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Comparative behavior, diet, and post-breeding strategies of two sympatric North Pacific albatross species (Phoebastria sp.)

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COMPARATIVE BEHAVIOR, DIET, AND POST-BREEDING STRATEGIES OF TWO SYMPATRIC NORTH PACIFIC ALBATROSS SPECIES

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Thesis Abstract

Comparative behavior, diet, and post-breeding strategies of two sympatric North Pacific albatross species (*Phoebastria sp.*)

Melinda Conners

A fundamental condition of the struggle for existence is resource limitation. Optimal foraging theory describes how individuals refine behavior to most efficiently exploit available resources. For colonial breeding animals, such as seabirds, competition for limited resources is amplified by a high density of competitors at feeding grounds near the colony, which can lead to a diversification of foraging strategies that best exploit available resources. Laysan and black-footed albatrosses (*Phoebatria immutabilis and P. nigripes*, respectively) breed sympatrically and synchronously in dense colonies on small atolls throughout the northwestern Hawaiian Islands. While the distributions and habitat preferences of these congeners are well described, the variability in foraging strategies driven by niche partitioning is not. In chapter 1, I used fine-scale behavioral data from GPS data-loggers to tease apart subtle behavioral nice partitioning between and within Laysan and black-footed albatrosses constrained to poor-nutrient tropical waters during the most energetically-demanding reproductive stage in birds: the brood-guard. Albatrosses showed discrete behavioral partitioning both between and within species, which was driven by differences in nocturnal and diurnal foraging and by sex-specific strategies. Black-footed albatrosses exhibited greater variability in foraging patterns suggesting they may experience strong intraspecific competition at Tern Island. In chapter 2, I employed a novel adaptation of a biochemical diet analysis, quantitative fatty acid analyses, to investigate dietary niche partitioning across the breeding season. This analysis characterized diet of individual adult albatrosses across the breeding season, from incubation to the chick-brood, for the first time in these species.

Additionally, this research extended beyond diet characterization to quantify dietary dependence on fisheries-associated resources for these two species. One of the primary threats to albatross is the incidental mortality of birds from fisheries bycatch, therefore, understanding the incidence of fisheries-associated food in the diet of a breeding colony of albatrosses could have important conservation implications. While older birds tended to consume more squid than younger birds, we did not identify an age bias in birds that exploited fisheries resources. Parallel with results from the behavioral analysis in chapter 1, I found that black-footed albatrosses had greater dietary flexibility than Laysan albatrosses at a population level, and a greater degree of dietary specialization at the individual level. In the final chapter, I looked at how the obligatory act of flight feather molt impacted activity levels and space use across the post-breed migrations, when albatrosses are freed from central place foraging constraints, but limited by demands of self-maintenance. I found that activity levels, but not habitat use, were impacted by molt extent. Habitat use appeared to be primarily driven by consistent individual preferences, with birds showing a high degree of site fidelity to their post-breeding molting grounds. A clear decrease in home range size with age indicated that birds spend less time searching for profitable feeding grounds when they are older, likely a product of accumulated memory and experience in these long-lived species.

This research was approved by the animal care and use committee of the University of California Santa Cruz (UCSC) and by permits from the Papahānaumokuākea Marine National Monument (PMNM-2008-006, PMNM-2009-004, PMNM-2011-015) and Special Use Permits (SUPs) from the US Fish & Wildlife Service (USFWS).

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Reproduction of this manuscript as Chapter 1 falls under BioMed Central's that "Copyright on any open access article in a journal published by BioMed Central is retained by the author(s)". This work was original research by Melinda G. Conners, with contributions from co-authors as minor revisions of text or of statistical advice. Supplementary materials from this published material from Conners et al. (2015) were integrated into Chapter 1.

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*

Dedication

To those who have yet to fledge their nests: Mason, Wyatt, Hudson, Ollie-bean and Emma,
may you grow up into a world where albatross still scour the seas and squid haunt the depths

*

To my grandparents for weaving me into a fabric of joy, grace, and love

*

To my one and only mom and dad for always encouraging me to explore
where the wild things are

You can know the name of a bird in all the languages of the world, but when you're
finished, you'll know absolutely nothing whatsoever about the bird ….
So let's look at the bird and see what it's doing — that's what counts.
— Richard Feynman

Mad as the sea and wind, when both contend
Which is mightier…
— William Shakespeare, *Hamlet*, 1601

Introduction & Synthesis

Seabirds are, in a sense, amphibious. While they rely exclusively on the marine environment for feeding, they nest and raise their young on land. This habitat duality imposes two interacting challenges on breeding seabirds: 1) given limited suitable land for nesting sites, seabirds often breed in dense colonies and therefore face intense competition for food in waters near the breeding colony (Ashmole 1971, Birt et al. 1987); and 2) foraging ranges are limited by the need to return to the nest to feed and guard chicks, amplifying competition over limited resources (Orians and Pearson 1979, Costa 1991). Competition at breeding colonies can further intensify if similar species also breed in the same place at the same time, which is often the case, since land suitable for breeding is rare and/or remote, and because most species, especially those breeding in temperate latitudes, sync their breeding cycles with seasonal booms in ocean productivity (Ainley 1977, Schreiber and Burger 2001).

Populations respond to competition by adjusting where or when they forage, or what they feed on, resulting in the development of distinct species-specific niches over time (Gause 1934). Furthermore, when food becomes scarce due to high density of competitors from the same species, the population will begin to exploit less preferred prey, broadening its dietary niche; but while the population niche broadens, individuals begin to specialize on what they feed on, narrowing their niche relative to that of the population (Roughgarden 1972, Holbrook and Schmitt 1992, Tinker et al. 2008). Alternatively, rather than responding by dietary niche, populations can respond behaviorally by foraging at different times of day or in different areas or by ranging farther from the colony where preferred prey is more abundant (Lewis et al. 2001). When different behaviors and strategies diversify within a population due to competitive pressures, it can result in different consequences from these different strategies, with some individuals foraging less efficiently than others or foraging in riskier areas (e.g. greater overlap with human development). This can have serious conservation implications, especially if risk (and thus mortality) varies for different subsets of the population.

While research on interactions between competing species is very common in ecology, interactions are much more difficult to study in elusive pelagic animals like seabirds. Albatrosses are the largest and most pelagic of seabirds, commonly ranging across entire ocean basins in a single foraging trip (Tickell 2000). Consequently, it is difficult to observe their behavior at sea, particularly their interactions with other species. Furthermore, estimating the diet of Procelleriform seabirds, such as albatross, has proven difficult, in part due to their hyperacidic stomachs (Grémillet et al. 2012) that rapidly digest prey into energy-rich stomach oil (Imber 1976, Warham 1977). The quick conversation of prey into oil is thought to be an adaptation to “lighten the load” for these highly transitory pelagic birds. Thus, how albatrosses partition their exploitation of marine resources is not well understood.

Black-footed (*Phoebastra nigripes*) and Laysan (*P. immutabilis*) albatrosses are two of three Phoebastria species in the North Pacific. They predominately breed throughout the tropical atolls of the northwestern Hawaiian Islands, while the third species, the short-tailed albatross (*P. albatrus*) breeds on a few islands in higher latitudes. Despite a near extinction from human exploitation in the early 1900s (Tickell 2000), both Laysan and black-footed albatross populations have recovered, although they are both listed as Near Threatened on the IUCN Red List (IUCN 2014). With growing populations and dense breeding colonies, these two species are likely to compete with each other, especially during the chick-brood season when foraging grounds overlap in subtropical waters (Hyrenbach et al. 2002, Kappes et al. 2015). While morphologically and functionally very similar, these two species show different patterns in their reproductive success, with Laysan albatross success fluctuating to a much greater degree than that of black-footed albatrosses (Arata et al. 2009, Flint 2009). Understanding how this community of albatross partitions resources through behavior and diet will potentially provide insight into the differences in reproductive success between the two species.

When seabirds complete their breeding season, they are released from the constraints of competition and central place foraging imposed on them by the dynamics of breeding in dense colonies. However, the post-breeding season (June - November in *Phoebastria* albatross species) is a critical part of the annual cycle for seabirds, in which they must replace flight feathers through molting activity, a process which is considerably energetically demanding (Murphy 1996). The costly activity of molt and high concentrations of birds in so-called ‘molting grounds’ likely imposes their own sets of constraints and limitations onto post-breeding albatrosses. Distributions of birds during the molting months are much more localized than one would expect after being freed from constraints of central place foraging, likely as a consequence of reduced flight efficiency, causing birds to switch to more sedentary foraging tactics. Additionally, the summer months of the North Pacific follow a seasonal spring bloom of phytoplankton, so birds are likely tracking areas of concentrated prey abundance that follows the spring bloom. Phoebastria albatrosses have a unique strategy to negotiate the constraints of molt in the post-breed season; in any given year individuals can initiate one of four molt patterns, providing them with flexibility in the extent of their molt. Molt extent is likely to have a large impact on movement patterns and habitat use in the post-breeding season, potentially rendering some birds more vulnerable than others.

Ultimately, this thesis aims to understand the causes and consequences of variability in behavior, diet, and movement patterns across the breeding and post-breeding seasons for two morphometrically and functionally similar species of albatross. While ship-based studies are highly valuable in their ability to map species distributions (Shuntov 1974, Kuletz et al. 2014), only by using electronic data-logging technology, can we link individual characteristics, such as breeding colony, breeding history and age, to behavior, movement patterns and habitat use. This dissertation used a combination of miniaturized electronic data-loggers in combination with a novel biochemical analysis to gather information on the movements and diets of a community of albatrosses.

Thesis Summary

In CHAPTER ONE, I use fine-scale GPS data-loggers and a novel behavioral classification analysis to tease apart subtle behavioral niche partitioning both between and within two species of albatross during the breeding phase when the two species have the highest spatial overlap. This research identifies behavioral differences previously unseen from tracking work and also placed these differences in the context of environmental (moon and wind) and intrinsic (sex and body size) factors. Both species were highly active, foraging across day and night; however, Laysan albatrosses relied on foraging at night to a greater extent. For both species, foraging along direct flight paths and foraging while drifting in a “sit-and-wait” strategy were just as prevalent as foraging in a searching flight mode, indicating flexibility in foraging strategies in Hawaiian albatross. Both species strongly increased drift forage on the darkest nights, suggesting Hawaiian albatross feed on diel vertically-migrating prey to some extent. Black-footed albatrosses showed a greater behavioral variability within the population which suggests a higher level of intra-specific competition.

In CHAPTER TWO, I use an adaptation of quantitative fatty acid analysis (QFASA), where I incorporate fatty acids and fatty alcohols from two separate lipid classes, to estimate the diet of individual Laysan and black-footed albatrosses. My objectives are 1) to characterize and compare the diet of two North Pacific albatrosses species across the incubation and chick-brood phases of the breeding season when both species switch from foraging in high latitude temperate waters to warmer subtropical waters, 2) to assess the relative importance of fisheries-associated resources in Laysan and black-footed albatross diet and to test whether year, breeding phase, species, sex or age influence fisheries-associations, and 3) to identify feeding strategies of Laysan and black-footed albatrosses along the spectrum of dietary

generalism or specialism. I found that fisheries-associated diet did occur in both albatross species across both the incubation and chick-brood stages but neither species relied on fisheries food as the dominant food source. Some individuals, however, appeared to specialize on fisheries food. Mesopelagic gelatinous squid was most dominate food source of both species, and older birds showed heavier reliance on squid than younger birds. Overall, black-footed albatrosses had a broader population niche width and greater dietary flexibility than Laysan albatrosses, which is consistent with recent behavioral analyses.

In CHAPTER THREE, I investigate space use, measured by activity and habitat, of Laysan and black-footed albatrosses from Tern Island across the post-breeding migration, when activities related to self-maintenance are paramount and manifest in two discrete stages: flight feather replacement through molt and the regaining of body condition to prepare for the breeding season. Using a long-term tracking study (8 years of data), I investigate how intrinsic characteristics (molt extent, sex and age) impact the activity and habitat use of Laysan and black-footed albatrosses during the post-breeding season. Finally, I measure the degree of site fidelity across the breeding season with a focus on the molting months. I found that molt extent (as classified as ‘large’, ‘medium’, or ‘small’) did indeed impact activity level, but not habitat, with birds with largest molt extents having the most significant reduction in space use that began earlier in the post-breeding season than other birds. Molt extent did not impact habitat use, likely because albatrosses showed a large degree of site fidelity to their molting grounds between years. Age influenced home range size, with sizes decreasing with age, most likely reflecting that birds accumulate memory and experience over time, thereby reducing searching effort when pursuing suitable feeding grounds. While the productive passes of the Aleutian Island archipelago and the California Current upwelling region were important habitats for molting albatrosses, many albatrosses spent the molting months in pelagic areas of the Transition Zone Chlorophyll Front, suggesting offshore oceanic zones can also have productivity levels high enough to support birds that switch to a high residency behavioral pattern due to flight feather molt. Sex had a strong influence on the timing of departure and arrival times but only a minor influence on habitat. While environmental factors certainly influence behavior of albatross at multiple scales, I showed that the intrinsic factors of molt extent, sex and age play a large role in dictating the spatial patterns of post-breeding albatross and are important factors to consider when examining this critical phase of the annual cycle.

Synthesis of Ecological Implications

An overarching theme that emerged from this body of work is that the metrics calculated from black-footed albatrosses repeatedly had greater variability during the chick-brood season than those measured in Laysan albatrosses. Black-footed albatrosses had twice the number of behavioral foraging patterns and a broader dietary niche in the chick-brood than Laysan albatrosses. Although I only measured fine-scale behavior from the chick-brood season, an analysis of landing rates from wet/dry archival tags across the entire breeding season (Kappes et al. 2015) showed a notable increase in the variance of landing rates in black-footed albatrosses, but not Laysan albatrosses, during the chick-brood. This, with our results from the diet analysis, indicates that the collapse of range and high overlap of competing birds during the chick-brood causes black-footed albatrosses to diversify their feeding strategies, while Laysan albatrosses do not show as strong a response. Within Laysan albatrosses, a subset of individuals during the chick-brood ranged significantly farther from the colony than average, suggesting that this species responds to competition by increasing range rather than by diversifying feeding strategy. Both diversification of strategies and range expansion align with theoretical and experimental theory describing population responses to intra-specific competition (Sokolowski et al. 1997, Svanbäck and Bolnick 2007, Araújo et al. 2008), however, our research cannot conclude that these responses are a direct response to competition. Brooding albatrosses forage in much different oceanic habitats than incubating or chick-rearing birds (Suryan et al. 2006, Kappes et al. 2015), and therefore, the behavioral and dietary responses seen in the chick-brood, might be a simple reflection of a different composition and availability of prey.

Less flexibility in behavior and diet within the Laysan albatross population agrees with recent findings of Thorne et al. 2015 who linked a weaker response of Laysan albatrosses to years of “poor” environmental conditions with reduced reproductive success, highlighting potential demographic consequences of behavioral plasticity between the species. The greater adaptability of black-footed albatrosses both across the breeding season, and inter-annually, indicates this species may be more resilient to changing climate than Laysan albatrosses, despite having much smaller population sizes (due to mortality from longline bycatch (Cousins et al. 2000, Lewison and Crowder 2003, Véran et al. 2007)). Despite greater flexibility in black-footed albatrosses, this thesis showed that both species rely heavily on squid (~ 50-60 % of diet for each species across the breeding season) whose distributions are predicted to shift north with the changing climate (Alabia et al. 2015). While breeding albatrosses might be able to track these shifting distributions during the less constrained incubation and chick-rear phases, the poleward shift of squid distributions could have negative consequences on brooding albatrosses given their highly constrained foraging ranges, ultimately impacting reproductive success. Reduced access to squid during the chick-brood season might also force birds to supplement their diet with more unnatural sources of food, such as fisheries-associated resources. So, while results from this thesis found incidence, but not dominance, of fisheries-associated food in the diet of these two species (~ 10 % of the diet of both species), we emphasize the importance of monitoring diet, including fisheries reliance, over time, because as the climate continues to change, squid distributions are predicted to shift, potentially having a large impact on optimal foraging strategies of breeding North Pacific albatrosses.

Finally, this thesis highlights intrinsic factors, such as sex, age and molt extent, as important factors driving measureable differences in albatross foraging and movement patterns. Older birds of both species ate more squid than younger birds, potentially using prior experience and memory of squid spawning cycles to better exploit this resource. Older birds additionally had smaller home ranges than younger birds in the post-breeding season, which suggests that they spent less time searching for profitable feeding grounds. Albatross, as long-lived *K*-selected species, are likely to use experience and memory in the development of optimal foraging strategies. That we found a high degree of site fidelity to post-breeding molting grounds further supports memory and experience as important factors shaping the behavior of Laysan and black-footed albatrosses. Finally, this work highlights the post-breeding season as an energetically-demanding phase in the annual cycle, critical for self-maintenance, where molt extent has strong impact on activity levels of birds.

