volume compared to *c.* 3% in most other birds (Bang 1966, 1971). Pennycuick (2002) proposed that the highly developed nasal sense organ in albatrosses functions both to receive dynamic pressure information (i.e. detection of changing wind speed and direction by sensing air pressure) and olfactory information (see next section). Dynamic pressure can indicate airspeed relative to wind speed and direction, contributing to individual decisions for timing and direction of movement in response to large-scale meteorological conditions and fine-scale wind and elevation conducive to efficient soaring flight (e.g. Murray et al. 2003, Catry et al. 2004a, Richardson 2011).

Olfactory Information

Olfactory cues (i.e. information from odours) are a probable source of navigational information for decisions of *when* and *where* to move. Olfaction is likely important for movements toward food resources when foraging out to sea, and toward the colony when returning to land. Olfactory information could be produced from phytoplankton (e.g. dimethyl sulfide released in response to grazing krill; Nevitt et al. 1995), from prey species (e.g. when macerated during consumption; Nevitt & Bonadonna 2005) or from other birds (e.g. social odours; Nevitt 2008). For albatrosses, it is unclear to what extent they rely on odours for navigating (e.g. Nevitt et al. 1995, Bonadonna et al. 2003a), but it is likely that olfactory cues play a role in guiding movement decisions (Nevitt et al. 2008, Mardon et al. 2010). Albatrosses and other seabirds have well-documented associations at sea with a number of inter-related biological and physical oceanographic features considered as proxies for primary and secondary productivity, including sea surface temperature, chlorophyll *a* concentrations, eddies and fronts, upwelling and currents, and bathymetry (Tremblay et al. 2009, Wakefield et al. 2009a, Kappes et al. 2010). An individual's movement decisions that result in these associations are likely influenced at least in part by olfactory cues.

Visual And Acoustic Information

Visual and acoustic cues are both probable sources of navigational information for more fine-scale decisions of *when* and *where* to move. Aggregations of other seabirds and subsurface predators at a fishing vessel or productive feeding area at sea could provide visual and acoustic information influencing the movement decisions of an individual albatross (e.g. Silverman et al. 2004, Sakamoto et al. 2009, Collet et al. 2015). Similarly, it seems reasonable to suggest that upon return to the colony from the open sea, the sight and sound of increasing numbers of sympatric birds nearer the colony likely serves as navigational information used to guide the direction of movement, followed by sight of the colony's physical land mass and familiar landmarks. Low frequency infrasound emitted when wind blows over physical barriers or when waves break against shore, can propagate great distances and may be detectable for guiding the movements of individual albatross (Åkesson & Alerstam 1998). Visual cues would also play a key role in influencing movement decisions when localizing and capturing target prey items upon encounter at sea, both above and below the water's surface (e.g. Martin 1998, Weimerskirch et al. 2007). On a larger scale, visual detection of wind streaks and ripples may aid in identifying likely areas of buoyant prey aggregation (Nevitt et al. 2008).

Interactions Between Navigation Capacity And The Internal State

The relative contribution of each source of navigational information will be determined by a bird's unique vector of intrinsic factors, represented in the ME framework as *navigation processes* acting between navigation capacity and the internal state (Figure 5.1). For example, an individual's age and experience will play an important role in determining which sources of information contribute to movement decisions. The movement path of a fledgling albatross is most likely influenced by movement "decisions" based on an inherited genetic program for movement bearing relative to geomagnetic or celestial cues, while more fine-scale movement decisions might be made in response to olfactory or visual cues (Riotte-Lambert & Weimerskirch 2013, Chapter Two). Memories and learned navigation skills will accumulate and improve with age, thus experience will become increasingly important in influencing cognitive movement decisions over an albatross's long lifespan (Weimerskirch et al. 2014).

Interactions Between Navigation Capacity And The External Environment

The availability of each source of navigational information will be determined by elements in the environment, represented in the ME framework as *navigation processes* acting between navigation capacity and the external environment (Figure 5.1). For example, the strength and reliability of geomagnetic cues vary between regions of the planet, and thus the influence of this cue on an individual's movement decisions will depend on its availability (Åkesson & Alerstam 1998). Similarly, the presence of olfactory cues depend on the biological and physical features of the environment that produce and concentrate odours, while the detectability of those cues for an individual at any location and time will depend on the transport of odours by wind and water current conditions (Bonadonna et al. 2003a, Nevitt et al. 2008). The presence of visual and acoustic cues rely directly on elements in the environment including the presence of prey or other predators, while the detectability of those cues for an individual at any location and time could be influenced by meteorological elements of the environment, such as fog, cloud cover or precipitation. Overall, the multidimensional vector of information inputs that comprise an individual's navigation capacity at a given moment in time depends on interactions with both the external environment and its internal state.

Motion Capacity – Modes Of Movement That Influence *How* To Move

The motion capacity component of the ME framework is defined here as comprising the various modes of movement available to an individual that determine *how* a movement path is generated (Nathan et al. 2008). The biomechanical and morphological traits of an individual will provide a set of motion machineries enabling movement. The *movement propagation process*, whereby bouts of different modes of movement are strung together to generate a movement path, could be considered the mechanistic bottleneck between all components and processes in the ME framework and the actual movement of the individual (Figure 5.1). Below I briefly review the different movement modes that may be available to an albatross. This is followed by a discussion of how an individual's unique motion capacity at any moment in time depends on its internal state, navigation capacity, and the external environment, and how these relationships and processes are represented in the ME framework.

Soaring Flight

Moving by dynamic soaring flight is the most iconic and hence widely recognized mode of movement available to an albatross. Dynamic soaring flight is sustained flight powered mostly by the energy of wind gradients rather than internal energy stores (Arnould et al. 1996, Weimerskirch et al. 2000a, Suryan et al. 2008). The low cost of soaring is made possible by unique anatomy, high wing aspect ratio paired with optimal wing loading, and a shoulder-lock mechanism enabling outstretched wings with little muscular contraction (Pennycuick 1982, Meyers & Stakebake 2005). Soaring flight is likely to comprise a high proportion of an individual's movement path when transiting long distances (Wakefield et al. 2009b, Mackley et al. 2010), but is certainly not the only mode of movement generating a movement path.

Flapping Flight

Moving by flapping flight is considerably less energetically efficient than soaring flight, but is nonetheless employed by albatrosses out of necessity when soaring alone is not possible (Suryan et al. 2008, Sakamoto et al. 2013). Albatrosses are thought to lack the necessary musculature to undertake sustained bouts of flapping flight (Pennycuick 1982, Meyers & Stakebake 2005). Instead, flapping is interspersed with soaring to varying degrees to determine *how* a movement path is generated. For example, a movement path out to sea could be comprised of just a few flaps interspersed with long bouts of soaring, while a movement path above or around the colony could be comprised of continuous alternating short bouts of flapping and soaring (*pers. obs.)*.

Takeoffs And Landings

To begin or end a bout of flight, a bird must takeoff or land. Takeoffs and landings are therefore a critical and distinct transitional mode of movement contributing to *how* a movement path is generated. To engage in a takeoff, an albatross orients into the wind and often runs along the sea or land surface while beating its wings to gain lift (Kabat et al. 2007). This is probably the most energetically costly mode of movement, especially under calm or light wind conditions (Weimerskirch et al. 2000b, Shaffer et al. 2001a, Suryan et al. 2008). Similarly, landing (on water or land) requires rapid rotations of the wings about the long axis to stall (Pennycuick 1982) and is also energetically costly (Weimerskirch et al. 2000b, Sakamoto et al. 2013). These transitional modes of movement can contribute importantly in the generation of an individual's movement path.