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CHAPTER ONE

Shadowed by scale: subtle behavioral niche partitioning in two sympatric, tropical breeding albatross species

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ABSTRACT

To meet the minimum energetic requirements needed to support parents and their provisioned offspring, the timing of breeding in birds typically coincides with periods of high food abundance. Seasonality and synchrony of the reproductive cycle is especially important for marine species that breed in high latitudes with seasonal booms in ocean productivity. Laysan and black-footed albatrosses breeding in the northwestern Hawaiian Islands have a dual reliance on both seasonally productive waters of high latitudes and on nutrient-poor waters of low latitudes, because their foraging ranges contract during the short but critical brood-guard stage. Therefore, these species face an additional constraint of having to negotiate nutrient-poor waters during the most energetically-demanding stage of the breeding cycle. This constriction of foraging range likely results in a higher density of foraging competitors. Thus, our aim was to understand how Hawaiian albatross partition resources both between and within species in this highly constrained breeding stage while foraging in less productive waters and simultaneously experiencing increased competition. High-precision GPS dataloggers were deployed on black-footed (*Phoebastria nigripes*, n=20) and Laysan (*Phoebastria immutabilis*, n=18) albatrosses during the brood-guard stage of the breeding season in 2006 (n=8), 2009 (n=13), 2010 (n=16) and 2012 (n=1). We used GPS data and movement analyses to identify six different behavioral states in foraging albatrosses that we then used to characterize foraging trips across individuals and species. We examined whether variations in behavior were correlated with both intrinsic factors (sex, body size, body condition) and extrinsic factors (lunar phase, wind speed, year). Behavioral partitioning was revealed both between and within species in Hawaiian albatrosses. Both species were highly active during chick-brooding trips and foraged across day and night; however, Laysan albatrosses relied on foraging at night to a greater extent than black-footed albatrosses and exhibited different foraging patterns at night. For both species, foraging along direct flight paths and foraging on the water in a “sit-and-wait” strategy were just as prevalent as foraging

in a searching flight mode, indicating flexibility in foraging strategies in Hawaiian albatross. Both species strongly increased drift forage at night when the lunar phase was the darkest, suggesting Hawaiian albatross feed on diel vertically-migrating prey to some extent. Black-footed albatrosses showed a greater variation in foraging behavior between individuals which suggests a higher level of intra-specific competition. This behavioral variability in black-footed albatrosses was not correlated with sex or body size, but differences in body condition suggested varying efficiencies among foraging patterns. Behavioral variability in Laysan albatrosses was correlated with sex, such that females exhibited greater flight foraging than drift foraging, had longer trip durations and flew farther distances from the breeding colony, but with no difference in body condition. Fine-scale movement data and an analysis of multiple behavioral states identified behavioral mechanisms that facilitate coexistence within a community of albatross during a critical life-history period when energetic demands are high, resources are limited, and competition for food is greatest.

1.1 BACKGROUND

Reproductive strategies in birds arise from a complex interaction among phylogenetic and morphological constraints and environmental conditions (Lack 1968, Martin 1987, Stearns 1992, Owens and Bennett 1995). Seabirds compared to other taxa, have low annual fecundity and older minimum breeding ages, accruing reproductive output over long lifespans (Ricklefs 1990, Weimerskirch 2001). Moreover, seabirds foraging in pelagic waters rely on efficient flight and tend to have the lowest fecundities and highest rates of adult survival (Weimerskirch 2001). These species are more likely to defer breeding if the cost of reproduction reduces adult survival beyond a critical threshold (Chastel et al. 1995, Crossin et al. 2013). To meet the minimum energetic requirements to support both parents and their offspring, breeding typically coincides with periods of high food abundance (Lack 1968, Perrins 1970, Le Corre 2001). Seasonality and synchrony of the reproductive cycle is especially important in seabirds that breed in temperate and polar regions where mesoscale features enhance ocean productivity and are predictable but occur in narrow temporal windows (e.g., seasonal coastal upwelling, ice-edge blooms) (Ashmole 1971, Ainley 1977, Nelson 1983, Bertram et al. 2001). In contrast, seabirds breeding in tropical and subtropical regions rely on less abundant, patchier resources (Ainley 1977, Seki and Polovina 2001), and associate with sub-mesoscale features such as eddies and filaments (Haney 1986a, 1986b, Tew Kai et al. 2009). Here, productivity peaks with less magnitude than in higher latitudes, and is episodic rather than confined to a single defined season (Ashmole 1971). Consequently, breeding of tropical seabirds, in general, shows weaker synchrony than their temperate counterparts (Harris 1969, Harrison 1990), is often protracted, and can occur throughout the year (Schreiber and Ashmole 1970).

Black-footed (*Phoebastria nigripes)* and Laysan (*P. immutibilis)* albatrosses that breed sympatrically and synchronously in dense colonies distributed throughout the northwestern Hawaiian islands are atypical for albatrosses in their reliance on tropical feeding grounds (sea-surface temperatures ≥ 25º C, Ballance and Pitman 1999) during the brood-guard reproductive stage (Hyrenbach et al. 2002, Kappes 2009), when chicks are too small to self-thermoregulate and are continually attended by at least one parent. The majority of albatross species breed in high latitudes in the southern hemisphere and match the brood-guard stage with seasonal highs in primary production in temperate or sub-polar waters (Tickell 2000). Hawaiian albatrosses exploit cooler and more productive waters associated with high latitudes during the longer foraging trips of the incubation and post-guard reproductive stages when they can range farther from the nest. However, they are limited to warm, tropical waters near the breeding colony while caring for small vulnerable chicks that require frequent feedings (Hyrenbach et al. 2002, Kappes 2009). The brood-guard is the most energetically demanding breeding stage in birds (Drent and Daan 1980, Ricklefs 1983), and it is common for adult albatrosses to lose body mass during this period (Weimerskirch and Lys 2000, Kappes 2009). It is therefore notable that Hawaiian-breeding albatrosses can rely on such suboptimal feeding grounds during this particularly constrained life history stage. The limited spatial extent of foraging grounds during the brood-guard increases the potential for competitive interactions within and among species (Ashmole 1963, Birt et al. 1987, Schreiber and Burger 2001). For most of the year, black-footed and Laysan albatrosses clearly segregate at sea with distinct habitat preferences (Fernández et al. 2001, Fischer et al. 2009, Kappes et al. 2010, Gutowsky et al. 2014), but during the brood-guard stage this spatial segregation breaks down and focal ranges (defined as the highest 50% utilization distribution) of the two species overlap by 75.4% (Kappes 2009) (Figure 1.1 GPS locations of incubating and chick-brooding Laysan (n=114) and black-footed (n=118) albatross breeding at Tern Island.). The radiation of foraging strategies among sympatrically-breeding seabirds to minimize competition and maximize resource allocation is well documented with species delineating strategies by time (e.g., Zavalaga et al. 2011), space (e.g.,Ballance et al. 1997), and morphology (e.g., González-Solís et al. 2000); however, how black-footed and Laysan albatrosses partition resources during the short but critical brood-guard stage remains unclear.

The original characterization of niche partitioning between these species — that Laysan albatrosses are nocturnal foragers of vertically-migrating squid while black-footed albatross are predominantly diurnal scavengers of fish roe and carcasses (Harrison et al. 1983) — was based on two lines of evidence: 1) Laysan albatrosses have relatively high levels of rhodopsin, a light-sensitive pigment typically found in high levels among nocturnal birds (*unpublished data,* Sillman 1981, Harrison et al. 1983), and 2) Laysan albatrosses have a larger component of squid in their diet than black-footed albatrosses who have greater proportions of fish eggs and carrion (Harrison et al. 1983). But more recent diet and tracking studies do not support nocturnal foraging in Laysan albatrosses and conclude that *both* species likely have daytime biased foraging (Fernández and Anderson 2000, Pitman et al. 2004, Walker et al. 2012). Additionally, activity budgets (based on data from wet-dry loggers) between the two species were found to be the most similar during the brood-guard (Kappes 2009), further complicating our understanding of how these albatross species partition resources in tropical waters. However, niche separation between species can be obvious, but it can also be quite subtle, like McArthur’s classic observation of congeneric warblers that forage simultaneously on insects in the same trees but at distinct heights and on different diameter branches (MacArthur 1958). Such subtlety can limit our understanding of niche partitioning among difficult to observe animals, such as wide-ranging pelagic marine species like albatross.

Niche partitioning within a species may also be important for central place foragers as it provides an additional mechanism for reducing competition (Araújo et al. 2007, Villegas-Amtmann et al. 2008, Masello et al. 2010). Often, within species variability of foraging strategies is linked to distinct intrinsic characteristics such as sex, body size, and age (Polis 1984, Shaffer et al. 2001, Jeglinski et al. 2013), but has even been correlated with personality (Patrick and Weimerskirch 2014a); this variability is important to understand as it can affect fitness (Watanuki 1992, Votier et al. 2004, Patrick and Weimerskirch 2014a, 2014b) and, therefore, population demographics. Within species niche partitioning is frequently more pronounced as the density of conspecifics increases, often as a result of short-term behavioral plasticity in foraging strategies (Svanbäck and Bolnick 2007, Tinker et al. 2008). Consequently, quantifying the level of individual variability both within populations and among closely related species can illustrate the degree of competitive stressors (Araújo et al. 2011).

Here, we propose that, given the reduction of spatial extent during the brood-guard, behavioral niche partitioning within and between species is likely occurring at finer scales than would be observable from the resolution of geolocation or Argos data used in previous studies. We used GPS data with greater precision in spatial (<10 m error in >95% locations) and temporal (1 fix 10 s^{-1}) scales to identify six different behavioral states along albatross foraging trips to: (1) investigate behavioral partitioning between black-footed and Laysan albatrosses during the brood-guard, particularly focusing on diurnal/nocturnal differences and the influence of the lunar cycle; (2) assess and quantify the amount of within species partitioning of foraging patterns; and (3) identify intrinsic drivers (body size, sex) and potential consequences (measured by body condition) of those patterns. Our ultimate objective was to understand the behavioral mechanisms facilitating coexistence within a community of albatross during a critical life-history stage when energetic demands are high, resources are limited, and competition for food is great.

1.2 METHODS

1.2.1 Study species and study location

Black-footed and Laysan albatrosses are highly migratory and pelagic surface feeders thought to depend primarily upon visual and olfactory cues to find prey at the ocean surface (Nevitt et al. 2008). They are the smaller-bodied of the three Phoebastria species breeding in the North Pacific, a trait thought to be related to the relatively lighter winds encountered in the lower latitudes of the central North Pacific during the breeding season (Suryan et al. 2008). Their populations primarily breed in the low-lying atolls of the northwestern Hawaiian Islands and, unlike albatrosses of the southern hemisphere, they time breeding with the winter season. Males and females are slightly sexually dimorphic, with males being marginally larger and heavier than females, but there is overlap in all of these morphometric measurements (Tickell 2000, this study). Single egg clutches are laid in November and December, chicks hatch in January and February, and chicks are guarded and fed frequently by adults into March. The post-guard period, when adults extend the range and duration of foraging trips and chicks are fed infrequent meals, extends into summer until chicks fledge (July-August).

The study colony at Tern Island in the French Frigate Shoals (23.870°N, 166.284°W, 712 km northwest of Kauai) supports ~4000 breeding pairs of black-footed albatrosses and ~3000 of Laysan albatrosses and is the only colony in the northwestern Hawaiian islands where the density of black-footed albatrosses is greater than that of Laysan albatrosses (Flint 2009). Although populations of both species have partially recovered since their decimation from the feather and egg trade in the early 1900s (Tickell 2000), they are listed as near-threatened species on the IUCN red list, and population stability for black-footed albatrosses is vulnerable to adult mortality from fisheries bycatch (Lewison and Crowder 2003, Véran et al. 2007, IUCN 2014).

1.2.2 Tracking methods

To collect fine-scale behavioral data on foraging albatrosses during the brood-guard season, we deployed GPS dataloggers on 18 Laysan and 20 black-footed albatrosses in February and March (2006: (n=8), 2009: (n=13), 2010: (n=16), 2012: (n=1)) at Tern Island. GPS dataloggers weighed either 35 g (iGot-U GT- 120, Mobile Action Technology Inc.) or 30 g (Technosmart GiPSY-2 logger). Tags recorded positions with a temporal resolution of 1 fix every 10 s to provide fine-scale foraging behavioral data without behavioral “noise” of fine-scale flight adjustments to the wind that are recorded with smaller sampling rates (Fritz et al. 2003). GPS dataloggers were housed in unlubricated condoms and polyethylene pouches and attached to 3-5 dorsal contour feathers using TESA cloth tape. For a subset of birds of each species, 3.6 g Lotek geolocators (LAT2500) were attached to the plastic auxiliary leg band with cable ties and epoxy for concurrent research (these data were not used in this study). Total tag weight represented 1.2-1.6% the weight of the bird, depending on species and datalogger combination; this range of percentages is well below the suggested maximum tag weight of 3% recommended for gliding seabirds such as petrels and albatrosses (Phillips et al. 2003, Vandenabeele et al. 2011).

1.2.3 Individual characteristics

To assess intrinsic factors as potential drivers of different foraging strategies, we created a body size index for each bird from morphometrics. Lengths of the culmen, tarsus, and minimum and maximum bill height were measured to ± 0.5 mm using vernier calipers. *Body Size and Body Condition:* For each species, we ran a principal components analysis (PCA) on standardized lengths of bill measurements and extracted single factor scores to construct a composite body-size index for each albatross (Shaffer et al. 2001). Tarsus was not included in the body-size PCA because measurements from 2006 were consistently smaller than those from other years, likely due to measurement bias of data recording personnel. Consequently the body size index includes only bill size, but provides an accurate score of size because bill size often correlates with body size. To increase the power of the PCA, we ran the analysis on a larger sample size of birds, from both species, by including morphometrics of birds from a concurrent study (Laysan, n = 163; black-footed, n = 167). Body mass was measured to ± 50 g on tag deployment and recovery using a spring-loaded Pesola scale. Subsequently, general body condition was calculated as an individual's residual distance from the regression of body mass at deployment against body size index (Shaffer et al. 2001). *Sex Determination:* Sex was recorded from either 1) a visual comparison when a pair was seen together attending the nest and size differences were observable, 2) predicted from a discriminant function analysis on morphometrics or 3) from DNA molecular identification (Shaffer et al. 2001). The sex of all birds from 2006 was identified with molecular DNA, so we included tarsus lengths along with both bill measurements when calculating the discriminant function. To increase prediction power, our discriminant function was calculated from measurements of birds of known sex (either molecular or visual confirmation) from this study as well as a concurrent study (black-footed, n = 43, Laysan, n = 35). Maximum bill depth, and culmen and tarsus lengths correctly assigned the sex of black-footed albatrosses 91% of the time using the following regression: 7.475 maximum bill depth + 1.197 tarsus + 0.832 culmen, and 94% of the time for Laysan albatrosses using: 2.174 culmen + 5.362 maximum bill depth + 0.697 tarsus, giving us a sample size of 12 male and 8 female black-footed and 12 male and 6 female Laysan albatrosses for further analyses.

1.2.4 Track analysis

All track and behavioral analyses were conducted in Matlab (2013a, The MathWorks, Inc.) with custom-built functions unless otherwise specified. High precision and accuracy (<10 m spatial error in >95% locations) of GPS dataloggers necessitated only minimal pre-processing of tracks. A simple speed filter removed locations from raw GPS data with speeds greater than 100 km hr^{-1} (< 0.1 % data removed); additionally, locations less than five kilometers from the breeding colony were excluded, and only a single foraging trip per bird chosen at random was included in the analysis. For a basic description of foraging trips, we calculated percent trip on water, maximum range (as defined as farthest distance (km) reached from colony), trip duration (days) and total distance traveled (km). To characterize movement behavior along a trip, we calculated the following parameters: flight speed (km/hr), turning angle (°), drift sinuosity, and landing rate (landings/hr). Birds were considered “on water” when speeds of three consecutive locations were below 6 km hr^{-1}. The high sampling rate of our GPS dataloggers allowed us to identify this cutoff speed, apparent in a bimodal distribution of speeds (Figure 1.2).

1.2.5 Foraging behavior

Area-restricted search (ARS) is often used to identify foraging behavior from animal tracking data, with the logic that foraging individuals are likely to spend more time and have more sinuous paths in profitable and predictable areas (Kareiva and Odell 1987, Fauchald and Tveraa 2003). However, albatrosses use a suite of foraging tactics, including area-restricted search, foraging along a direct (transiting) flight path and foraging while drifting at the surface of the water using a “sit-and-wait” strategy (Harper and PC 1987, Catry et al. 2004, Weimerskirch et al. 2007). To identify multiple foraging behaviors, we first calculated three behavioral metrics (residence time (ARS), landing density, and drift sinuosity) then incorporated all three metrics into a custom behavioral state classification routine outlined below.

1.2.5.1 Behavioral metrics

Residence time: To identify areas of high search intensity (ARS), we calculated residence time values at every location along a track using the Pascal program (translated to Matlab) provided in Barraquand and Benhamou 2008. Residence time is a scale-dependent metric that imposes a virtual circle with a user-defined radius over each consecutive location and sums the time spent along all track segments within the circle, both forward and backward (Barraquand and Benhamou 2008). To avoid overinflating residence times in locations where birds were drifting on the water, drift segments greater than two minutes were re-discretized as if the birds were flying at a constant speed (50 km hr^{-1}) (see Weimerskirch et al. 2007). The selection of the radius of the virtual circle in residence time analysis defines the spatial scale of identified ARS, and therefore the radius requires justification. We selected a 10 km radius (20 km circle), because we were interested in small-scale flight searching behavior, the scale in which albatrosses would be reacting to prey through vision or scent (Nevitt et al. 2008), rather than large-scale reactions of birds to environmental features, as behavior at that scale has been identified previously in these species (Kappes et al. 2010). Trips were temporally re-discretized with a constant interval of 10 sec. The number of steps allowed outside the virtual circle was set at 720 steps (equivalent to two hours). Finally, a Hampel filter detected and replaced local outliers along the residence time series with appropriate local values (Pearson 2005).

Landing density: Within the virtual circles (r = 10 km) calculated at each consecutive location for residence time, we additionally calculated the number of landings for all track segments that fell within the circle, both forward and backward. This approach allowed us to calculate foraging effort at the same spatial scale as flight search intensity, allowing us to decipher active versus non-active flight modes.

Drift sinuosity: To identify active drifts, indicating “sit-and-wait” foraging, drifting bouts were defined as locations where the bird was sitting on the water (speeds < 6 km hr^{-1}) for a minimum of ten minutes (see Weimerskirch et al. 2007). Drifts that were separated by less than three consecutive fixes (i.e. 30 sec) were combined as a single drift to avoid the artificial discretization of drifts due to short spikes of speeds above 6 km/hr. We then calculated the track sinuosity of each drift as the ratio of the straight-line distance from the beginning to end of the drift and the summed distance between all consecutive locations in the drift. Sinuosity values ranged from zero, representing a completely tortuous path, to one, a perfect line. To ensure that drift sinuosity reflected albatross behavior, we tested if sinuosity was simply a reflection of wind-induced roughness of the sea-surface (wind chop), or of fine-scale looping currents induced by near-inertial oscillations. A linear mixed model regression of wind speed on drift sinuosity with species included as a fixed cofactor and individual bird as a random effect indicated no relationship between wind and drift sinuosity for either species (Figure 1.3). Inertial currents are fine-scale looping surface currents with a strictly anti-cyclonic flow (clockwise in northern hemisphere) (Bograd et al. 1997). However, the directions of arcs in albatross drifts were both clockwise and counter-clockwise. Additionally, the loop radius of inertial currents is on average much larger (>10^{3} m, Chaigneau et al. 2008) than loops in drifts of albatrosses (<10^{1} m).

1.2.5.2 Behavioral state classification:

Each location along a trip was assigned one of six behavioral states using residence time, landing density, and drift sinuosity (Figure 1.5). An individual was assigned to one of two flight behaviors: ‘Transit’ or ‘ARS’, identified by either low or high residence times, respectively. A high landing density at that location indicated that the individual was in a foraging mode of that flight behavior (Figure 1.5, ‘Transit Forage’ or ‘ARS Forage’), since albatross are required to land on the surface of the ocean to forage, and likely limit their landings to foraging activity given the high energetic cost of take-offs and landings (Weimerskirch et al. 2000). Thresholds classifying residence time and landing density values as ‘High’ or ‘Low’ were unique to each individual, with ‘High’ defined as values greater than the 60th percentile of an individual’s distribution of residence times and greater than the 60th percentile of an individual’s distribution of landing densities. Percentile-based threshold values were selected to reflect biological and behavioral relevance based on a visual inspection of different threshold scenarios on a subset of tracks from both species. Drifts were classified as either passive drifts (low sinuosity) where the bird was resting, or active foraging drifts (high sinuosity), indicating “sit-and-wait” behavior (Figure 1.5, ‘Drift Forage’) (see Weimerskirch et al. 2007; Zavalaga et al. 2011). The threshold value for drift sinuosity was fixed at 0.65 for all individuals of both species, identified as the local minima of a bimodal distribution of drift sinuosity values for both species.

1.2.6 Environmental data:

We classified locations as day, night, or nautical twilight using local sun zeniths extracted at each position along a foraging trip in Matlab (‘sun_position.m’). Moonrise and moonset along each trip were identified by extracting moon elevation above the horizon at each location (‘LunarAzEl.m’). Moon phase was defined as the proportion of lunar disc illuminated obtained from the U.S. Naval Observatory. Three day composites of ocean surface wind speeds derived from the quikSCAT (2006, 2009 data) and ASCAT (2010, 2012 data) scatterometer observations were extracted along tracks using the Thematic Real-time Environmental Distributed Data Services within NOAA’s Environmental Research Division.

1.2.7 Statistical analyses:

Except where noted, all statistical analyses were run using the ‘nlme’ (Pinheiro et al. 2015), ‘mgcv’ (Wood 2011), ‘multcomp’ (Hothorn et al. 2008), and ’pvclust’ (Suzuki and Shimodaira 2006) packages in R 3.1.1 (R Core development Team, 2014). When necessary, variance structures were included in regression models to account for heterogeneity in residuals using the ‘varComb’ and ‘varIdent’ functions in the ‘nlme’ package. Significance was defined as $P \leq 0.05$ and marginal significance as $P \leq 0.10$. Permutational MANOVA and simper analyses (Clarke 1993) were run in PRIMER statistical software.

1.2.7.1 Movement parameters and general track characteristics

Linear mixed effect models tested differences in movement parameters (flight speeds and turning angles, landing rates, drift durations, drift sinuosities and percent of trip in flight). Species, astronomical state (day, night or twilight), and their interaction were fixed effects and individual birds were used as random factors. The fixed effects of sex and year were found insignificant and not included in final models. Landing rate and turn angle distributions were log transformed and percent trip in flight was arcsin transformed to meet assumptions of normality. Posthoc multiple comparisons using Tukey contrasts identified diurnal differences both between and within species. General track characteristics (total trip distance, maximum distance reached, mean daily distance traveled and trip duration) were compared using general linear models with species, sex and year as fixed effects. Maximum distance was square root transformed before analysis.

1.2.7.2 Behavioral state species comparison

Multiple permutational MANOVA analyses tested for differences in behavioral composition of trip (% trip in each behavioral state) between species. Species differences were tested for both overall trip behavioral composition as well as behavioral composition of day and of night portions of trip. The resemblance matrix was calculated using Euclidean distance, an unrestricted permutation method, and Type III (partial) sums of squares. Then, a similarity percentage analysis (simper, Clarke 1993)) identified the relative contribution of behavioral states to the dissimilarity between species.

1.2.7.3 Effect of lunar phase on behavioral state

To understand how albatross foraging behavior responded to lunar phase, we ran a series of generalized additive mixed models. Each behavioral state was examined separately and modeled as a binomial dependent variable. Lunar phase, as an explanatory variable, was included in the model using a cyclical smoothing spline and nested under astronomical state to isolate the smoother at night, when behavior would be potentially affected by the moon. To account for the contribution of individual variability to the error term, individual bird was included as a random effect. A first order autoregressive correlation structure was incorporated to account for temporal autocorrelation.

1.2.7.4 Identifying and characterizing foraging patterns within species

Within each species, a hierarchical clustering analysis grouped individuals into discrete foraging patterns based on the duration of the trip (%) in each of the six behavioral states (‘pvclust’, following Louzao et al. 2014). This method identifies significant clusters by calculating approximately unbiased (AU) p-values using multiscale bootstrap resampling. We used Euclidean distance and the Ward agglomeration method to identify significant clusters at the $P \geq 0.95$ level, but then applied the 50% similarity level to define population-level foraging patterns (see Louzao et al. 2014). Once birds were clustered into overall foraging patterns, we further characterized strategies by comparing additional behavioral parameters and track characteristics between clusters. Behavioral parameters included the proportions of day and night the birds were in the foraging mode of each behavioral state (‘% Day in Transit Forage’, ‘% Night in Transit Forage’, etc.) and day and night landing rates (landings hr^{-1}), while track characteristics included mean daily distance traveled (km day^{-1}), total cumulative distance traveled (km), maximum range (km), and total trip duration (days). Means of behavioral parameters and track characteristics were compared between clusters using linear models. Tukey contrasts identified significantly different clusters.

1.2.7.5 Foraging patterns compared with environmental conditions

To test whether foraging strategies reflected intrinsic behavioral differences, rather than responses to extrinsic environmental conditions, we compared year, wind strength and lunar phase among population-level clusters (for each species). Years were compared among clusters using chi-squared tests. To compare average wind regimes experienced by birds across clusters, winds were extracted at each location along a track (subsampled to 1 fix every 5 min^{-1}) and then a mean was calculated for each bird. Mean winds and mean lunar phase experienced by birds were compared between clusters with ANOVAs and a post hoc Tukey test if clusters were significantly different. Lunar phase was square-root transformed to meet assumptions of normality.

1.2.7.6 Foraging patterns and intrinsic factors

To explore potential drivers of foraging strategies we examined sex, body size, and body condition among birds of different clusters. A chi-squared test tested for sex differences while generalized least squares models tested for differences among clusters in body size and body condition indices.

1.3 RESULTS:

Black-footed and Laysan albatrosses predominantly foraged north and northeast of Tern Island in pelagic waters, with a subset of birds from each species (n=6 (30%) black-footed; n=5 (28%) Laysan) visiting the sharp bathymetric slope of the northwestern Hawaiian island seamount chain (Figure 1.4). Additionally, individuals from both species (n=2 (10%) black-footed, n=8 (44%) Laysan) visited deeper seamounts in pelagic waters along their trips both north and south of the breeding colony. Laysan albatrosses ranged farther north than black-footed albatrosses (Figure 1.4, Table 1.2) however this was predominately driven by a small subset of individuals that ranged much farther than the mean population.

1.3.1 Individual characteristics:

As expected, black-footed albatrosses were slightly heavier in mass than Laysan albatrosses, and within each species, females weighed less than males (Table 1.1). Despite their larger mass and overall size, black-footed albatrosses had shorter culmen lengths but thicker bill depth than Laysan albatrosses (Table 1.1). Culmen length versus bill depth showed a distinct clustering between species and between sexes (Figure 1.6). Black-footed albatross had a shorter range of body size indices, ranging from -2.57 to 1.68, compared to -1.87 to 3.61 for Laysan albatrosses. Black-footed albatrosses had greater overlap in bill morphometrics between the sexes than Laysan albatrosses (Figure 1.6). Body size accounted for 20% of the variation in black-footed albatross adult body mass ($F_{1,166} = 42.6$, $P < 0.001$) and only 6.2% of the variation in adult Laysan albatross body mass ($F_{1,161} = 11.2$, $P < 0.001$).

1.3.2 Species and diurnal differences in movement parameters:

Movement parameters did not differ between species until examined separately between day and night, with the exception of drift duration and landing rates (Table 1.3, Table 1.4). Both species spent a similar proportion of total trip in flight, but while time in flight was similar across day and night for black-footed albatross, Laysan albatross spent less of the night in flight. Mean drift duration was overall longer in black-footed albatross than Laysan, and while both species had shorter drifts during the day, this diurnal/nocturnal discrepancy was more pronounced in Laysan albatrosses. There was no difference in mean drift sinuosity between species, and no diurnal differences of mean drift sinuosity within species. Mean landing rates of overall trips were almost identical between the species, but Laysan albatrosses had significantly higher landing rates at night than black-footed. There were no significant differences in overall flight speeds or flight angles between the species and both species decreased speeds and increased turn angles at night.

1.3.3 Species differences in general track characteristics*:*

All general track characteristics differed between the species (Table 1.2). Means of daily distance traveled, maximum distance reached, trip duration, and total distance traveled were all greater in Laysan albatrosses (Table 1.2). Additionally, compared to males, female Laysan albatrosses reached significantly greater maximum distances (female = 767.1 ± 352.4 km, male = 363.3 ± 281.2 km, Table 1.2) and had significantly longer trip durations (female = 2.4 ± 0.2 days, male = 1.9 ± 0.6 days, Table 1.2). In contrast, there were no differences between sexes in black-footed albatross (Table 1.2).

1.3.4 **Behavioral states – diurnal and species differences**

The overall behavioral state composition of trips (percent of trip in each behavioral state) between species was not different (t = 0.19, P = 0.91) with both species spending the largest proportion of trip duration in ‘Transit’, followed by ‘ARS’ and then ‘Drift’ (Table 1.5). However, when separated into day and night, the behavioral composition of trips varied significantly different between species (day: t = 3.47, P = 0.03 and night: t = 2.18, P = 0.07). Simper analyses identified which behaviors contributed the most to species dissimilarity (Figure 1.7). Percent of trip in ‘Transit Non-Forage’ behavior was the largest contributor to species dissimilarity, contributing 35.6% in day segments and 32.4% in night, followed by ‘Drift Forage’ (day: 18.3%, night: 25.7%), ‘Drift Non-Forage’ (day:10.4%, night: 21.9%) and ‘Transit Forage’ (day: 20.5%, night: 4.3%). Both ‘ARS Forage’ and ‘ARS Non-Forage’ contributed <10% to species dissimilarity, both day and night. All three foraging states (Transit Forage, ARS Forage, and Drift Forage) were greater contributors to species dissimilarity at night in Laysan albatrosses and in day in black-footed albatrosses (Figure 1.7). On average, both species were in an active foraging mode for almost half their foraging trips (Table 1.5, 46.4 ±

11.2%, 44.6 ± 17.6% for black-footed and Laysan, respectively), however total foraging activity was partitioned between day and night differently for each species (Table 1.5, 55.8 ± 21.6% of day and 36.6 ± 21.5% of night for black-footed albatrosses and 44.6.6 ± 17.6% of day and 49.3 ± 19.6% of night for Laysan albatrosses.

1.3.5 Relationship between lunar phase and behavioral states of albatrosses

Behavioral states associated with drifting on the water had the greatest response to lunar phase for both species. Black-footed and Laysan albatrosses both increased 'Drift Forage' behavior on the darkest nights (Figure 1.8, black-footed: F = 7.30, P < 0.001; Laysan: F = 7.48, P < 0.001). Both species also increased 'Drift Non-Forage' behavior on the darkest nights. However, this was a weak response in Laysan albatrosses (Figure 1.8, F = 1.17, P = 0.06), and black-footed albatrosses also increased 'Drift Non-Forage' on the brightest nights (Figure 1.8, F = 5.12, P < 0.001). 'Transit Non-Forage' behavior increased with the moon phase for both black-footed and Laysan albatrosses (Figure 1.8, F = 2.99, P = 0.002 and F = 2.49, P = 0.007, respectively). None of the other flight modes were significantly affected by moon phase, although black-footed albatrosses showed a weak increase in 'ARS Non-Forage' during the full moon (Figure 1.8, F = 0.96, P = 0.07).

1.3.6 Within species foraging patterns

The '*pvclust*' hierarchical clustering algorithm identified three times as many behavioral clusters in black-footed (six clusters) than Laysan albatrosses (two clusters) at the P > 0.95 significance level (indicated by red vertical lines, Figure 1.9). Defining population-level foraging patterns at the 50% similarity level resulted in three behavioral clusters in black-footed and two in Laysan albatrosses (dark grey shaded boxes, Figure 1.9) which we used in subsequent analyses.