Floating, Paddling, Sitting And Walking

Floating, paddling, sitting and walking are modes of movement with varying degrees of low mobility (or immobility for sitting) that are likely to contribute to *how* a movement path is generated. Recall that a movement path is defined as a sequence of locations occupied by an individual during some definitive duration within its lifespan (Nathan et al. 2008). If the duration of a path encompasses time spent on the colony, sitting as a "mode of movement" could contribute in generating the path (i.e. sequential locations at a regular time interval are observed in the same place). Paddling and walking are leg-propelled modes of movement often associated with a bout of floating or sitting. While out to sea, time spent floating is interspersed with active paddling (*pers. obs.*, Conners et al. 2015). While on land, all albatrosses must cope with the necessity of walking when commuting between a landing or takeoff site, and a nest or resting site, despite their limited terrestrial maneuverability (Weimerskirch et al. 2000b, Kabat et al. 2007).

Diving

Diving is wing or foot-propelled swimming under the water, and is used when a target prey item is deep enough that submersion of the head from a floating position would be insufficient. Diving as a mode of movement is available to only some species of albatross (e.g. black-browed, grey-headed, shy, light-mantled; Prince et al. 1994, Hedd et al. 1997, Huin & Prince 1997). These species regularly dive to depths of 2-5 m, with dives up to 12 m recorded for light-mantled albatross (Prince et al. 1994). For some species, diving as a mode of movement will contribute to *how* an individual's movement path is generated when foraging out to sea.

Interactions Between Motion Capacity And The Internal State

The modes of movement available to an albatross will depend on its unique intrinsic factors, represented in the ME framework as *motion processes* acting between the internal state and motion capacity (Figure 5.1). For example, a bird's breeding phase will influence the relative contribution of flight and sitting that contribute to an observed movement path; during the incubation phase, sitting could comprise a high proportion of a bird's path if the duration included an incubation bout (e.g. Weimerskirch 1995). The modes of movement that generate a movement path have important feedbacks to the internal state, represented in the ME framework as *internal dynamics* acting between the movement path and internal state component (Figure 5.1). Because different modes of movement require different energetic expenditure, the movement path feeds back to a bird's body condition. For example, during the incubation phase, long bouts of sitting are followed by foraging trips requiring all other modes of movement (i.e. sitting followed by walking, takeoff, flapping, soaring, then landings, takeoffs and possibly diving for prey capture, and so on). The relative contribution of each of these movement modes to a movement path will have a net energetic cost to the individual that will feed back to its body condition (Weimerskirch 1995, Weimerskirch et al. 2002).

Interactions Between Motion Capacity And Navigation Capacity

The modes of movement employed by an albatross also depend in part on its navigation capacity, represented in the ME framework as *movement propagation processes* acting between navigation capacity and motion capacity (Figure 5.1). An individual's decision to move in a particular direction at a particular time will influence which mode of movement is employed to generate the movement path. For example, if a bird uses olfactory and visual cues to navigate toward an aggregation of foraging conspecifics at a fishing vessel, this movement 'decision' will influence which modes of movement contribute to the movement path (i.e. landing, paddling and floating, as opposed to continued soaring flight).

Interactions Between Motion Capacity And The External Environment

The modes of movement available to an albatross will depend on elements in the environment, represented in the ME framework as *motion processes* acting between the environment and motion capacity (Figure 5.1). For example, the proportion of a movement path generated by flapping and soaring flight will be closely linked to wind conditions (Weimerskirch et al. 2000a, Sakamoto et al. 2013). The wind conditions experienced will depend on the movement path that resulted in a bird's location (i.e. *external dynamics* acting between the movement path and the external environment). Whether the wind is used in making a decision of *when* and *where* to move will depend on intrinsic factors that influence *why* a bird would move, and ultimately *how* it does so, thus generating its movement path.

Applying A Custom ME Framework To A Literature Review

I've now demonstrated that, despite the breadth of material, it is feasible to summarize and relate cross-disciplinary literature pertaining to movement for a particular system or organisms under the ME framework (Figure 5.1). By explicitly defining each of the four major components of the basic ME framework, I've identified 45 factors likely to contribute in determining the movement path of any individual albatross. The custom ME framework built here for albatrosses is admittedly over-simplified with non-exhaustive coverage of the published literature; a full review of all relevant research to-date would entail a book-sized volume. Yet the exercise of populating a custom ME framework has utility in that it reveals areas that are generally well understood, and areas where the literature pertaining specifically to albatross movement is lacking. This begs the question of whether there are identifiable gaps between a conceptual understanding of the drivers of albatross movement and the areas of the framework that receive the most practical attention in terms of applied studies of movement. I therefore used my customized conceptual ME framework as a lens through which to explicitly evaluate the field of research whereby biologging technologies are used to record the movement paths of individual albatrosses. I survey the literature for the factors most commonly measured or suggested as important in determining observed movement patterns. This allows for the recognition of components and factors within the framework that have received the most consideration, and those in need of attention in order to develop a more holistic understanding of albatross movement through the use of biologging tools.

Literature Review Methods

This review is based on the analysis of contents from published research articles selected with the 'ISI Web of Knowledge' (Thomson Reuters) search engine with the search criteria: "Topic = (albatross AND (biologging OR biologger OR telemetry OR satellite OR GPS OR GLS OR geolocator)). The results were narrowed to include peer-reviewed journal articles (i.e. not books or reports) where bird-borne biologging tools were used to produce positional data for individuals, and hence the movement paths of individuals could be inferred. This yielded a total of 117 papers published between 1990-2015 (search completed on December 31st, 2015; a separate bibliography of assessed publications can be found in Appendix 1).

To provide a general overview of trends in the albatross-biologging movement literature, each article was assessed for: 1) the number of individual birds with recorded movement paths, 2) the study species, and 3) device types used. Because the conceptual ME framework is built from the perspective of explaining individual movement, I also determined for each study whether biologger-derived movement data were used to examine the movement paths of individuals independently (i.e. to explore the drivers of movements at the individual-level), or to examine movement paths of all device-equipped birds collectively (i.e. to describe general movement patterns at the group-level). For each article I then determined which of the 45 factors from my custom ME framework were either measured (quantitatively or qualitatively) or suggested (speculated as potentially important) as potential drivers of movements. Because so few published studies investigate specific sources of navigational information, I also assessed whether navigation capacity was discussed in general terms of whether albatross use inherited genetic programs in making "decisions" of when and where to move, or whether they use cues based on memory and learning experiences.

General Trends In Albatross-Biologging Research

Not surprisingly, the number of albatross-biologging movement studies published has increased steadily over the past 25 years, as have the number of individual birds contributing biologger-derived movement data to a given study (Figure 5.2). Since 2005, it has become commonplace for a single study to incorporate movement data from 50 or more individuals. Of the ten studies published in 2015, seven included movement data from >100 individual birds (mean 180 birds ± 170 SD; Figure 5.2). This trend is driven by a combination of decreased device costs, accumulation of large datasets over time, increasing collaborations among researchers, and improved online repositories for data sharing.

The albatross-biologging movement literature has been subject to a species-bias toward wandering albatrosses since the landmark paper tracking this species 25 years ago (Jouventin & Weimerskirch 1990). Movement paths of biologger-equipped wandering albatrosses were included in 40% (46 of 117) of the articles assessed (including multi-species studies). Twenty-five articles include black-browed albatross, while black-footed, grey-headed, and Laysan albatross have also been relatively well represented in the movement literature (16, 14, and 13 articles, respectively). Another 46 articles are shared among 15 less-studied species (Table 5.1). Neither Salvin's nor Atlantic yellow-nosed albatross have been the subject of published articles, although movements of individuals from both species have been tracked with biologging devices (Taylor et al. 2004).

Positional data have been derived from three main types of bird-borne biologging devices: satellite transmitters, GPS receivers, and light-based geolocators (deployed in 84, 31, and 17 articles, respectively (some articles use variations of the three, and some use multiple device types)). Ancillary in-situ data have been recorded by additional sensors or animal-attached devices in 22% of the assessed papers. These include: 25 studies incorporating wet/dry state data to identify periods of saltwater immersion, seven employing stomach temperature loggers to infer ingestion events, two using accelerometers for fine-scale 3-dimensional movements, two using heart-rate recorders to quantify energetic expenditure, and one using bird-borne cameras to capture images of the surrounding environment.

Regardless of sample size, study species or device type, 87% of published studies use individual-based movement data to describe movement patterns collectively for all birds in a dataset, and to then make inferences regarding movement for a higher-level group that the tracked birds are taken to represent. Only 15 studies (13%) to-date have focused on describing or comparing the movements of the tracked individuals themselves. Of these 15 individual-focused studies, nearly half have been published in the past two years.

Common Factors Thought To Drive Movement Patterns

Overwhelmingly, factors within the internal state and external environment components are most commonly measured or suggested as probable drivers of observed movements for biologger-equipped albatrosses (Figure 5.3). Within the internal state component, breeding phase is routinely considered as a primary explanation for *why* birds move via a given movement path. Half of all published articles assessed include breeding phase as an explanatory variable, with another 8% speculating on the likely importance of this factor. Sex is also commonly included as a potential driver of movement patterns, with 35% of publications including this factor in analyses. This is likely due in part to the prevalence of studies conducted on wandering albatross, where sexual dimorphism makes sex relatively easy to assign (i.e. genetic sexing is not required). Species is explicitly examined as a factor determining movements in 29% of papers, where studies are designed to investigate if and *why* individuals of different species move differently.

Within the external environment component, bathymetry is quantified or qualified in 37% of albatross-biologger research, and discussed as a probable abiotic element driving movements in an additional 9%. The next most commonly measured external elements are wind and sea surface temperature (both quantified in 23% of assessed articles), followed closely by fishing vessel activity (quantified in 22% of articles). Overall, the presence of prey and fishing vessels are the two most common elements of the external environment considered to impact albatross movements, each being empirically or speculatively discussed in approximately half of all published articles (Figure 5.3).

Factors Less Commonly Considered

Within the internal state component, age only emerged as a topic of interest in albatross movement research beginning in 2005, and has gradually increased in the literature since. There are now 17 published studies (15% of the assessed articles) investigating the role of age in determining movements, ten of which were published in the past 5 years. Many focus on individuals from younger age classes, but some also include older, senescent-aged individuals.

Personality (i.e. consistent behavioural tendencies) is rarely investigated as an important intrinsic factor influencing observed movement paths (Figure 5.3). Individual moult has never been quantified in the published albatross-biologger movement literature, and has only been speculated as potentially important in four studies.

Within the motion capacity component, flapping as a mode of flight is often suggested as an important contributor in generating movements (20% of published articles), but the proportion of a movement path comprised of flapping has been quantified in only one study (Figure 5.3). The two modes of movement used to accomplish short-distance movements at-sea (paddling and diving) are rarely, if ever, measured or discussed as important in albatross-biologging movement research. Further, despite recorded movement paths encompassing time spent at the colony, location data on-land is typically filtered out for analyses, leaving time spent walking or sitting un-quantified (Figure 5.3).

As a whole, navigation capacity has not been commonly discussed as important to movement, nor quantified relative to specific types of navigational information used by individuals (Figure 5.3). In more general terms, inherited navigational abilities were suggested to be important in determining movements in nine published articles (<8%), while learnt abilities were suggested as important in 17 published articles (<15%). Overall, 20% of assessed studies consider some aspect of navigation capacity in their discussions of potential drivers of observed movement patterns from biologger-equipped albatrosses.

Limitations In Albatross Movement Research

Many of the weaknesses in our current understanding of albatross ME can be attributed to two limitations that have both lessened over time: 1) a tendency to ignore the individual to which biologging devices are attached, and 2) the accessibility of quantifying or qualifying factors. In light of these limitations, I discuss gaps in our understanding of what drives a bird to move via a given movement path, I identify trends toward change in the drivers we explore with biologging, and I recommend future research directions.

There has been a propensity within the albatross-biologging movement research to generalize the movements of individual equipped birds to represent the movements of a much larger group. Mostly these extrapolations are made at the level of the species, colony, sex, or age class (87% of published articles). We thus have a tendency to ignore the individuals from which positional data are derived, missing out on identifying the unique intrinsic factors that drive individuals to move via a given observed movement path. However, an emerging shift among seabird scientists away from inferring group-level movement patterns and toward investigating individual specialization in movement was reflected at the recent 2nd World Seabird Conference ('WSC2', Cape Town, South Africa, October 26th-30th, 2015). Three complete symposia, comprising 19 oral presentations, at the WSC2 were dedicated to showcasing research on the causes and consequences of individual variability and specialization in movement, foraging and migration strategies. This growing interest in individual seabird movement is likely to manifest in the albatross-biologging movement literature as well.

There are a number of intrinsic factors that are unique to a focal individual that are likely to receive increasing attention as studies focus in on individual equipped birds. Measures of body condition are becoming more common and sophisticated in terms of the physiological variables considered (e.g. aerobic capacity, energetic, and endocrine state from non-destructive blood and feather sampling), and are likely to become key in studies of movement and carry-over effects (i.e. internal dynamics acting between the movement path and the internal state). Investigations explicitly examining 'personality' may be less common, but are expected to increase beyond the two published papers where personality is quantified in relation to movement, and the three papers where personality is suggested to exist (all of which have been published in the past five years). In contrast, interest in moult status as an important intrinsic factor in determining individual movements is not yet apparent, and represents an area of albatross movement ecology research with great potential for exploration.

Our ability to quantify or qualify each of the 45 factors identified in the custom ME framework built here present practical limitations to their study. It was only 25 years ago that it became possible to infer individual movement paths from sequential location data, let alone identify multiple intrinsic and extrinsic variables likely influencing the observed patterns. On average, each of the assessed studies attempted to measure only *c.* 4 of the 45 factors identified (3.9 ± 2.2, mean ± SD), and invoked only *c.* 3 additional factors as potential contributors to observed movement patterns (3.3 ± 2.8, mean ± SD). Study designs traditionally have not included measurement of factors relevant to individual movements beyond those easily acquired such as breeding phase, sex (for sexually dimorphic species), and age-class (i.e. immature or mature), often paired with readily available coarse-scale satellite-derived external elements such as bathymetry, SST, wind, and celestial conditions (i.e. moon phase or day versus night). Ideally, study designs where biologging devices are attached to individual birds would include attempting to identify a minimum of sex, age, breeding success and experience, and some measure of body condition and moult status, to allow for future explorations of the role of these internal state factors in determining movements.

As for the external environment, the presence and behaviour of fishing vessels and prey are both commonly discussed as important but are much less often quantified. Cooperation from fisheries operations in recording and providing quality data on vessel position and activity is paramount in improving quantitative assessments of bird movements relative to fisheries. Historically, national and international fisheries bodies have been reluctant to release data on vessel activities (i.e. Vessel Monitoring System, or 'VMS', data,) but access to VMS data is improving, as is the quality of the data (e.g. Granadeiro et al. 2011, Torres et al. 2011, 2013, Collet et al. 2015, Sugishita et al. 2015). Incidental mortality through drowning on baited longline hooks, entanglement in nets, and collisions with trawl warps are primary threats to albatross populations worldwide. Therefore, determining how vessel activity impacts bird movements is key in generating effective conservation management solutions.

Gathering reliable data on the availability and behaviour of potential prey in relation to the movements of individuals also remains challenging. Of the 13 studies assessed as having measured prey in some respect, only two quantified the availability and distribution of prey in the environment that individuals moved through (i.e. the prey field). These studies used acoustic transducers to assess the presence of squid aggregations (Rodhouse & Boyle 2010) or size of krill swarms (Veit & Prince 1997) where birds had been detected. Rather, the majority of studies have measured prey in terms of what birds successfully captured and consumed throughout their movements; seven studies used stomach temperature loggers to infer ingestion events along the movement path, while three analyzed general prey consumption from stomach contents of biologger-equipped individuals and one estimated long-term diet using chemical signatures of stable isotopes. Better understanding movement in relation to the presence and behaviour of prey will require efforts to obtain in-situ measurements of prey fields combined with accurate information of feeding events and dietary composition. Because albatross diets are variable and prey are patchily dispersed throughout their vast ranges, successfully quantifying prey fields in relation to individual movements remains a great challenge. Regardless, foraging is a central theme throughout the albatross-biologging movement literature, and investigating how prey in the environment interacts with an individual's internal state, navigation capacity and motion capacity will be necessary to advance the study of the drivers of albatross movement.