1.3.7 Foraging patterns of black-footed albatrosses

Cluster 1 – BF1 (Figure 1.9, Table 1.6): Individuals from Cluster 1 (BF1) spent the majority of their foraging trips in flight. Of all black-footed albatrosses, birds in BF1 allocated the most foraging time to the 'Transit Forage' behavioral state, which predominantly occurred during the day; although compared to birds from BF2 and BF3, they also spent the largest proportion of the night in this foraging mode. Birds from BF1 also spent the largest proportion of night in 'Transit Non-Forage'. This cluster had the highest percent trip in both the 'ARS Non-Forage' and 'ARS Forage' behavioral states. Most of 'ARS Non-Forage' behavior occurred during the night while 'ARS Forage' was allocated equally between day and night. Birds from BF1 spent very little of their foraging trips drifting on the surface of the water, and both the 'Drift Non-Forage' and Drift Forage' behavioral states occurred during the day more than at night. Correspondingly, these birds had the lowest landing rates, both day and night, and had the highest values for all trip distance and duration metrics. Overall, these birds spent more time foraging during the day than at night, and in flight forage mode, rather than drift.

Cluster 2 – BF2 (Figure 1.9, Table 1.6): Individuals from Cluster 2 (BF2) spent the majority of their foraging trips in on the water. These birds had the lowest allocation of time to either flight foraging mode, and predominantly foraged in the 'Drift Forage' state, mostly during the night. BF2 birds had a very large percentage of trip in 'Drift Non-Forage', also mostly during the night, but they also had the largest percentage of the day in 'Drift Non-Forage' behavior, compared to the other clusters. All four flight behaviors (Transit Forage/ Non-Forage, ARS Forage/ Non-Forage) occurred more during the day than at night. These individuals had the highest landing rates at night and had the lowest values for all trip distance and duration metrics.

Cluster 3 – BF3 (Figure 1.9, Table 1.6): Cluster 3 (BF3) birds relied on both flight and drift behavior. While BF3 birds spent a significant amount of the trip in flight, they predominantly foraged using the 'Drift Forage' behavioral state. Although overall time on water was lower than for BF2 birds, they had a higher proportion of the trip in ‘Drift Forage’ mode, and while ‘Drift Forage’ occurred more frequently at night than day within BF3 birds, these birds spent a larger proportion of the day in ‘Drift Forage’ when compared to birds from other clusters. Overall, birds from BF3 allocated the most time to non-foraging flight behaviors compared to the other clusters, and despite the prevalence of flight, they foraged predominantly while drifting, both day and night.

1.3.8 Foraging patterns of Laysan albatrosses

Cluster 1 – LA1 and Cluster 2 – LA2 (Figure 1.9, Table 1.7): Both Laysan albatross clusters spent, on average, about one third of their foraging trips in the ‘Transit Non-Forage’ behavioral state, but for LA2 birds, this predominantly occurred during the day, while LA1 birds spent equal amounts of day and night in ‘Transit Non-Forage’. Although both clusters had similar overall behavioral composition of trips, LA1 birds spent comparatively more time foraging in flight, while LA2 birds spent more time drift foraging than LA1 birds. ‘Transit Forage’ at night was more important for LA1 birds, but ‘ARS Forage’ at night was similarly important for both clusters. Overall, LA2 birds spent the majority of the day in ‘Transit Non-Forage’ while spending the majority of the night in ‘Drift Non-Forage’ and especially ‘Drift Forage’, while LA1 birds spent the majority of the day in ‘Transit Forage’ and ‘ARS Forage’ and the majority of the night in ‘Transit Non-Forage’ and ‘ARS Non- Forage’. LA1 and LA2 birds had similar landing rates during the day, but landing rates at night were higher in LA2 birds. Birds from LA1 had greater distance and duration metrics.

1.3.9 Intrinsic factors and foraging patterns

There were neither sex nor body size differences among clusters in black-footed albatrosses (sex: $\chi^2 = 3.40$, $P = 0.18$; body size: $F_{2,16} = 0.93$, $P = 0.42$); however, a posthoc Tukey HSD test revealed a trend towards higher body condition in birds of Cluster 2 (Figure 1.10a), but this was not significant ($t = 1.38$, $P = 0.19$), probably because of the small number of individuals in Cluster 2. Laysan albatrosses did trend towards sex and body size differences between clusters, with the first cluster being composed of smaller birds ($F_{1,14}$ = 2.22, P = 0.16) and more females than males (χ^2 = 2.53, P = 0.11, Figure 1.10a). Body condition was the same between the two clusters of Laysan albatross ($F_{1,14}$ = 0.01, P = 0.92). To explore the potential for competitive exclusion within each species, we used a linear regression to test the effect of body size on maximum distance reached from the colony. There was a significant relationship in Laysan albatrosses, with smaller (and female) individuals reaching farther maximum distances (Fig. 8a, $F_{1,14}$ = 6.73, P = 0.02) than larger (and male) individuals (Figure 1.11). Regressions run separately for the sexes showed different slopes between the sexes (Figure 1.11 Female Laysan albatrosses reach more distant foraging grounds than malesa, -0.18 for male and 0.24 for females), but sample sizes of sexes nested within species were small and sex-specific regressions did not show a significant relationship between body size and maximum distance. There was no relationship with body size and maximum distance reached for black-footed albatrosses (Figure 1.11b, $F_{1,17}$ = 1.26, P = 0.28) but sex-specific regressions also had different slopes (Figure 1.11b, 0.52 for male and 0.0001 for females). Year as a cofactor had no effect for either species and was removed in final regression models.

1.3.10 Extrinsic factors (year, wind and lunar phase) and foraging patterns

There was no difference in distribution of years among clusters in both black-footed and Laysan albatrosses (χ-squared = 6.12, P = 0.19 and χ -squared = 5.4, P = 0.15, respectively, Figure 1.10b). Lunar phase was not significantly different between clusters in black-footed albatrosses ($F_{2,17}$ = 1.65, P = 0.22), but wind strength experienced by birds was marginally different between two of the three clusters ($F_{2,17}$ = 2.44, P = 0.12), with birds from Cluster 1 experiencing lower mean winds than Cluster 3 (Tukey's HSD, P = 0.09). However, flight behaviors were more important in Cluster 1 birds experiencing lower winds (mean wind strength = 5.40 ± 0.25 m/s) than Cluster 3 birds (mean wind strength = 6.52 ± 1.66 m/s), directly contradicting what one would expect if behavioral clusters were being driven by wind speeds alone. Mean wind was not different between the two Laysan albatross clusters ($F_{1,16}$ = 0.30, P = 0.59). Laysan albatrosses in Cluster 1 did experience a fuller lunar phase (52.0 ± 33.4 % disc illuminated) than did birds from Cluster 2 (22.0 ± 20.0 % disc illuminated) ($F_{1,16}$ = 4.01, P = 0.06). However, Cluster 1 birds also flew more during the day than birds from Cluster 2, suggesting the heavy reliance on flight in these birds was not just an artifact of lunar conditions.

1.4 DISCUSSION

1.4.1 Beyond “Area-Restricted Search” foraging behavior

Many studies classify short duration landings as foraging activity, whereas long drifting bouts that occur at night are interpreted as resting, non-foraging periods. However, drift sinuosity and ingestion events captured by GPS and stomach-temperature data-loggers indicate that these drifts are often associated with active “sit-and-wait” foraging (Jodice et al. 2003, Catry et al. 2004, Weimerskirch et al. 2007, Zavalaga et al. 2011, Cruz et al. 2013). Although prey consumed in this manner tend to have smaller mass (Catry et al. 2004, Weimerskirch et al. 2007), the energetic content of prey available at night (e.g., myctophids and pelagic crustaceans) can be high (Roby et al. 1997, Paredes et al. 2014), and the “sit-and-wait” strategy may, at times, be the most optimal strategy (i.e., most energy gained for energy used) (Jodice et al. 2003, Louzao et al. 2014).

Foraging in direct flight and “sit-and-wait” foraging tactics were as frequently used as area-restricted search flight for brood-guarding Hawaiian albatross, but the use of ARS as the only proxy of foraging behavior is widely prevalent in seabird foraging studies. ARS is an informative metric valuable in identifying areas of high-use and for understanding spatial scales employed by foraging animals. However, ARS is often measured as a two dimensional spatial metric (Fauchald and Tveraa 2003) and if the aim is to understand foraging behavior and/or activity budgets, our results caution against only considering ARS behavior, at least for albatrosses and other species that have flexible foraging tactics. Methods like first passage time and residence time are useful in identifying where animals spend the most time, but by themselves do not incorporate behavioral variability within those areas. Using ARS metrics alone, it would be possible to delineate "sit-and-wait" foraging from foraging in flight due to the large differences in spatial scales (10^2 m vs 10^4 m) these behaviors operate on; however, it would not be possible to effectively delineate the difference between the two flight-based foraging strategies that operate on similar spatial scales. For example, it is possible to calculate the same value of residence time within a virtual circle for a bird flying in a straight line (direct flight) and landing frequently as for a bird flying in a tortuous path but not landing at all. Therefore, by incorporating a measure of both spatial-temporal use (residence time) and activity (landings), we were able to identify behaviors that would likely be masked if using ARS metrics alone.

Fractal landscape methods that quantify track convolution (i.e. searching intensity) within ARS regions (Nams 1996, Tremblay et al. 2007) circumvent some limitations of ARS methods that use time as their metric; however, at least for brood-guarding Hawaiian albatrosses, it was quite common for birds to fly in tortuous paths but not land, especially for black-footed albatrosses at night. If we were evaluating the movement of birds solely by identifying path tortuosity without landing activity we could make the erroneous assumption that these birds were actively foraging, e.g. both searching for food *and* landing to feed. In the case of black-footed albatrosses, without considering landing densities within regions of high residency times, we would calculate that they are in ARS flight ~29% of the night versus ~24% of the day and might conclude the importance of nocturnal foraging in this species. However, when delineating ARS flight into 'ARS Forage' and 'ARS Non-Forage' by looking at landing densities, we see that ~19% of the night is in 'ARS Non-Forage' while only 10% of that is in 'ARS Forage', an important distinction that leads us to a different conclusion. Thus, incorporating measurements of activity, such as stomach-temperature loggers (Weimerskirch et al. 2007), accelerometers (Weimerskirch et al. 2006), altimeters (Weimerskirch et al. 2004), wet/dry data (Cairns et al. 1987), etc., within analyses of spatial use is critical for understanding the sometimes nuanced behavior of animals.

1.4.2 Nocturnal and diurnal niche partitioning between Hawaiian albatross species

Overall foraging behavior was remarkably similar between black-footed and Laysan albatrosses. However, clear species differences emerged when delineating behavior by day and night. Our results support greater nocturnality in Laysan albatrosses at least during the brood-guard. While both species appear to rely on daylight for foraging while in transit, Laysan albatrosses spent more of the night foraging in area-restricted search flight and foraging while drifting than black-footed albatrosses. Black-footed albatrosses appear to rely on daylight for both flight foraging modes, and they also drift foraged in daylight as much as they did at night (Table 1.5, Figure 1.7). Although Laysan albatross foraging behavior suggests greater nocturnality of the two Hawaiian albatrosses, foraging occurred across day and night, to varying degrees, in both species. Foraging trips of Hawaiian albatross were very active (~ 50% trip in active forage mode) - likely a reflection of the high provisioning demands on parents during the brood-guard.

Seabirds can adjust their dependency on nocturnal and diurnal foraging in different marine habitats (Dias et al. 2012) or under conditions of increased competition (Zavalaga et al. 2011); the occurrence of nocturnal foraging in Hawaiian albatross, therefore, may be a behavioral response to foraging in a tropical environment during a period of high competition. The oligotrophic waters around the Hawaiian islands are generally described as patchy and nutrient-poor (Seki and Polovina 2001), but they do support a large biomass of micronekton associated with steep gradients of the archipelago and nearby seamounts (Boehlert and Genin 1987, Drazen et al. 2011). This micronekton is associated with the diel vertically migrating prey community – the primary prey resource in oceanic waters (Drazen et al. 2011) – that has a more pronounced migration in lower than higher latitudes (Ashmole 1971).

Indeed, a recent investigation of stomach contents of fishery by-caught Laysan albatrosses found myctophids to occur more frequently in the stomachs of birds from the Hawaiian fishery compared to the Alaskan fishery (Walker and Fitzgerald 2012). Given the greater abundance of this prey field in surface waters at night in tropical, pelagic waters, nocturnal foraging would provide enhanced feeding opportunities for Hawaiian albatrosses given the relatively long nights (~10-11 hours) of the boreal spring. Brood-guarding birds that need to maximize provisioning rates while minimizing trip duration (Shaffer et al. 2003) would have an energetic advantage if able to exploit the abundant micronekton in surface waters at night (see (Louzao et al. 2014)), especially considering half the duration of foraging trips occurs at night for brood-guarding Hawaiian albatrosses (48.0 ± 11.7% and 50.5 ± 4.8%, for black-footed and Laysan albatrosses, respectively).

How albatrosses search for and locate prey at night is poorly understood; however, foraging by flight in seabirds requires visual cues. The eyes of Laysan albatrosses have high concentrations of rhodopsin, a light sensing pigment (16.30 optical density units (D/g), as compared to 3.90 D/g for black-footed albatrosses and 19.50 D/g for the barn owl, *unpublished data* Sillman 1981), indicating a morphological adaptation for higher visual acuity at night. Indeed, foraging in ARS flight remained important at night for Laysan albatrosses – behavior that implies an ability to search and locate prey through visual cues at night. Additionally, nocturnal foraging in flight for Laysan albatrosses was not limited to birds foraging under bright moonlight conditions (cluster 1 birds). While cluster 1 birds did spend more time in transit forage at night, cluster 2 birds, which foraged under darker nocturnal conditions, spent a similar proportion of night actively foraging in area-restricted search behavior as cluster 1 birds. Laysan albatrosses appear to rely less upon moonlight to forage in flight than black-footed albatrosses; however, moonlight likely assists navigation and orientation given the predominance of transit behavior on bright nights (cluster 1 birds, also Figure 1.8).

In contrast, black-footed albatross behavior showed a significant reduction of nighttime flight forage behaviors and relied predominately on the “sit-and-wait” strategy at night to forage. Despite a reduction of foraging in flight under dark conditions, black-footed albatrosses spent a large proportion of night on the wing, perhaps commuting to areas where the “sit-and-wait” foraging strategy was profitable. Interestingly, BF1 (cluster 1) birds experienced the brightest moon conditions (Figure 1.10b) and were the only cluster of birds within black-footed albatrosses that spent a substantial proportion of the night in both flight foraging strategies, further supporting our conclusion that black-footed albatrosses have a greater reliance on moonlight compared to Laysan albatrosses for flight foraging. Both species showed a strong reduction in drift forage behavior on full moon nights (Figure 1.8), likely due to the reduced accessibility of diel-migrating prey on bright nights. Increased transit but decreased foraging behavior suggests a reduced foraging efficiency on bright moonlit nights as compared to darker nights as seen in other seabird species (Phalan et al. 2007, Mackley et al. 2011, Dias et al. 2012, Cruz et al. 2013) but see (Regular et al. 2011).

1.4.3 Within- and among- species niche partitioning in a community of albatross

The mechanisms that facilitate coexistence within a community is a central question in ecology (Amarasekare et al. 2004). Intraspecific competition may be more intense than competition between species, because smaller morphological differences lead to fewer opportunities for niche partitioning (Begon et al. 2006). Indeed, colonies of conspecific seabirds that are in close proximity often have highly delineated foraging grounds reducing intraspecific competitive interactions (Grémillet et al. 2004, Masello et al. 2010, Wakefield et al. 2013). Within a colony, density-dependent competition can select for individuals with “roving” strategies (Sokolowski et al. 1997, Lewis et al. 2001) – increased range, longer trips, decreased time at resource patches – sometimes with reduced fitness (Lewis et al. 2001). In Laysan albatrosses, birds from cluster 1 (LA1) traveled more, reached further maximum distances, and spent less time on water *(*Table 1.7*),* consistent with such a “roving” strategy.

Birds from cluster 1 were smaller, and were mostly females, such that differences could reflect sex-specific foraging strategies in brood-guarding Laysan albatrosses. Sex-specific foraging occurs across seabird taxa in dimorphic (see review in Lewis et al. 2002), reversed dimorphic (Weimerskirch et al. 2005), and, increasingly, in monomorphic species (Lewis et al. 2002, Thaxter et al. 2009, Pinet et al. 2012, Hedd et al. 2014). Compared to black-footed albatrosses, there was less overlap between the sexes in bill dimensions suggesting a potential morphological mechanism of intraspecific niche separation. Thus these differences in foraging behavior appear not to be the result of short-term behavioral plasticity but rather fixed trait-mediated niche specialization between the sexes (Shaffer et al. 2001), although these morphological differences are very slight compared to other dimorphic albatross species. The longer trip durations and further maximum ranges of female Laysan albatrosses might reflect enhanced flight efficiency of the smaller sex, as is seen in other Procelleriform species that use gliding flight (Shaffer et al. 2001, Phillips et al. 2004). But if it is flight efficiency driving these behaviors, we would expect to additionally see a relationship between body size and maximum range *within* each species, and that is not the case (Figure 1.11), although sample size are small. Competitive exclusion of smaller females by larger males from foraging grounds near the colony also seems unlikely as there remains significant spatial overlap in core foraging grounds between the sexes.