The possibility of quantifying some previously immeasurable factors within the framework is becoming a reality thanks to rapid technological advancements in the field of biologging. Devices are becoming increasingly sophisticated and miniaturized, enabling multiple on-board sensors with higher precision and sampling rate of positional data, as well as the recording of concurrent ancillary data. High quality location data paired with immersion state, depth, or accelerometry data are likely to allow for investigations addressing the contribution of all modes of movement generating a movement path, including flapping flight, diving, and paddling on the water's surface. Bird-borne cameras are another promising technology that can provide insight into the external surroundings immediately relevant to a focal individual. These technologies can reveal important interactions between an individual and various elements of the environment, including conspecifics, congeners, other predators, vessels, and prey. Further, we may also be able to determine important localized abiotic elements that are not readily measured from coarse-scale satellite-derived data, such as waves, cloud cover, precipitation, fog or celestial conditions. By considering more detailed information on the intrinsic factors and external elements relevant to each biologger-equipped individual, we can begin to disentangle how interactions among the internal state, external environment, and motion capacity of individuals determine an individual's movements.

Empirical study of animal orientation and navigation under natural conditions remains exceedingly challenging, and thus the contribution of an individual's navigation capacity in determining movements recorded by biologgers remains a major 'black box' in albatross ME (Figure 5.3). The inadequacy of investigations and established hypotheses of the mechanisms controlling pelagic seabird movement decisions is recognized in the literature (e.g. Guilford et al. 2011, Åkesson & Weimerskirch 2014). There are recent indications, all from 2015, of advancements in the general area of animal navigation research, and also for seabirds and albatrosses in particular. Qin et al. (2015) discovered the likely protein molecule complex that acts as a compass in animals' geomagnetic sense, representing an enormous step toward understanding the role of geomagnetic cues in influencing movement decisions. Wikelski et al. (2015) combined biologging, sensory manipulations and translocations to assess the role of olfactory cues in guiding migratory navigation in gulls. They show that birds with severed olfactory nerves traveled with clear directional preference but were unable to compensate for displacements, lending support to the importance of olfactory information to navigation capacity. Collet et al. (2015) investigated the influence of visual cues on albatross movement decisions in relation to fishing vessel activity. The results indicate that birds detect fishing vessels from up to 30 km away, at the limit of what was considered their theoretical maximum visual range. Also in 2015 at the WSC2, seabird navigation was the focus of a presentation session. One topic of discussion was the 'exploration-refinement hypothesis' (originally proposed by Guilford et al. 2011), which suggests that some seabirds rely on large-scale exploratory movements during the immature years, rather than strict genetic or cultural control, which become refined over time through learning and memory into an individual movement strategy. Ultimately, understanding navigation capacity will require combining biologging research with field and lab-based behavioural experiments, and exploration of internal mechanisms determining sensory perception. With cross-disciplinary collaboration, there is hope that the black box of albatross navigation will continue to open.

It should also be noted that some factors remain impossible to realistically measure, such as an individual's unique history of experiences that influence both its motivations to move and its decisions of when and where to move. Regardless of our ability to quantify the entirety of an individual's past experiences, this should still be recognized as a potentially significant contributor to both intra- and inter-individual variation in movement paths. Building a custom conceptual ME framework is thus a valuable exercise in identifying all factors likely to influence an individual's movements, whether or not those factors are typically measured or discussed in the biologging literature.

Conclusions

The review presented here identifies general trends, strengths, and weaknesses in the albatross-biologging movement literature. As the number of studies published in a given year and the number of individuals comprising each dataset continues to grow, hopefully so too will the breadth and complexity of questions asked about the drivers of albatross movement. In brief, future work should look to overcome the heavy species-bias toward wandering albatross in the published literature, as well as move away from tendencies to record only easily quantified or qualified intrinsic factors and external elements. We should explore more thoroughly the interactions within and among components in driving individual movements. This will require attempting to quantify, for each unique biologger-equipped individual, as many factors as possible within the multidimensional vector of interacting intrinsic factors, rather than assuming all individuals are ecologically equivalent. The works accomplished to-date have laid the groundwork in exploring and describing albatross movements and suggesting probable drivers of the observed patterns, mostly at the group-level. As cross-disciplinary technological and analytical toolboxes develop, in-depth investigations of movement in terms of individual specialization due to unique internal states, navigation capacity and motion capacity will inevitably become more common. Biologging research has an important role to play in both the development of effective conservation and management strategies for all threatened species, including the albatrosses (Table 5.1; Cooke 2008, Burger & Shaffer 2008, IUCN 2015), as well as gaining a more comprehensive understanding of the complex movement ecology of these magnificent animals.

I've shown that the basic conceptual ME framework proposed by Nathan et al. (2008) is well suited to integrating cross-disciplinary movement research into a customized framework built for a specific target taxa. Explicitly populating and visualizing a ME framework helps to elucidate complex relationships among a multitude of probable drivers of movement. Custom frameworks can be used as a guide in conducting reviews, as accomplished here with a survey of the published albatross-biologger movement literature. A similar exercise could be valuable for any group studied with biologging technologies that record sequential positional data, as the fundamental unit will always be the unique individuals contributing movement paths, and individual movement paths are the central tenet of the ME framework.

Tables

Table 5.1 – There are presently 22 recognized species of albatross (Order: *Procellariiformes*, Family: *Diomedeidae*). Included in the table are the number of published biologging studies of movement for each species (from 1990 to 2015), current IUCN Red List category, and oceanic regions of residence (from IUCN 2015). Categories include: Near Threatened (NT), Vulnerable (VU), Endangered (EN) and Critically Endangered (CR). Asterisks (0*) indicate species for which no biologging research has been published in peer-reviewed journals but for which biologging studies have been carried out and published in reports.

Common name (all ending in 'albatross')	Scientific name	Number of published biologging movement studies	IUCN Red List Category	Oceanic regions of residence
Amsterdam	*Diomedea amsterdamensis*	3	CR	Southern Indian
Antipodean	*Diomedea antipodensis*	2	VU	South Pacific
Atlantic Yellow-nosed	*Thalassarche chlororhynchos*	0*	EN	South Atlantic
Black-browed	*Thalassarche melanophris*	25	NT	Southern Indian, South Pacific, South Atlantic
Black-footed	*Phoebastria nigripes*	16	NT	North Pacific
Buller's	*Thalassarche bulleri*	4	NT	South Pacific
Campbell	*Thalassarche impavida*	1	VU	South Pacific
Chatham	*Thalassarche eremita*	2	VU	South Pacific
Grey-headed	*Thalassarche chrysostoma*	14	EN	Southern Indian, South Pacific, South Atlantic
Indian Yellow-nosed	*Thalassarche carteri*	3	EN	Southern Indian, South Pacific
Laysan	*Phoebastria immutabilis*	13	NT	North Pacific
Light-mantled	*Phoebetria palpebrata*	8	NT	Southern Indian, South Pacific, South Atlantic
Northern Royal	*Diomedea sanfordi*	3	EN	Southern Indian, South Pacific, South Atlantic
Salvin's	*Thalassarche salvini*	0*	VU	Southern Indian, South Pacific
Short-tailed	*Phoebastria albatrus*	5	VU	North Pacific
Shy	*Thalassarche cauta*	2	NT	Southern Indian
Sooty	*Phoebetria fusca*	1	EN	Southern Indian, South Atlantic
Southern Royal	*Diomedea epomophora*	2	VU	Southern Indian, South Pacific, South Atlantic
Tristan	*Diomedea dabbenena*	2	CR	South Atlantic
Wandering	*Diomedea exulans*	46	VU	Southern Indian, South Pacific, South Atlantic
Waved	*Phoebastria irrorata*	6	CR	Central Pacific
White-capped	*Thalassarche steadi*	2	NT	Southern Indian, South Pacific, South Atlantic

Figures

Figure 5.1 – A custom movement ecology framework for the drivers of albatross movement (adapted from Nathan et al. 2008). The basic framework is composed of four interacting components that together determine an individual's movement path (as depicted in the upper left diagram). Arrows indicate the processes acting within and between components. Albatross-specific factors within each component of the full framework are detailed in the four cut out panes at the bottom of the figure.