The prevalence of studies showing sex-specific foraging strategies in monomorphic or slightly sexual dimorphic species suggests sex differences can be unrelated to body size (Thaxter et al. 2009, Stauss et al. 2012, Pinet et al. 2012). An alternative explanation is that the foraging differences between the sexes in Laysan albatrosses are not related to size but to different parental roles influence foraging differences, with shorter trips of males reflecting male-biased provisioning. During incubation, male Laysan albatrosses spend more time incubating the egg than females who spend more time foraging at sea (Rice and Kenyon 1962), likely regaining body condition lost in egg production (Tickell 2000). It is possible that male-biased nest attendance continues into the brood-guard stage as females continue to allocate more energy to self-maintenance than males. Parental roles can switch across the breeding season with one sex contributing more time and energy to the nest early in season, and the other sex contributing more later in season (Thaxter et al. 2009, Pinet et al. 2012), so it would be informative to conduct a study of fine-scale foraging behavior across the breeding season to see if sex-specific differences persist into the post-guard stage.

The breeding population of black-footed albatrosses in the French Frigate Shoals (Tern Island and surrounding atolls) is ~30% larger than that of Laysan albatrosses (Arata et al. 2009). Despite larger numbers of breeding birds, black-footed albatrosses have shorter maximum ranges and trip durations than Laysan albatrosses (Table 1.2). We can thus expect higher densities of black-footed albatrosses at-sea that should result in greater intra-specific competition in foraging grounds near Tern Island. Often, a high level of individual variability unrelated to morphological traits is a flexible behavioral response to increased intraspecific competition (Svanbäck and Bolnick 2007, Tinker et al. 2008, Villegas-Amtmann et al. 2011). Therefore, it is not surprising we see greater levels of variability in foraging strategies in black-footed albatrosses, independent of body size or sex. Conducting a similar study at a different breeding colony, such as Midway Atoll, where densities of Laysan albatrosses are greater than that of black-footed albatrosses would help to clarify whether intraspecific variability in these species is a short-term behavioral response dictated by density of conspecifics or is a fixed intrinsic characteristic of the species.

Greater population-level behavioral plasticity in black-footed albatrosses might serve as a buffer against environmental variability on breeding decisions. Indeed, black-footed albatrosses breeding at Tern Island show more behavioral flexibility to poor environmental conditions than Laysan albatrosses and have higher reproductive success at Tern Island in “poor” years (Thorne et al. 2015). Furthermore, different behavioral patterns within black-footed albatrosses appear to have varying efficiencies, at least for cluster 2 birds (BF2), although the higher mean body condition of these birds was not statistically significant (Figure 1.10a). However, it is interesting that the birds with higher mean body condition were the birds that predominantly foraged while drifting and spent a much larger proportion of their foraging trips on the water. Foraging on the water in “sit-and-wait” was found to be the most energy efficient foraging strategy in a study of wandering albatrosses during the brood-guard (Louzao et al. 2014). Variable efficiencies of foraging patterns are likely to have a more measurable effect on individuals in the brood-guard when constraints are high (Walter et al. 2014) and when birds are foraging in challenging environmental conditions (Lescroël et al. 2010).

1.5 CONCLUSION

We quantified behavioral mechanisms that enable coexistence within an albatross community constrained to poor-nutrient tropical waters during the most energetically-demanding reproductive stage in birds: the brood-guard. Albatrosses showed discrete behavioral partitioning both between and within species which was driven by differences in nocturnal and diurnal foraging and by sex-specific strategies. Our results are the first to observe nocturnally-biased foraging behavior in Laysan albatrosses, but we emphasize foraging behavior occurred across day and night in both species. Black-footed albatrosses exhibited greater variability in foraging patterns suggesting they may experience strong intraspecific competition at Tern Island. While foraging patterns in Laysan albatrosses were less variable, behavioral differences were primarily associated with gender. Examining variability in foraging strategies across breeding phases, when birds experience large regime shifts in oceanic habitat and levels of competition will provide further understanding of behavioral plasticity and capacity for short-term adaptation in Hawaiian albatross.

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Table 1.1 Mass and morphometrics (means ± SD) of Laysan and black-footed albatross breeding on Tern Island

	Laysan albatross (163)		**Black-footed albatross (167)**	
	Female (77)	*Male (86)*	*Female (80)*	*Male (87)*
Mass Initial (kg)	2.37 ± .03	2.52 ± .03	2.76 ± .04	3.01 ± .04
Tarsus (cm)	10.32 ± .04	10.61 ± .05	10.81 ± .05	11.48 ± .04
Culmen (cm)	10.64 ± .03	11.37 ± .04	10.23 ± .05	10.78 ± .04
Minimum Bill Depth (cm)	2.25 ± .01	2.38 ± .01	2.53 ± .01	2.68 ± .01
Maximum Bill Depth (cm)	2.40 ± .01	2.57 ± .01	2.68 ± .01	2.87 ± .01

Table 1.2 Track characteristics by species and the effects of species and sex on track characteristics.

Coefficient ± SD are given for linear model results for each movement parameter. Results for the effects of species and sex nested under species are shown. Additionally, Mean ± SD are given for summary statistics of each movement parameter. BFAL = black-footed albatrosses and LAAL = Laysan albatrosses.

	Summary Statistics		**Linear Model Output**								
	BFAL	LAAL	Species			Sex [BFAL]			Sex [LAAL]		
	µ ± SD	µ ± SD	Coef. ± SD	t	P	Coef. ± SD	t	P	Coef. ± SD	t	P
Total Distance *(km)*	886.1 ± 476.9	918.6 ± 496.6	686.1 ± 363.9	1.9	0.07*	402.2 ± 210.1	1.9	0.23	480.9 ± 351.5	-1.4	0.52
Daily Travel *(km/day)*	468.2 ± 176.4	499.2 ± 163.6	198.4 ± 92.2	2.2	0.04**	73.6 ± 74.1	1.0	0.75	186.8 ± 86.4	-2.2	0.15
Max. Distance *(km)*	368.4 ± 215.3	500.2 ± 365.8	11.9 ± 3.4	3.6	0.001**	3.7 ± 2.7	1.4	0.53	10.2 ± 3.1	-3.2	0.01 **
Trip Duration *(days)*	1.9 ± 0.65	2.0 ± 0.5	1.5 ± 0.4	4.2	< 0.001**	0.5 ± 0.3	1.7	0.32	1.2 ± 0.3	-3.6	0.01 **

Table 1.3 Movement parameters by species and astronomical state

	Black-footed Albatross				**Laysan Albatross**			
PARAMETERS (μ ± SD)	Overall Trip	Day	Night	Twilight	Overall Trip	Day	Night	Twilight
Landing Rate *(landings/hr)*	2.1 ± 1.4	3.2 ± 2.3	2.0 ± 1.6	1.7 ± 1.5	2.6 ± 1.2	2.8 ± 1.6	3.6 ± 1.8	1.0 ± 0.9
Drift Duration *(min.)*	20.8 ± 11.1	18.8 ± 13.6	20.4 ± 13.4	14.1 ± 10.5	14.3 ± 5.1	9.8 ± 2.6	16.6 ± 8.8	7.7 ± 2.4
Flight Speed *(km/hr)*	44.4 ± 3.6	45.6 ± 4.0	42.7 ± 3.8	45.5 ± 3.6	44.4 ± 2.9	46.9 ± 4.0	40.3 ± 3.1	46.1 ± 3.4
Flight Turning Angle *(°)*	50.1 ± 7.3	47.0 ± 7.6	53.5 ± 8.4	48.4 ± 8.0	51.0 ± 10.2	48.8 ± 9.3	54.9 ± 13.3	49.3 ± 10.2
Time in Flight *(%)*	67.7 ± 17.0	67.6 ± 19.5	65.2 ± 27.5	83.1 ± 12.2	70.2 ± 14.8	81.9 ± 0.1	55.8 ± 24.0	94.5 ± 5.8

Table 1.4 Results from linear mixed models testing the effects of species, diurnal states and their interactions on albatross movement parameters.

Posthoc multiple comparisons using Tukey contrasts identified diurnal differences both between and within species

		Movement Parameters					
Model Effects		***Landing Rate***	***Drift Duration***	***Drift Sinuosity***	***Flight Speed***	***Flight Turning***	***In Flight (%)***
Species	Coef. ± SD	0.44 ± 0.24	10.5 ± 3.07	0.02 ± 0.04	1.08 ± 1.27	0.03 ± 0.08	0.17 ± 0.10
	t	1.84	-3.42	0.51	-0.85	0.39	1.82
	P	**0.08***	**0.002****	0.62	0.4	0.7	0.08
Day [Species]	Coef. ± SD	0.30 ± 0.19	8.22 ± 2.57	0.03 ± 0.04	1.10 ± 1.11	0.00 ± 0.07	0.21 ± 0.08
	z	1.59	-3.2	-0.8	0.98	-0.04	2.71
	P	**0.5**	**0.01****	0.96	0.89	1	**0.06***
Night [Species]	Coef. ± SD	0.58 ± 0.19	8.01 ± 2.68	0.01 ± 0.04	2.07 ± 1.11	0.01 ± 0.07	0.18 ± 0.14
	z	3.07	-2.99	0.26	-1.86	-0.18	-1.3
	P	**0.01****	**0.02****	1	0.33	1	0.75
Twilight [Species]	Coef. ± SD	0.23 ± 0.19	10.23 ± 4.77	0.03 ± 0.08	0.52 ± 1.12	0.03 ± 0.08	0.26 ± 0.06
	z	1.2	-2.15	0.37	0.46	-0.34	4.18
	P	0.77	0.21	0.99	0.99	0.99	**< 0.001****
BFAL [Day/Night]	Coef. ± SD	0.29 ± 0.00	5.76 ± 1.65	0.01 ± 0.02	2.93 ± 0.07	0.13 ± 0.01	0.02 ± 0.11
	z	-73.82	3.5	-0.76	-44.54	23.33	0.15
	P	**< 0.001****	**0.004****	0.97	**< 0.001****	**< 0.001****	1
BFAL [Day/Twilight]	Coef. ± SD	0.08 ± 0.00	1.64 ± 4.29	0.01 ± 0.03	0.29 ± 0.11	0.04 ± 0.01	0.24 ± 0.05
	z	-13.17	-0.38	0.23	-2.69	4.56	4.98
	P	**< 0.001****	0.99	1	**0.05***	**< 0.001****	**< 0.001****
BFAL [Night/Twilight]	Coef. ± SD	0.20 ± 0.00	7.40 ± 4.34	0.02 ± 0.03	2.62 ± 0.11	0.09 ± 0.01	0.22 ± 0.10
	z	31.94	-1.7	0.61	24.55	-9.7	2.14
	P	**< 0.001****	0.47	0.99	**< 0.001****	**< 0.001****	0.23
LAAL [Day/Night]	Coef. ± SD	0.01 ± 0.00	5.97 ± 0.93	0.03 ± 0.02	6.09 ± 0.07	0.12 ± 0.01	0.37 ± 0.08
	z	-1.83	6.44	1.48	-88.21	20.49	-4.72
	P	0.33	**< 0.001****	0.63	**< 0.001****	**< 0.001****	**< 0.001****
LAAL [Day/Twilight]	Coef. ± SD	0.16 ± 0.00	3.68 ± 0.71	0.07 ± 0.06	0.86 ± 0.11	0.02 ± 0.01	0.29 ± 0.03
	z	-24.5	-5.16	1.03	-7.99	2.19	8.98
	P	**< 0.001****	**< 0.001****	0.89	**< 0.001****	0.17	**< 0.001****
LAAL [Night/Twilight]	Coef. ± SD	0.15 ± 0.00	9.65 ± 1.03	0.04 ± 0.06	5.23 ± 0.11	0.10 ± 0.01	0.66 ± 0.07
	z	-22.81	-9.35	0.62	47.16	-10.63	9.33
	P	**< 0.001****	**< 0.001****	0.99	**< 0.001****	**< 0.001****	**< 0.001****

Nested effects indicated with brackets.

Table 1.5 Percentage of time in each behavioral state.

Means ± SD are given for the time spent in each behavioral state across the whole trip and across day and night portions of the trip, for each species. All three active foraging states are grouped together to provide a summary of time spent actively foraging across the whole trip and across day and night portions of the trip.

	Black-footed Albatross			**Laysan Albatross**		
Behavioral State	% Total Trip	% Day	% Night	% Total Trip	% Day	% Night
Transit Non-Forage	27.2 ± 7.7	24.3 ± 16.1	31.3 ± 21.9	28.2 ± 7.3	37.7 ± 14.1	17.9 ± 14.2
Transit Forage	14.5 ± 10.6	22.6 ± 16.0	6.2 ± 7.4	15.2 ± 7.9	21.8 ± 10.7	8.3 ± 7.6
ARS Non-Forage	13.9 ± 4.7	7.9 ± 5.6	19.2 ± 12.0	14.0 ± 3.6	10.9 ± 8.2	17.3 ± 8.6
ARS Forage	13.8 ± 5.4	17.6 ± 7.0	9.7 ± 9.1	15.0 ± 5.5	15.7 ± 10.7	14.5 ± 9.5
Drift Non-Forage	10.5 ± 12.7	8.8 ± 10.9	12.1 ± 18.7	8.8 ± 10.2	3.5 ± 6.3	13.8 ± 15.4
Drift Forage	18.1 ± 10.6	15.6 ± 14.9	20.6 ± 17.0	16.3 ± 9.2	7.1 ± 5.5	26.5 ± 19.2
Active Forage	46.4 ± 11.2	55.8 ± 21.6	36.6 ± 21.5	46.5 ± 7.3	44.6 ± 17.6	49.3 ± 19.6

Table 1.6 Mean values of behavioral parameters and track characteristics for each black-footed albatross behavioral cluster.

				Cluster BF1 *(n=6)*	**Cluster BF2** *(n=4)*	**Cluster BF3** *(n=10)*
	Test	F	P	Mean ± SD	Mean ± SD	Mean ± SD
Behavioral Parameters						
% Day in Transit	gls	9.8	0.001**	11.6 ± 1.9	28.9 ± 13.3 [a]	30.1 ± 18.3 [a]
% Night in Transit	lm	3.0	0.08*	36.3 ± 16.7 [a]	11.9 ± 8.9	36.0 ± 25.0 [a]
% Day in Transit Forage	lm	12.7	0.0004**	43.0 ± 7.6	12.3 ± 2.6 [a]	14.4 ± 10.5 [a]
% Night in Transit Forage	gls	5.8	0.01**	13.7 ± 9.8	2.2 ± 2.6 [a]	3.4 ± 2.6 [a]
% Day in ARS	lm	0.7	0.51	6.3 ± 6.6	10.5 ± 4.8	7.8 ± 5.4
% Night in ARS	gls	5.1	0.02**	27.1 ± 12.4 [a]	7.8 ± 5.2	19.1 ± 10.4 [a]
% Day in ARS Forage	lm	0.5	0.62	20.0 ± 7.9	15.9 ± 6.9	16.9 ± 6.9
% Night in ARS Forage	gls	2.0	0.17	15.0 ± 12.2	5.0 ± 4.7	8.3 ± 7.3
% Day in Drift	gls	2.7	0.10*	5.5 ± 6.2 [a]	18.4 ± 16.3	7.0 ± 9.3 [a]
% Night in Drift	gls	18.5	.00001**	2.0 ± 2.8 [a]	47.1 ± 9.3	4.2 ± 5.0 [a]
% Day in Drift Forage	lm	0.8	0.47	10.2 ± 5.3	11.5 ± 12.8	20.5 ± 18.6
% Night in Drift Forage	lm	5.0	0.02**	5.3 ± 6.6	25.2 ± 14.0 [a]	28.0 ± 17.1 [a]
Day Landing Rate	lm	0.3	0.75	1.37 ± 0.39	1.7 ± 0.74	1.76 ± 1.03
Night Landing Rate	lm	2.7	0.10*	0.47 ± 0.28 [a]	1.60 ± 1.43 [b]	1.04 ± 0.49 [a,b]
Track Characteristics						
Daily Travel (km)	gls	9.9	0.001**	650 ± 115	337 ± 135 [a]	412 ± 139 [a]
Max Range (km)	gls	2.8	0.09*	551 ± 284	254 ± 107 [a]	305 ± 129 [a]
Total Distance (km)	gls	6.5	0.008**	1352 ± 520	565 ± 140 [a]	735 ± 328 [a]
Trip Duration (km)	lm	0.35	0.71	2.04 ± 0.667	1.77 ± 0.485	1.75 ± 0.742

[1] log$_{10}$-transformed for gls or lm

[2] square-root transformed for gls or lm

[a,b] indicate which clusters did not significantly differ at P ≤ 0.05 in a multiple comparison post-hoc Tukey test.