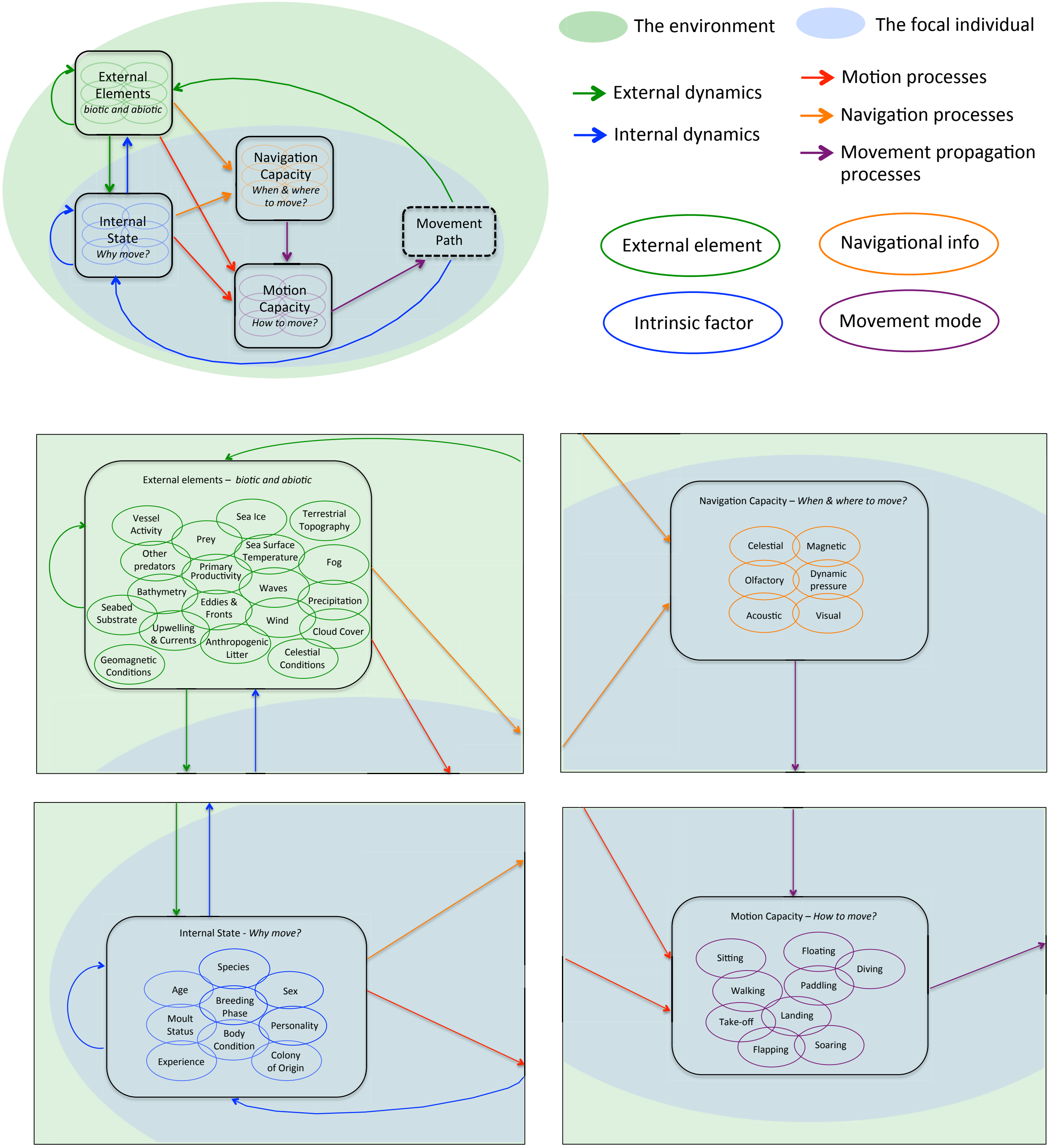

The environment
The focal individual
External dynamics
Internal dynamics
Motion processes
Navigation processes
Movement propagation processes
External element
Navigational info
Intrinsic factor
Movement mode
External Elements
biotic and abiotic
Internal State
Why move?
Navigation Capacity
When & where to move?
Motion Capacity
How to move?
Movement Path
External elements – biotic and abiotic
Vessel Activity
Sea Ice
Terrestrial Topography
Prey
Sea Surface Temperature
Other predators
Primary Productivity
Fog
Bathymetry
Waves
Seabed Substrate
Eddies & Fronts
Precipitation
Wind
Upwelling & Currents
Cloud Cover
Anthropogenic Litter
Celestial Conditions
Geomagnetic Conditions
Navigation Capacity – When & where to move?
Celestial
Magnetic
Olfactory
Dynamic pressure
Acoustic
Visual
Internal State - Why move?
Species
Age
Sex
Breeding Phase
Moult Status
Personality
Body Condition
Experience
Colony of Origin
Motion Capacity – How to move?
Sitting
Floating
Diving
Walking
Paddling
Take-off
Landing
Flapping
Soaring

Figure 5.2 – Temporal trends in albatross-biologging movement research. Boxplots show the number of individual albatross equipped with positional biologging devices in each of 117 assessed studies. Published articles are grouped into 5 year bins from 1990-2014, and 2015 is shown alone. Boxplots show the median and interquartile range (IQR) with whiskers extending to 1.5xIQR. Outliers are shown as filled circles, and y-values for extreme outliers are reported with an asterisk*. The number of published articles (*n)* contributing to each box plot is shown on the x-axis.

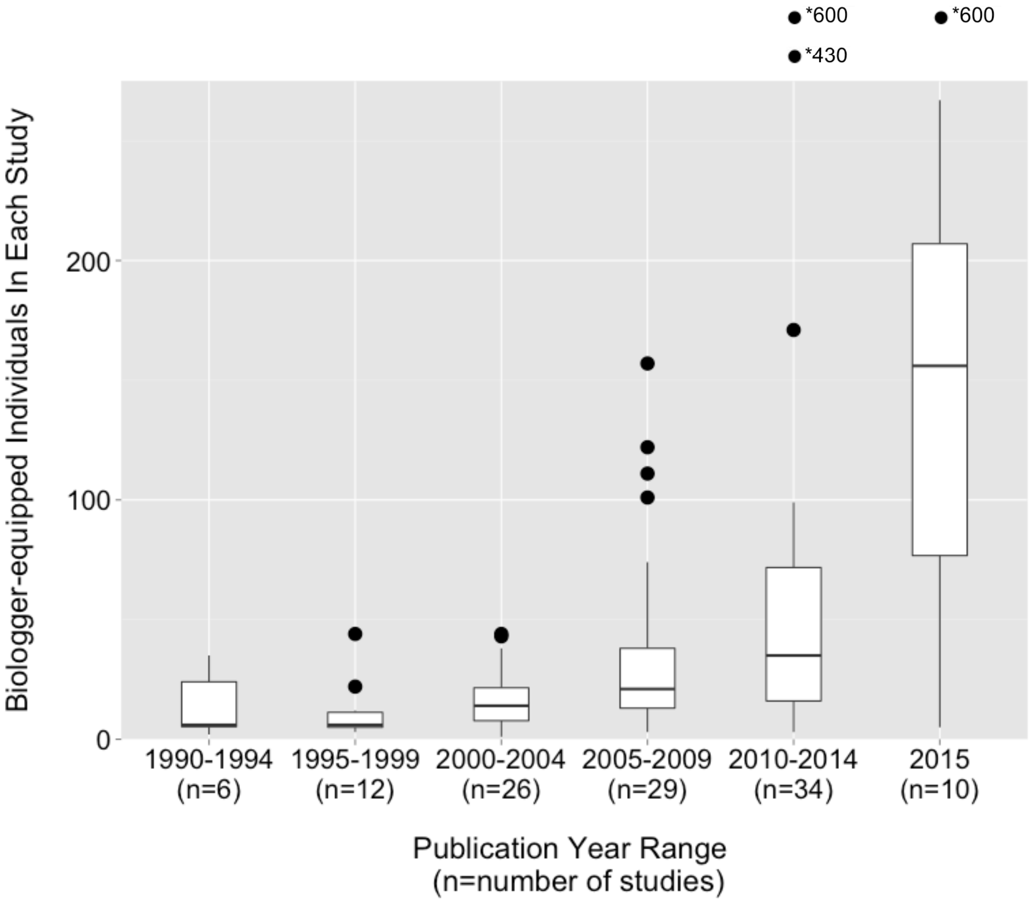
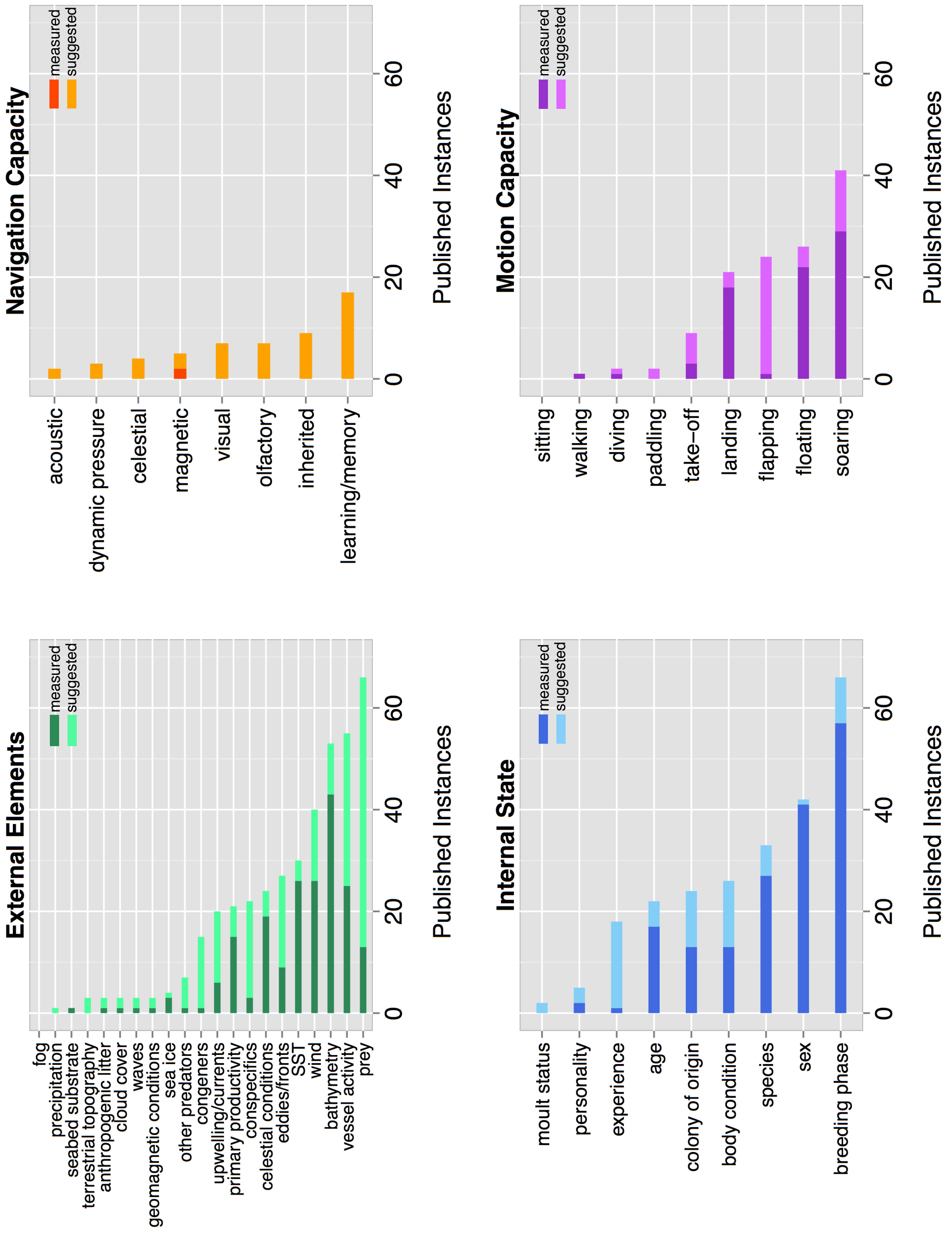


Figure 5.3 – Results from a survey of factors measured or suggested as drivers of movement in published albatross-biologging research. The custom movement ecology framework was used as a guide in conducting a literature survey of the most commonly measured (dark bars) or suggested (light bars) factors in driving movement patterns (where movement paths of individuals are known from biologging devices). A total of 117 studies, published from 1990 to 2015, were assessed.


External Elements
fog
precipitation
seabed substrate
terrestrial topography
anthropogenic litter
cloud cover
waves
geomagnetic conditions
sea ice
other predators
congeners
upwelling/currents
primary productivity
conspecifics
celestial conditions
eddies/fronts
SST
wind
bathymetry
vessel activity
prey
measured
suggested
0
20
40
60
Published Instances
Navigation Capacity
acoustic
dynamic pressure
celestial
magnetic
visual
olfactory
inherited
learning/memory
measured
suggested
0
20
40
60
Published Instances
Internal State
moult status
personality
experience
age
colony of origin
body condition
species
sex
breeding phase
measured
suggested
0
20
40
60
Published Instances
Motion Capacity
sitting
walking
diving
paddling
take−off
landing
flapping
floating
soaring
measured
suggested
0
20
40
60
Published Instances

Chapter 6: Discussion

The overarching objectives of my thesis were to 1) identify and address weaknesses in our understanding of seabird movements with a focus on the albatross family and, 2) identify and address weaknesses in the approaches used to describe and evaluate seabird movement based on biologger data. Below, I briefly summarize how my findings contributed to meeting each of these objectives. Then, I review the conservation status of Laysan and black-footed albatrosses and of pelagic seabirds in general, and recommend future movement research avenues for each group. In light of my PhD work in concert with the recent work of others, I share some perspectives on important future research directions that will continue to advance ecological knowledge and improve our ability to develop effective conservation solutions for threatened seabirds.

Summary Of Dissertation Findings

To meet my first objective, I examined the dispersive movements of fledgling black-footed albatross (Chapter Two), and assessed detailed movements of non-breeding adult Laysan and black-footed albatrosses (Chapter Three). The results revealed some unexpected movements and behaviours of birds in both age-classes. I am hopeful that my findings will inspire future research to examine in more detail the drivers of movements during the periods of immaturity and non-breeding for these and other threatened wide-ranging seabirds. Toward the first objective, I also evaluated general weaknesses in our understanding of albatross movement ecology by building a conceptual framework of the drivers of movement (Chapter Five). I then used this framework to conduct a review of the albatross-biologger movement literature. The outcome of this work can serve as a guide to identifying interesting and important areas for further biologging efforts. To meet my second objective, I developed a multi-step approach for examining biologger-derived immersion state data in combination with positional data to generate daily activity budgets for non-breeding seabirds (Chapter Three). Before this work, non-breeding activity budgets were typically evaluated according to broad stages of the non-breeding period, such as averages of time spent in flight during migratory and over-winter stages of non-breeding. My work demonstrates how immersion state data can be used to examine non-breeding movements and behaviour in greater detail. Toward the second objective, I also critically evaluated a common analytical approach for describing the space use of seabirds, with Laysan and black-footed albatrosses as model wide-ranging species (Chapter Four). The results suggest that caution is warranted when extrapolating movement and space use from a small sample of biologger-equipped individuals to represent a larger group such as a colony due to high potential for individual variation in movements. The outcome of this work has particularly important conservation implications in terms of using biologger data to assess spatially and temporally explicit threats. Perhaps most critically, the results demonstrate how sizeable at-sea areas used by birds may be entirely undetected depending on the number and identity of the biologger-equipped individuals contributing data to a sample.