Table 1.7 Mean values of behavioral parameters and track characteristics for each Laysan albatross behavioral cluster.

				Cluster LA1 *(n=6)*	**Cluster LA2** *(n=12)*
	Test	F	P	Mean ± SD	Mean ± SD
Behavioral Parameters					
% Day in Transit	lm	9.2	0.008**	24.7 ± 8.6	43.1 ± 12.3
% Night in Transit	lm	4.4	0.05**	28.4 ± 15.1	13.6 ± 11.9
% Day in Transit Forage	lm	17.2	0.0009**	33.6 ± 7.4	16.9 ± 7.6
% Night in Transit Forage	lm	7.3	0.02**	15.0 ± 9.7	5.5 ± 4.6
% Day in ARS	lm	4.9	0.04**	4.8 ± 6.8	13.4 ± 7.5
% Night in ARS	lm	5.8	0.03**	24.3 ± 6.3	14.4 ± 8.1
% Day in ARS Forage	lm	8.6	0.01**	25.5 ± 6.4	11.7 ± 9.5
% Night in ARS Forage	lm	0.1	0.74	15.8 ± 5.5	14.0 ± 11.0
% Day in Drift	gls	2.7	0.10*	2.7 ± 2.5	3.8 ± 7.4
% Night in Drift	gls	18.5	0.00001**	7.0 ± 9.0	16.7 ± 16.9
% Day in Drift Forage	lm	0.8	0.48	4.9 ± 3.6	8.0 ± 6.1
% Night in Drift Forage	lm	16.3	0.001**	8.1 ± 8.8	34.2 ± 17.0
Day Landing Rate	lm	0.81	0.38	1.59 ± 0.43	1.37 ± 0.64
Night Landing Rate	lm	7.8	0.01**	0.86 ± 0.37	2.12 ± 1.36
Track Characteristics					
Daily Travel	gls	7.6	0.02**	635 ± 124	443 ± 147
Max Distance	gls	2.0	0.17	691 ± 355	421 ± 354
Total Distance	gls	9.9	0.009**	1425 ± 380	716 ± 385
Trip Duration	lm	1.6	0.23	2.57 ± 0.6	2.03 ± 0.9

[1] $\log_{10}$-transformed for gls or lm

[2] square-root transformed for gls or lm

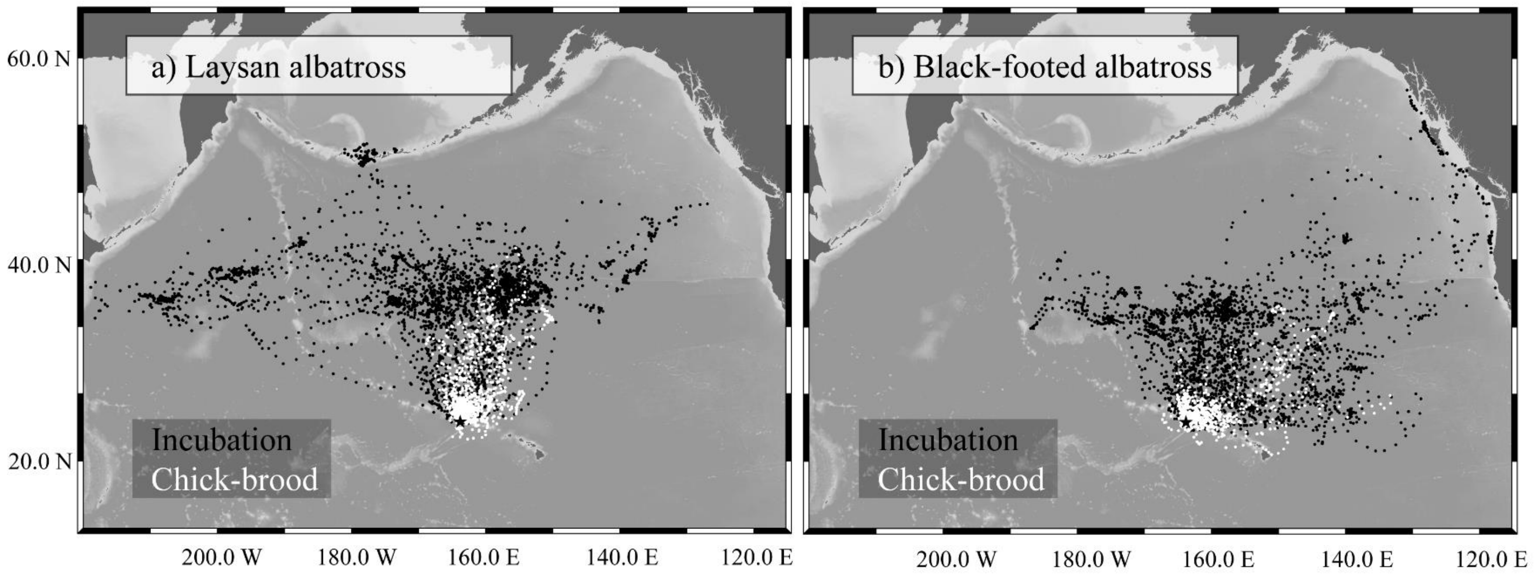


Figure 1.1 GPS locations of incubating and chick-brooding Laysan (n=114) and black-footed (n=118) albatross breeding at Tern Island.

Tracks used for this figure were collected for this study and a concomitant long-term tracking study from 2006, 2009, 2010, 2011 and 2012. Tracks were interpolated to 1 position every 5 hours. Incubating birds of both species spend the majority of time in higher latitudes in the North Pacific Transition Zone as well as coastal locations around the Pacific Rim. Clear spatial segregation between the species occurs during the incubation stage (focal range overlap of 50.8% (Kappes 2009)) but spatial segregation breaks down during the chick-brood stage (focal range overlap of 75.4% (Kappes 2009)). Tern Island is indicated with a star.

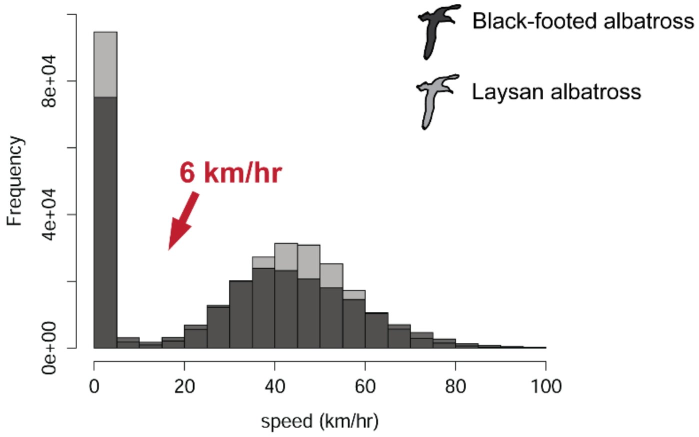


Figure 1.2 A bimodal distribution of speeds in both species, indicating a speed threshold of ~6 km/hr below which birds do not remain aloft

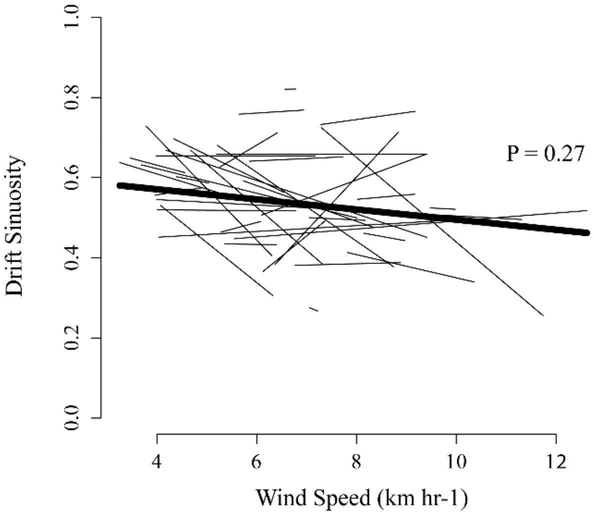


Figure 1.3 Wind speed did not affect sinuosity of tracks in drifting birds, validating the use of drift sinuosity as a proxy for drift foraging activity.

A linear mixed model was constructed with drift sinuosity as a continuous response variable to wind speed with species as a fixed factor. Individual bird was included as a random effect since birds had numerous drifts within a foraging trip. Slopes of individual birds were allowed to vary and are represented by the thinner lines, while the population mean slope (of both species) is the bold line. Wind speed, nor species, had a significant effect on sinuosity ($t_{35,655}$ = -1.11, P = 0.27).

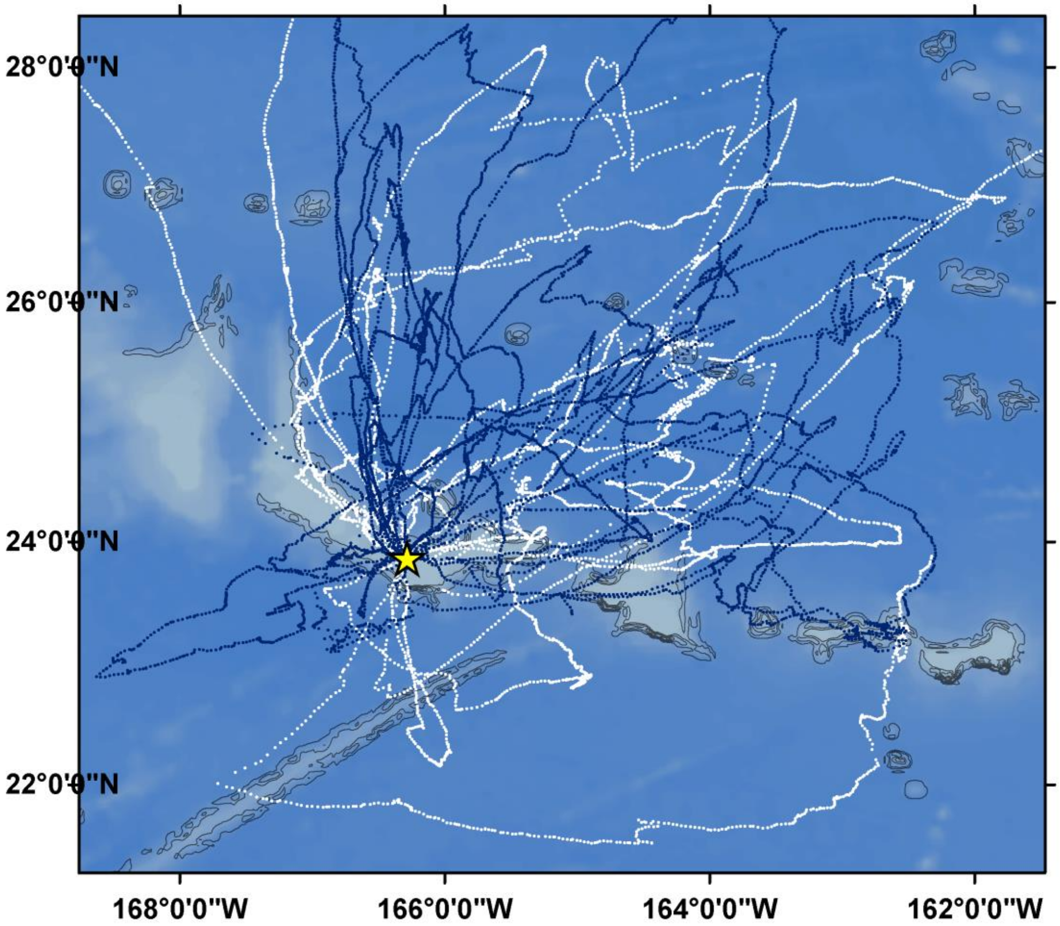


Figure 1.4 Black-footed (black) and Laysan (white) albatross GPS tracks deployed at Tern Island (black star) in 2006, 2009, 2010 and 2012.

Tracks were subsampled to 1 location every 5 minutes for the purpose of this illustration. Some individuals of both species visited both the steep bathymetric slope of the northwestern Hawaiian Islands as well as deeper submerged seamounts in pelagic waters. Both species predominately foraged north and northeast of Tern Island with a few individuals from both species foraging south and southwest. The vast majority of trip durations were spent in pelagic waters.

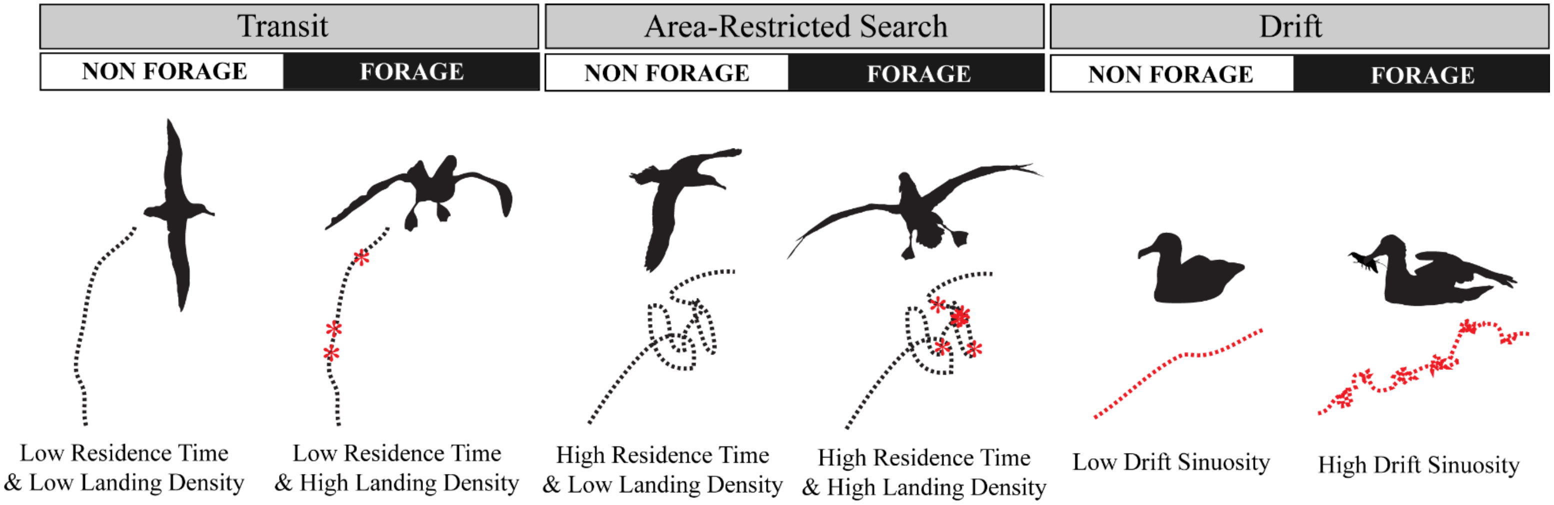


Figure 1.5 Behavioral state classification schematic showing forage and non-forage modes for two flight behaviors (Transit and ARS) and for drifting behavior.

Red indicates when bird is on the water.