Conservation And Future Movement Research For Hawaiian Albatrosses

Throughout human history, Laysan and black-footed albatrosses have been dealt an onslaught of detrimental anthropogenic impacts. Populations of both species recovered from the decimation of the feather and egg trade in the early 1900s (Tickell 2000), but contemporary impacts continue to threaten their population stability (IUCN 2015). In the long-term, breeding success of both species is predicted to be highly vulnerable to effects of climate change, including breeding site inundation from sea-level rise (Reynolds et al. 2015) and increased variability in the location of their primary foraging region during breeding, the Transition Zone Chlorophyll Front (TZCF; Thorne et al. 2015). More immediately, survival of birds from both species is threatened by fatal entanglement in fishing gear resulting from the attraction of birds to vessels to feed on bait and discards (Lebreton & Véran 2012, Edwards et al. 2015). A critical step in addressing these marine-based threats is developing a more comprehensive understanding of the at-sea movements and behaviour of these species throughout the life cycle (Naughton et al. 2007, IUCN 2015).

The results of Chapters Two, Three and Four of this thesis collectively demonstrate the wide-ranging, pelagic nature of both Laysan and black-footed albatrosses. Across age-classes and annual phases, these species make use of most of the North Pacific. Importantly, space use varies to differing degrees among individuals, age-classes and life stages. In Chapter Two, I found remarkable consistency in movements among fledgling black-footed albatross, where fledglings used relatively warm and unproductive waters compared with adults. I suggested that differing habitat associations between fledglings and adults might be due to different energetic demands and experience. In light of recent work by Thorne et al. (2015), it is also possible that there is a contemporary spatial mismatch occuring between fledgling movements and what was previously predictable ideal habitat. Over the past 30 years, the subtropical gyre has been expanding and the TZCF has been shifting northward (Thorne et al. 2015). The apparently innate early dispersive movements of fledglings may have been more adaptive historically if they resulted in overlap with regions of high prey availability. Climate models suggest that sea surface temperatures in the expanding subtropical gyre, where tracked fledglings were found to concentrate, will continue to increase dramatically (Polovina et al. 2011). Therefore, a potential mismatch between fledglings and productive foraging regions may be exacerbated in the future. Similar work to Chapter Two should be carried out for Laysan albatross and at other colonies, to examine whether younger age-classes of other populations and species also exhibit ontogenetic niche differences during the early dispersal period. More detailed research on movements and behaviour during the early-life stages will be crucial to understanding how climate-change induced shifts in the marine environment will impact Hawaiian albatrosses at the population level. Differential vulnerability between age-classes to fisheries interactions could also have important demographic consequences. As shown in Chapter Five, consideration of age as an important driver of individual movements has been increasing in the albatross-biologging literature, especially over the course of my PhD research. The continuation of this trend will benefit our understanding of the role of age in the movement ecology and conservation of North Pacific albatrosses.

The results of Chapters Two, Three and Four indicate there is greater variability in movements among mature breeding-aged birds than juveniles, especially outside of the early chick-rearing period. In general, I found that adult black-footed albatross exhibited higher variability among individuals in movements than Laysan albatross. This general pattern aligns with recent work investigating individual foraging strategies of Laysan and black-footed albatrosses at a fine spatiotemporal scale (Conners et al. 2015). Conners et al. (2015) found that birds of both species exhibited identifiable individual foraging strategies based on their use of six distinct behaviours, but black-footed albatross showed greater intraspecific variation in strategies. Interestingly, this work was carried out during early chick rearing, suggesting that birds were partitioning resources behaviourally rather than spatially (based on relatively restricted ranges during chick rearing for both species, Chapter Four). Individual specialization may then be a behavioural mechanism that facilitates coexistence during periods of high energetic demand, limited resource availability, and high competition (Conners et al. 2015). Future research could potentially pursue the question of whether individual foraging strategies persist throughout the annual cycle, despite a possible reduction in competitive pressure as birds spread out across the North Pacific following early chick rearing.

Chapter Three revealed a 'quasi-flightless stage' during the overwinter period that is behaviourally consistent across individuals and species, despite different geographic regions where this relatively immobile stage was spent. For both species, apparent higher constraints to movement during this period likely limit the use of some foraging strategies, such as 'fly-and-forage' tactics (Strandberg & Alerstam 2007). Limited foraging strategies could result in the loss of body condition observed during this time when active flight feather moult is likely taking place (Edwards 2008). Future research building on Chapter Three should examine in greater detail how moult influences movements in terms of the extent and duration of reduced flight activity experienced by birds during the non-breeding period, the availability of resources in overwintering areas, and how birds forage. This could be accomplished through at-sea observations, captures, and biologging efforts in overwintering areas. Further, these species are somewhat unique among albatrosses in their complex multi-year moult strategies (Edwards & Rohwer 2005). Following individuals across multiple years in a longitudinal study would provide insight into whether individual specialization in foraging strategies persists throughout the annual cycle and across years, and the importance of moult in driving individual movements. Further, individual specialization in foraging strategies (behaviourally and spatially) likely lead to differential risk of fisheries interactions among birds, as suggested for black-browed albatross (*Thalassarche melaophris*; Granadeiro et al. 2011), and more recently for Laysans (Edwards et al. 2015). Important next steps for both focal species of this dissertation will include looking more closely at individual variation in movement, subsequent impacts on detrimental ecological interactions at sea, and ultimately, how this may influence population dynamics.

Conservation And Future Movement Research For Seabirds Worldwide

Albatrosses are the focus of Chapter Five, but the conceptual framework that I developed could be broadened to cover a larger group, such as pelagic seabirds in general. Pelagic seabirds are birds that are entirely dependent on deep water or neritic continental shelf habitats for at least part of their life cycle (i.e. birds that do not use primarily coastal inshore waters; Croxall et al. 2012). Because of this reliance on the pelagic environment and associated patchy resources, these birds are arguably the most mobile of all marine top predators in terms of the distances and rates at which they move throughout the world's oceans in search of food. Their movements, and subsequent individual fitness and population dynamics, can be some of the most rapidly responsive to changes in ocean conditions (Durant et al. 2009). It follows that seabirds have been widely recognized as excellent potential indicators of the health of the marine environment both regionally and globally (Piatt & Sydeman 2007), and as surrogates for biodiversity hotspots in marine spatial planning (Ronconi et al. 2012, Lascelles et al. 2016). Unfortunately, of the 199 species of pelagic seabirds, nearly half are known or suspected to be experiencing population declines (Croxall et al. 2012). The oceans are rapidly changing as a result of human activities and global climate change, and pelagic seabird populations are declining in response (Paleczny et al. 2015). Increasing our understanding of the complex drivers of seabird movements will be essential now more than ever in addressing declines and in ensuring seabirds can continue to act as useful bioindicators for marine ecosystems. An important step toward a holistic understanding of seabird movement ecology could be to expand the conceptual framework developed in Chapter Five to encompass all pelagic seabirds, and to conduct a similar but more comprehensive literature review in order to identify priority research areas for future biologging movement research.