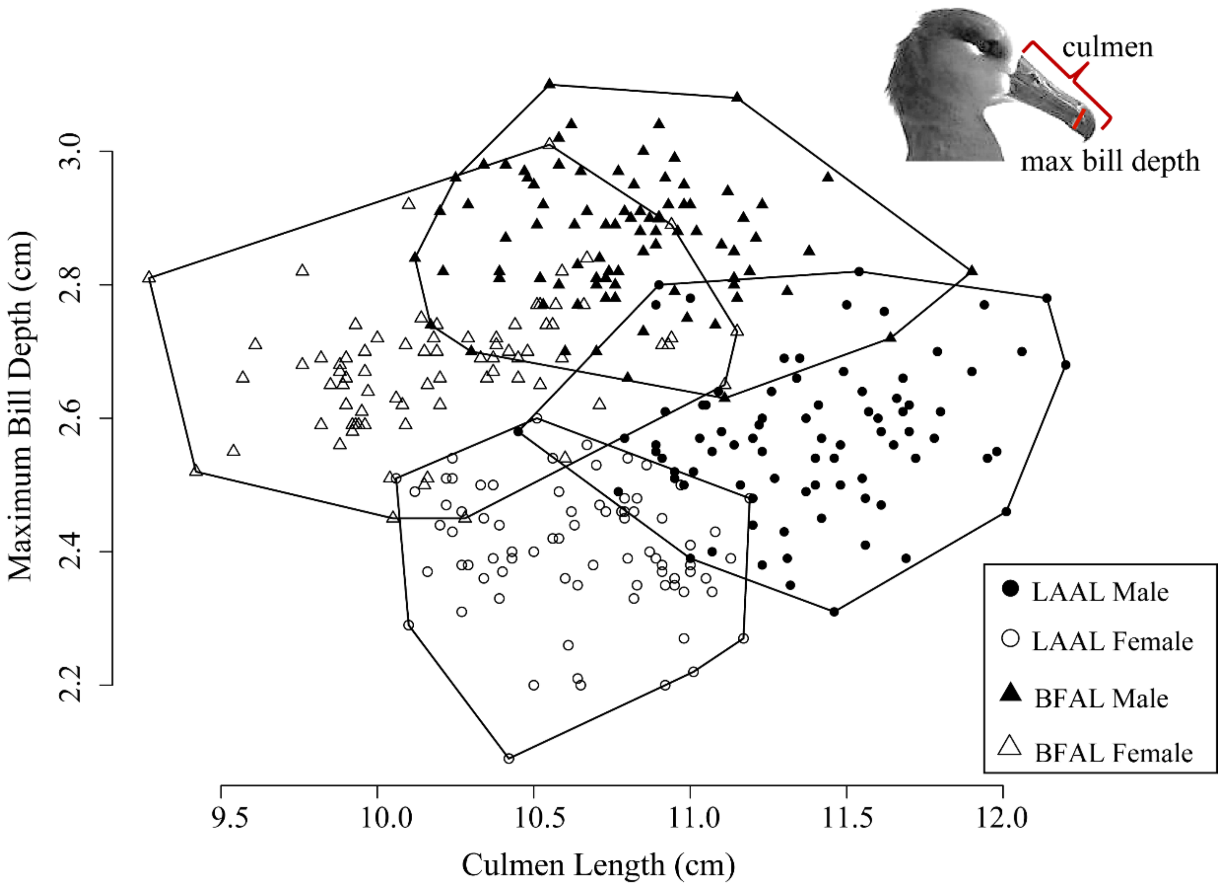


Figure 1.6 Scatterplot of bill morphometrics indicates clustering in morphological space. Morphometrics cluster by species (shorter, thicker bills in black-footed albatrosses (BFAL)) and by sex within species (female bills generally shorter and less deep). Bill measurements between the sexes overlap more in black-footed albatrosses than they do in Laysan albatrosses

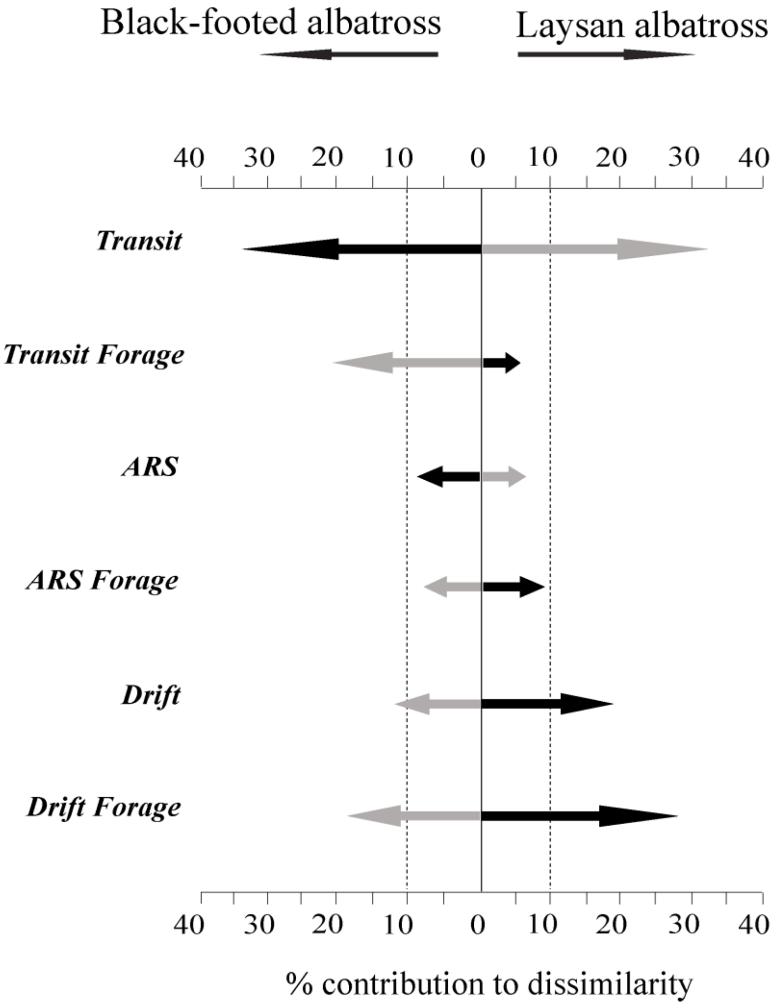


Figure 1.7 A simper analysis indicates that nocturnal foraging is more prevalent at night in Laysan albatross than it is in black-footed, while the opposite is true for diurnal foraging.

Black arrows were calculated on behavior during the night and light grey arrows during the day. The percent contribution to dissimilarity between species is represented by the length of the arrows, and the direction of the arrow is towards the species in which behavior was greatest (measured by duration). Dashed lines at 10% contribution represent a cutoff below which behavioral states were considered as less important variables driving the dissimilarity between species.

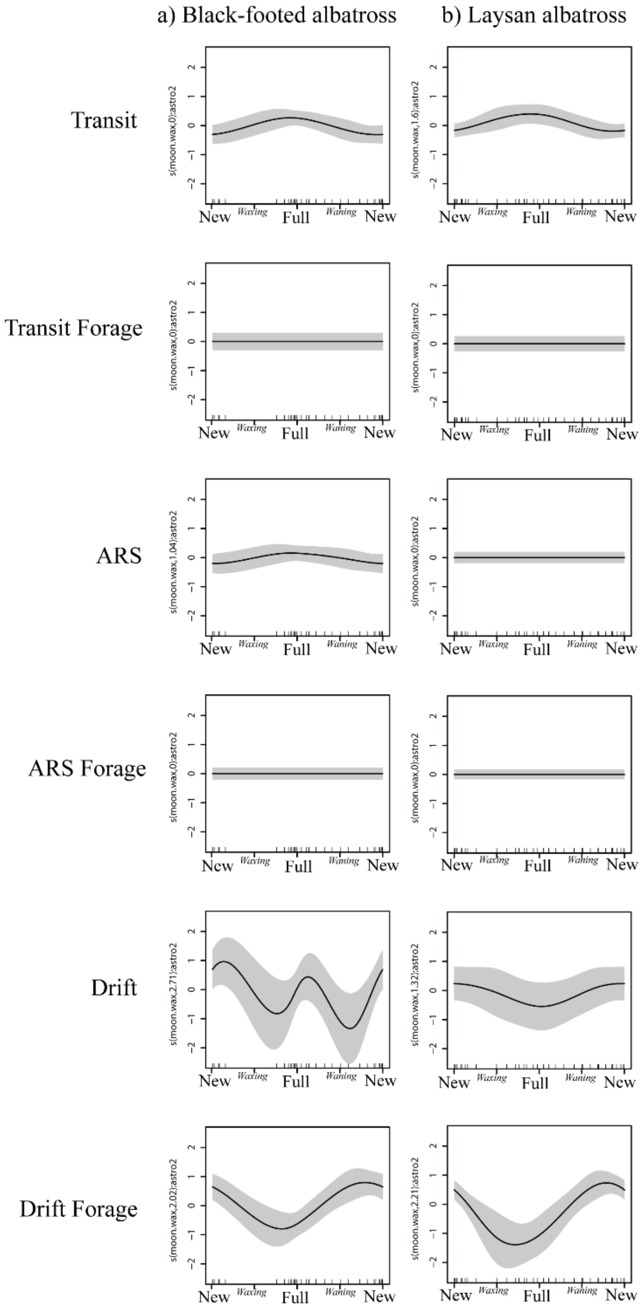


Figure 1.8 Effects of lunar phase on each behavioral state in albatrosses.

Lunar effect isolated for night portions of trips only. Shaded areas represent 95% Bayesian confidence intervals (Nychka 1988).

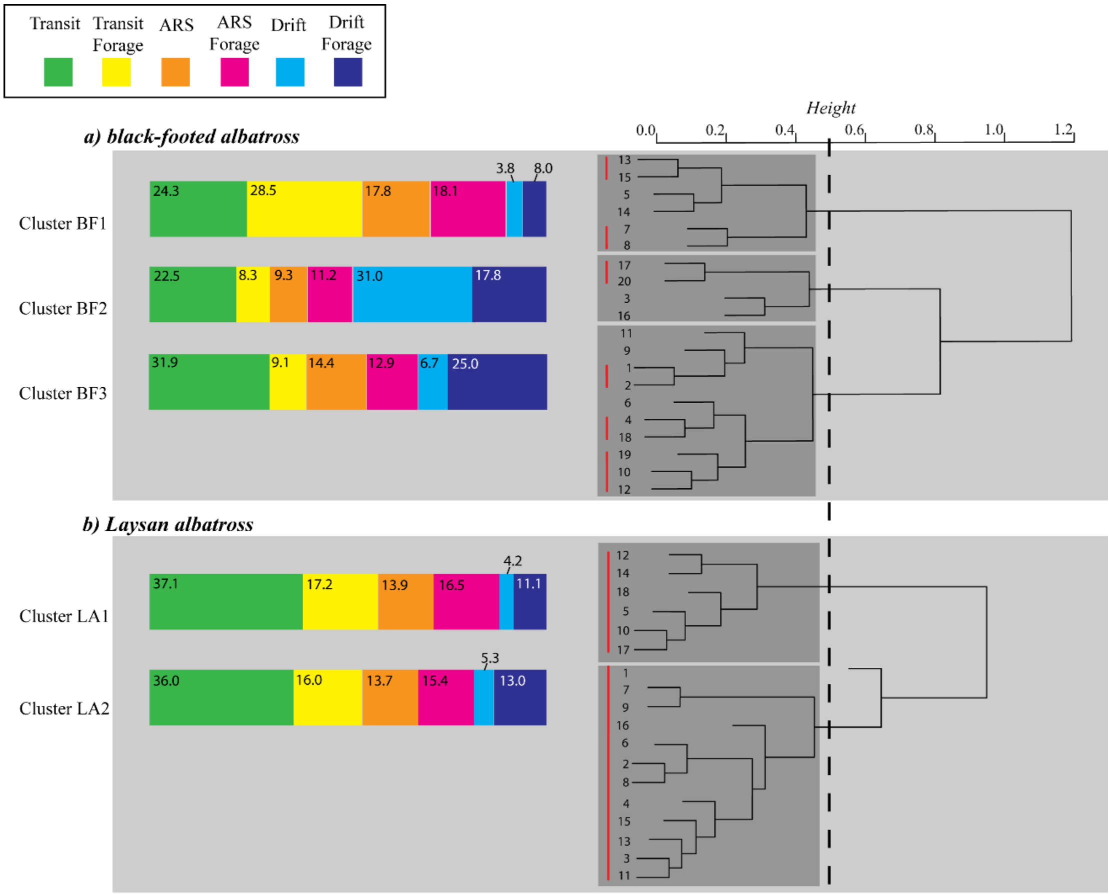


Figure 1.9 'Pvclust' clustering output with the corresponding population-level foraging patterns shows higher population variability for black-footed albatrosses than for Laysan albatrosses.

The 50% similarity level is indicated with the dotted black line providing the threshold for population-level foraging patterns (dark grey shaded rectangles). Clusters significant at the P > 0.95 significance level are indicated with the vertical red lines. The mean behavioral composition of trips of birds in each cluster are given as colored bar diagrams with normalized means of each behavioral state (% trip).

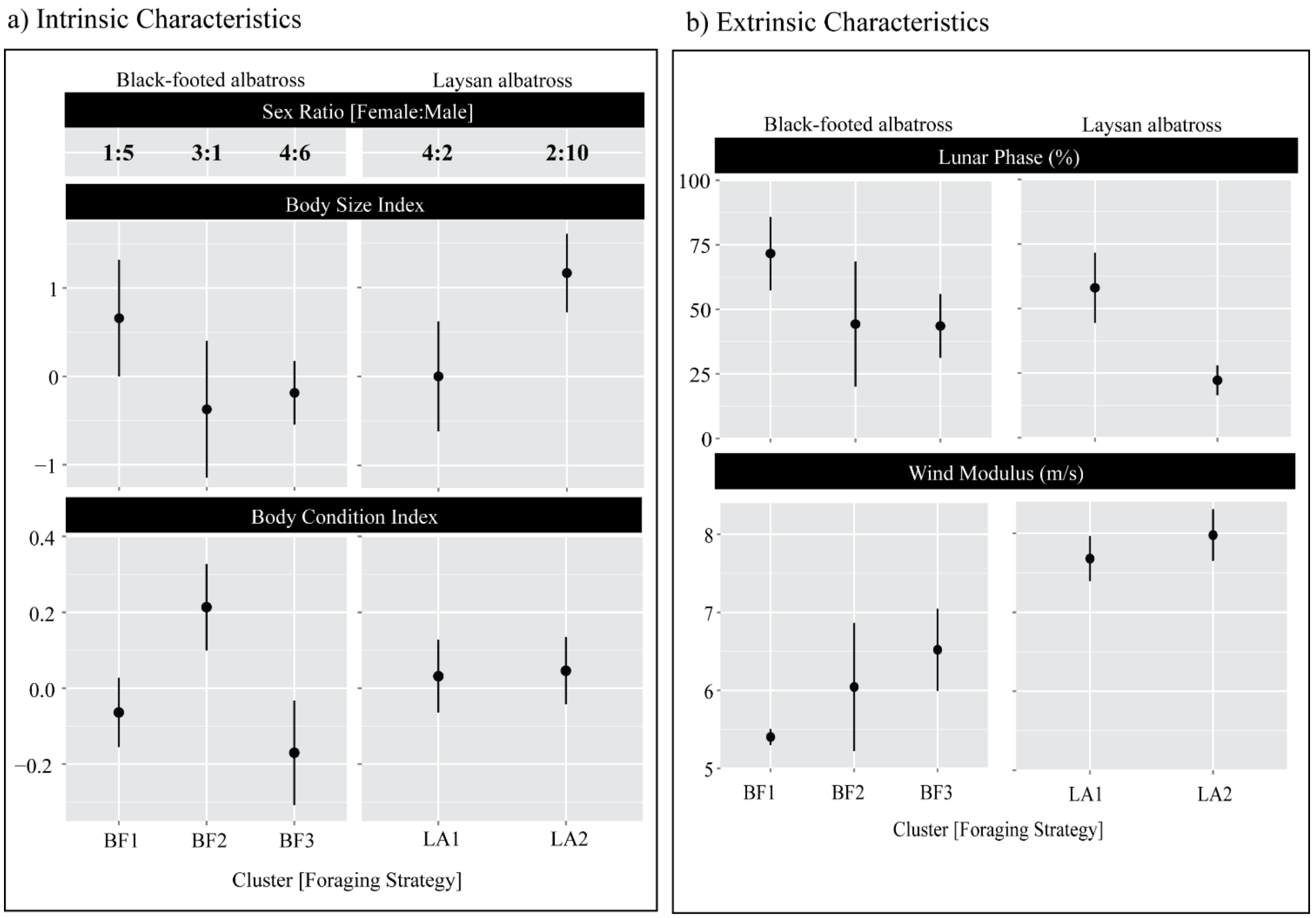
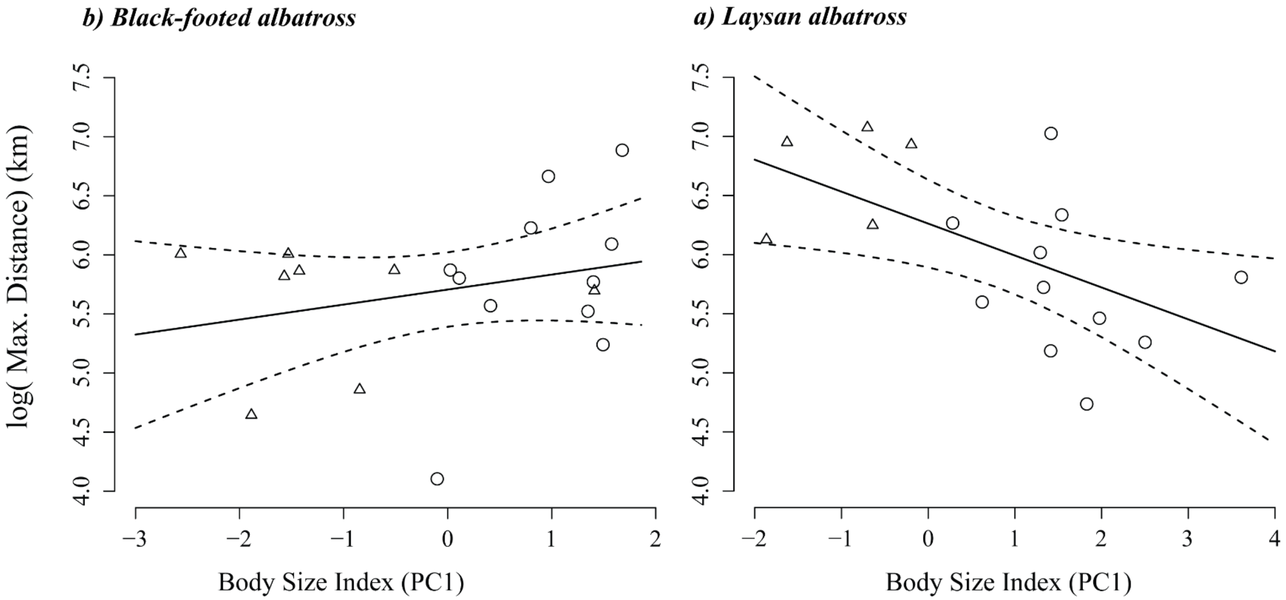


Figure 1.10 The effect of intrinsic and extrinsic factors on foraging patterns in black-footed and Laysan albatross.