Chapters Three and Four demonstrate that the continuous emergence of new biologging technologies and the accumulation of data over time must be matched by the continuous evolution of analytical techniques used to examine the data. The multi-step analytical approach developed in Chapter Three offers a new means of examining positional and immersion-state data to provide insights into movement and activity budgets of pelagic seabirds during the non-breeding period. Without this new approach, the 'quasi-flightless stage' found during overwinter might have gone undetected due to the high degree of individual variation in the timing of non-breeding events. The results of Chapter Three lead me to speculate that observed periods of reduced flight and increased floating may indicate constraints from flight feather moult. Since the publication of Chapter Three (Gutowsky et al. 2014b), similar work has been carried out with the primary objective of verifying the hypothesis that the 'quasi-flightless stage' during non-breeding is explained by flight impairment during active wing moult (Cherel et al. 2016). Immersion-state data from a species with a known moult chronology, the blue petrel *Halobaena caerulea*, were used to determine a behavioural signal in the data that identified active moulting, marked by increased time floating and decreased time in flight. This signal, or 'behavioural moult criterion' was applied to identify for individuals the location and duration of a quasi-flightless stage of overwinter, which did indeed coincide with moult. The criterion was then used to determine moulting areas and timing for two other species of petrel, the Antarctic *Pachyptila desolata* and thin-billed *P. belcheri* prions. Further, Cherel et al. (2016) conducted a review of seabird studies that used immersion-state sensors to investigate movements and behaviour during non-breeding. They found that quasi-flightless stages are likely identifiable for most species of tubenoses (Order: *Procellariiformes*), and that moult is a probable primary driver of movements during the non-breeding period. Taken together, the work from Chapter Three and Cherel et al. (2016) calls for a re-analysis of the high volume of at-sea activity data already acquired for albatrosses, petrels and shearwaters to investigate variations in the intensity, duration and timing of quasi-flightlessness that would be expected from different moult patterns (Bridge 2006). Future work should look to identifying when and where seabirds renew the plumage that is critical to their long distance travels, and to identifying potential threats birds may face during the energy-demanding period of moult.

Differences between analytical approaches employed in Chapter Two and Chapters Three and Four are further testament to the constant advancements in data processing that are occurring within the field of biologging. Specifically, the techniques used to infer positional estimates for wide-ranging animals like seabirds from light-based geolocator devices, or GLS, have been rapidly evolving over the course of this dissertation. In Chapter Two, I employed a common and relatively simple filtering approach to GLS positional estimates, which were first derived from proprietary automated template-fitting software (Lotek Wireless, St. John's, Newfoundland). This filtering approach accounted for spurious location estimates common in seabird GLS data, but has the drawback of removing up to 20% of daily locations estimated for an individual. The remaining estimated positions retain a likely mean error of within approximately 200-400 km of the true positions (Phillips et al. 2004, Shaffer et al. 2005). Between the time of writing and publication of Chapters Two and Three, more powerful approaches for processing GLS data became attainable due to collaboration with experts in implementing new and analytically more complex methodologies. Thus, in Chapters Three and Four, I adopted a state-space modelling (SSM) approach for refining location estimate uncertainty and avoiding unnecessary data loss by incorporating device-specific error and movement dynamics into estimates of true daily positions (Jonsen et al. 2005, Winship et al. 2012). Still, there remains considerable uncertainty in my SSM-estimated locations (estimated as Bayesian 95% credible limits from the posterior distributions of location estimates, mean ± standard error, 0.89 ± 0.08° latitude and 0.92 ± 0.06° longitude, Chapter Four). SSM approaches are also computationally difficult to implement and understand without sufficient training or expert guidance, and cannot reliably estimate positions around the equinox period. A number of research groups have been working toward the development of open-source software packages within the R computing environment (R Core Team 2015) with the explicit function of processing GLS light data. The most recently released package, 'FlightR', optimizes a hidden Markov model to estimate the most probable location of an individual on a given day based on raw light-level data, and provides positional estimates with credible intervals (Rakhimberdiev et al. 2016). Double-tagging experiments (high-precision GPS and GLS) on migrating black-tailed godwit *Limosa limosa* provided GLS-based positional estimates from 'FlightR' that deviated from true positions by a mean of 43 km (± 51 km SD, with equinoxes included). This work represents an exciting advancement over the approaches that were available at the time of data analysis and publication from this dissertation, and illustrates the active state and constant progress within the field of biologging.

In Chapter Four, I demonstrate that in addition to developing and adopting new approaches to processing and analyzing biologger-derived data, it is also important to re-examine approaches that become commonplace over time. Estimating the space use of a larger group such as a colony based on a sample of biologger-equipped individuals can be misleading if individual variation in movements is not taken into account, especially when pooled Kernel Density Estimation techniques are applied to small datasets for wide-ranging seabird species (Chapter Four). The recommendations made in Chapter Four (and published in Gutowsky et al. 2015) are supported by a number of past studies (e.g. Lindberg and Walker 2007, Hebblewhite and Haydon 2010, Schofield et al. 2013, Soanes et al. 2013), and most recently by Lascelles et al. (2016). Coincidentally, concurrent with my work for Chapter Four, BirdLife International had been collaborating with top seabird scientists from six nations to develop new recommendations for analyzing seabird space use from movement data (M. Dias, *pers. comm.*). Their work also recognizes the issues borne of pooled datasets and offers a new approach to better incorporate the influence of sample size and individual variation into analyses of space use. While recent publications have still been applying pooled Kernel Density Estimation approaches to small datasets without also reporting individual variation in movements (e.g. Burke et al. 2015, Fayet et al. 2015), I am hopeful that future work will heed the advice offered in Chapter Four (Gutowsky et al. 2015) and by BirdLife International (Lascelles et al. 2016); exercise caution, transparency, and analytical rigour when extrapolating from individual-based movement data to infer higher-level spatial patterns for groups, particularly for wide-ranging pelagic seabirds.

Much of the published seabird biologging movement research to-date has focused on ecological questions at the level of species, colony, sex, or age class, often with limited acknowledgement or consideration of the variation among the individuals carrying the devices. Rather, the movements and behaviours of individuals are taken together to represent the likely movement and behaviour of a larger group. For albatrosses, only 13% of published articles have explicitly investigated individual variation or specialization with respect to movement (Chapter Five). Due to a number of constraints, the work in Chapters Two and Three of this thesis in some ways contribute to this disparity. But throughout the process of producing this dissertation, I recognized that seabird movement biologging research has been somewhat subject to a 'tyranny of the Golden Mean' not unlike that pointed out by Bennett (1987) in the fields of comparative and ecological physiology. Bennett (1987) identified an almost complete focus on central tendencies in physiological studies, and proposed that focusing instead on inter-individual variability would open new doors in physiological research. I would suggest that seabird scientists using biologging tools have also had a propensity over the past 25 years to focus on central tendencies when investigating seabird movement ecology, without also fully appreciating the causes and consequences of the degree of variation among individuals. But the tide seems to be turning away from generalizing group-level movement patterns and toward also investigating individual specialization in movement (Chapter Five). This paradigm shift, paired with innovations in biologging technologies and analytical approaches, will continue to provide exciting new opportunities to investigate the multitude of factors that determine why, when, where and how individual seabirds move. These ecological insights can in turn guide conservation and management initiatives, in concert with on-colony population monitoring and research, ship-based at-sea surveys, fisheries monitoring and reporting, and large-scale climatic and oceanographic modeling. A multi-faceted approach is critical to successfully detecting shifting population dynamics, and disentangling the mechanisms driving change.

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Appendices

Appendix 1 – Results of albatross-biologging movement literature review

Results of a literature search of published research articles selected with the 'ISI Web of Knowledge' (Thomson Reuters) search engine with the search criteria: "Topic = (albatross AND (biologging OR biologger OR telemetry OR satellite OR GPS OR GLS OR geolocator)). The results were narrowed to include peer-reviewed journal articles (i.e. not books or reports) where bird-borne biologging tools were used to produce positional data for individuals. This yielded a total of 117 papers published between 1990-2015 (search completed on December 31st, 2015).

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Appendix 2 – Co-authorship and copyright release

Chapter 2: Post-breeding distribution and habitat associations of fledgling and adult black-footed albatrosses in the North Pacific

While the work is my own, this research chapter is a collaborative effort among a number of researchers and government scientists. All co-authors provided feedback on the manuscript, which has been published with the following citation:

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Chapter 3: Daily activity budgets reveal a quasi-flightless stage during non-breeding in Hawaiian albatrosses.

This study is my own yet there are a number of co-authors whose contributions were invaluable to its completion. All co-authors provided feedback on the manuscript, which has been published with the following citation:

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Chapter 4: Individual-level variation and population-level interpretations of space use in wide-ranging species: An albatross case study of sampling effects.

Although the research is my own, this study could not have been completed without the help of a number of co-authors. All co-authors provided feedback on the manuscript, which has been published with the following citation:

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