Factors are plotted as means ± SE.


b) Black-footed albatross

a) Laysan albatross

Figure 1.11 Female Laysan albatrosses reach more distant foraging grounds than males

A linear regression shows no relationship between body size and maximum distance in black-footed albatrosses ($F_{1,17}$ = 1.26, P = 0.28, R^2 = 0.07), whereas maximum distance shows a significant negative correlation with body size in Laysan albatrosses ($F_{1,14}$ = 6.73, P = 0.02, R^2 = 0.33). For both species, males are plotted with an open circle and females with an open triangle. Dotted lines represent 95% confidence intervals.

2 CHAPTER TWO

Identifying fisheries-associated diet in the stomach oil of tube-nosed seabirds using quantitative lipid analysis.

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Daniel Costa, Scott A. Shaffer

ABSTRACT

Mortality from incidental bycatch in longline fishery operations is a global threat to seabird populations, and especially so for the albatross family (Diomedeidae) in which seventeen out of twenty-two species are threatened. Despite the risks, fisheries remain attractive to many species of seabird by providing access to high-energy foods in the form of discarded fish and offal, target fish, and baited hooks. Current policy regarding fisheries management is increasingly aimed at discard reform, and the first discard ban recently passed in the European Union Fisheries Common. While there is global agreement in the importance of minimizing the waste inherent in bycatch and discards, there is also growing concern that there is a lack of understanding the extent to which seabirds rely on fisheries-associated resources, especially at the colony and individual levels. We used a novel adaptation of quantitative fatty acid analysis (QFASA), to assess the fisheries-associated reliance of two threatened North Pacific albatross species at the colony and individual levels. Albatross diet was estimated with QFASA using multiple lipid classes from stomach oil collected from two species of sympatrically-breeding adult albatrosses across multiple breeding seasons. Prey-specific error was estimated by comparing QFASA estimated diets from known "simulated" diet, which allowed us to interpret diet results on a prey-specific basis. Fisheries-associated diet occurred in both albatross species across both the incubation and chick-brood stages however neither species relied on fisheries food as the dominant food source (~ 10 % of the diet for both species). Despite low overall population dependence, there were some individuals whose diet consisted almost entirely of fisheries-associated food, indicating that some individuals might specialize on this foraging tactic. Our analysis also showed significant species differences in the type of fisheries resource consumed, with black-footed albatrosses scavenging target fish species (swordfish) to a greater extent and Laysan albatrosses predominately consuming fish species used to bait longline hooks, a behavior also observed directly on vessels by fisheries observers. Overall diet characterization of the species highlighted mesopelagic gelatinous squid to be the most dominate food source for both Laysan and black-footed albatrosses, and the amount of squid in the diet increased with age. Both species had similar diet composition during the incubation phase of the breeding cycle, however during the chick-brood phase, black-footed albatrosses showed a significant dietary shift towards flying fish eggs and crustaceans. Overall, black-footed albatrosses showed greater dietary flexibility, which is consistent with recent behavioral analyses. Quantitative fatty acid analysis proved a tractable method for estimating the importance of fisheries-associated resources in the diet of albatrosses, which could be an important management tool for future conservation efforts.

2.1 INTRODUCTION

Incidental mortality from fisheries bycatch is the principle threat to seabird biodiversity, particularly so for albatrosses (Croxall and Gales 1998). Eighteen out of twenty-two recognized species of albatrosses are currently threatened or endangered from extinction, of which four are critically endangered (Gales 2008). Population declines of at least ten albatross species are attributed at least in part to adult mortality from fisheries bycatch, and specifically to demersal and pelagic longline operations (Weimerskirch et al. 1997, Gales and Robertson 1998, Tuck et al. 2001, Lewison and Crowder 2003, Véran et al. 2007).

The widespread impact of fishery bycatch on seabird populations, along with a large economic impact to the fishing industry due to bait loss from scavenging birds (Løkkeborg 2008, Gandini and Frere 2012), incited a global movement in the 1990s to understand seabird-fishery interactions (Brothers 1991, Løkkeborg 2011, Melvin et al. 2014). Subsequent research led to the development of vessel gear such as tori lines and weighted sinker hooks and to operational changes such as night setting and underwater setting chutes (Brothers 1999). When implemented, these changes to fishing operations significantly reduce seabird bycatch (summarized in Gilman et al. 2005), however, the global efficacy of these measures is limited by a non-unanimous implementation among international longline fleets; and fishery interactions, although reduced from historic levels, remain a significant threat to seabird populations.

Despite the risk of injury or death, fisheries remain attractive to many albatross species by providing lipid-rich meals in the form of target fish (Bisson 2008), baited hooks, and discarded bait and offal (Furness 2003, Bicknell et al. 2013). Unwanted fish and offal alone enter the oceans as fisheries waste at the rate of ~ 7.3 million tons a year (Kelleher 2005), and some longline fisheries lose up to 13-14 % of bait due to scavenging birds (Gandini and Frere 2012). High energy content meals made accessible to seabirds through fishery operations, along with fishery-induced collapse of higher trophic level fish stocks, has led to a restructuring of marine communities since the advent of industrial fishing (Pauly et al. 1998, Dayton et al. 2002, Coll et al. 2008). Many seabird species now show behavioral (i.e., Torres et al. 2011, Collet et al. 2015), breeding (i.e., Furness and Tasker 2000, Frederiksen et al. 2004), and dietary (i.e., Bearhop et al. 2001, Votier et al. 2008) responses to industrial fishing efforts. Understanding the degree to which seabird populations rely on fisheries subsidies remains an important, yet, in some cases, intractable problem. Particularly challenging is identifying fisheries-associated food in diet analyses relying on stomach contents. This is especially true for species in the Procelleriformes order, like albatrosses, that rapidly digest prey into a homogenous stomach oil (Warham 1977, Tickell 2000), thereby reducing, if not eliminating, the ability to visually identify fisheries-associated diet in stomach contents.

In addition, while vessel-based studies have significantly advanced our understanding of seabird-fishery interactions, much less is understood about the impact on seabirds at the colony and individual levels (but see Bearhop et al. 2001, Votier et al. 2008, 2010, 2013, Navarro et al. 2009), especially for pelagic seabirds. Colony-specific studies are important for predicting the response of seabird populations to changes in fishery management, such as the recent discard ban of the EU Common Fisheries Policy.

Furthermore, measuring how dependency on fishery-associated resources changes across an annual cycle increases understanding of when populations are most at-risk to both changes in fishing practices (i.e. reduced discards) and to incidental mortality from bycatch. Populations that rely on fishery-associated resources during critical phases of the breeding cycle are vulnerable to changes in fishery policies if they lack flexibility in foraging strategies or if natural resources are difficult to exploit (Oro et al. 1995).

Furthermore, understanding individual variability in response to fisheries is critical for long term management of seabird populations. Generalist seabirds, especially those that scavenge, such as albatross, tend to consume more fisheries discards than others (Bicknell et al. 2013), and, generalist populations are often comprised of individual specialists (Bolnick et al. 2003, Svanbäck and Bolnick 2007, Araújo et al. 2011). Given the skill required for successful capture of bait from hooks during longline setting operations (Bisson 2008), it is likely that some individuals within albatross populations are specializing in a fisheries-dependent foraging pattern over their lifespans, as is seen in other seabird species (Patrick et al. 2015). Additionally, there is growing evidence that individuals in many long-lived seabird species are consistent in the foraging and/or spatial patterns they use (Woo et al. 2008, Patrick et al. 2013, 2015, Patrick and Weimerskirch 2014b, Wakefield et al. 2015), potentially throughout their lifespans. Therefore, when considering fisheries management with regards to seabird populations, it is important to consider not just colony-specific dependence on fishery subsidies, but also the level of consistency in foraging strategies.

Laysan (*Phoebastria immutabilis*) and black-footed (*P. nigripes*) albatrosses are generalist scavengers of the North Pacific and their population trajectories are vulnerable to incidental mortality from fisheries by-catch (Lewison and Crowder 2003, Naughton et al. 2007); particularly so for black-footed albatrosses (Lewison et al. 2004, Véran et al. 2007). Although bycatch rates of albatrosses in U.S. pelagic longline operations dropped after the implementation of mitigation gear on vessels (Anderson et al. 2011), there is little information on birds taken in Japanese and Taiwanese fleets in the North Pacific. Furthermore, the degree of dependence on fisheries subsidies among breeding colonies in the North Pacific is unknown. Likewise, there is no information on the frequency of fisheries-associated individual diet specialization in these albatross species.

An analysis of bulk stable isotopes in the tissues of Laysan albatrosses from a recently established breeding colony on Guadalupe Island off Mexico revealed that birds were more likely to be consuming fish than squid (Henry et al. 2007), however, it is not known whether this reliance on fish was specific to naturally occurring prey in the California Current or to fish exploited from pelagic longline fishery operations. The only comprehensive diet study of both albatross species from breeding colonies in the northwestern Hawaiian Islands was predominately based on accumulated squid beaks that represented feeding that occurred during the late chick-rearing season, and as such does not represent diet across the breeding season (Harrison et al. 1983, Pitman et al. 2004a). Considering the dramatic change in feeding grounds from incubation to chick-guard and to chick-rear stages (Hyrenbach et al. 2002, Kappes et al. 2015), there remains a critical need to understand how diet, including the degree of fisheries exploitation, varies within a breeding season for North Pacific albatrosses.

Traditional diet analyses have provided invaluable insight into Hawaiian albatross feeding ecology (Gould et al. 1997, Pitman et al. 2004a, Walker et al. 2012), however, the methods used in these analyses are limited by their omission of rapidly digested soft-bodied prey (e.g. jellyfish, chunks of swordfish meat). This is especially true for scavenging birds such as albatrosses, that have hyper-acidic stomachs with a pH that can dissolve bone over short periods of time (Grémillet et al. 2012). The foraging trips of adult Laysan and black-footed albatrosses can be very long (up to 30 days) and adults often return with stomachs full of stomach oil and nothing else (*personal obs*.), especially during the incubation and early-chick-guard phases; as a result, there is currently no information about diet of these two species during these critical phases in the breeding cycle.

Biochemical dietary analyses, such as stable isotope, fatty acid, and DNA barcoding, were developed to circumvent the biases of traditional dietary methods using stomach contents and are becoming increasingly important in characterizing diet of free-ranging animals that are difficult to observe and/or sample, such as albatross. Lipids, and specifically fatty acids, have long been used in the forensic detailing of trophic webs both in terrestrial and marine ecosystems (Ackman and Eaton 1966, Connan et al. 2005). Since fatty acids are found in great diversity and, for many, can only be synthesized *de novo* in certain organisms, they can serve as traceable biomarkers in food web studies (Budge et al. 2006).

Initial assessment of lipid composition of procellariform stomach oil indicated high volumes of wax esters and triacylglycerides (Imber 1976) - lipid classes commonly found in storage tissues of marine organisms. Quantitative fatty acid analysis (QFASA) employs a robust statistical model to quantitatively estimate predator diet by identifying the combination of prey lipid signatures most similar to that of the predator while accounting for predator metabolism, and is a proven method that has been used to estimate diet of free-ranging seals, sea lions, seabirds, porpoises and polar bears (Beck et al. 2007, Iverson et al. 2007, Thiemann et al. 2008, Meynier et al. 2010, Bromaghin et al. 2013, Jansen 2013). A critical requirement of QFASA is the collection of a comprehensive library of lipid signatures from potential prey, which is exceedingly challenging for generalist pelagic predators, such as albatross, which regularly forage across entire ocean basins and consume diverse prey. Nevertheless, given access to a comprehensive prey library, procellariform stomach oil is highly suitable for quantitative fatty acid analysis as it is dietary in origin (Place et al. 1989) and thus requires no calibration for predator metabolism, eliminating a large source of error in the model (Bromaghin et al. 2015). Additionally, stomach oil represents diet integrated from days to weeks, and can be treated as longitudinal sampling of the same individual, opening up the possibility of examining individual-based differences in foraging strategies and dietary specialization.

Here, we employ a novel adaptation of QFASA using both fatty acids and fatty alcohols from triacylglycerol and wax ester lipid classes to estimate the diet of individual Laysan and black-footed albatrosses from stomach oil samples. Our objectives were 1) to characterize and compare the diet of two North Pacific albatrosses species across the incubation and chick-brood phases of the breeding season when both species switch from foraging in high latitude temperate waters to warmer subtropical waters, 2) to assess the relative importance of fisheries-associated resources in Laysan and black-footed albatross diet and to test whether year, breeding phase, species, sex or age influence fisheries-associations, and 3) to identify feeding strategies of Laysan and black-footed albatrosses along the spectrum of dietary generalism or specialism.

2.2 METHODS

2.2.1 Study Species

Black-footed and Laysan albatrosses are highly migratory, pelagic surface feeders thought to depend primarily upon visual and olfactory cues to find prey at the ocean surface (Nevitt et al. 2008). Black-footed albatrosses are slightly bigger than Laysan albatrosses by nearly all morphometrics, except for bill length. Within both species, males and females are slightly sexually dimorphic, with males being marginally larger and heavier than females, but there is overlap in all of these morphometric measurements (Tickell 2000, Conners et al. 2015). Single egg clutches are laid in November and December, chicks hatch in January and February, and chicks are guarded and fed frequently by adults into March. The post-guard period, when adults extend the range and duration of foraging trips and chicks are fed infrequent meals, extends into summer until chicks fledge (July-August). The study colony at Tern Island in the French Frigate Shoals (23.870°N, 166.284°W, 712 km northwest of Kauai) supports ~4000 breeding pairs of black-footed albatrosses and ~3000 of Laysan albatrosses and is the only colony in the northwestern Hawaiian islands where the density of black-footed albatrosses is greater than that of Laysan albatrosses (Flint 2009).

2.2.2 Stomach Oil

Procellariform stomach oil is derived directly from prey (Place et al. 1989). The unique gastro-intestinal anatomy of procellariforms results in the build up of neutral lipids inside the stomach following slow gastric-emptying that is biased towards proteins, carbohydrates and aqueous fluid, following mechanical rupture of ingested prey (Place et al. 1989). This unique characteristic of procellariforms is thought to be advantageous for pelagic species relying heavily upon gliding flight as a mechanism to increase transportability of calories (Warham 1977).

Sampling of Albatross Stomach Oil: We collected small aliquots of stomach oil (5-10 mL) from 47 adult black-footed albatrosses and 48 adult Laysan albatrosses breeding at Tern Island, French Frigate Shoals (23.870°N, 166.284°W) across the incubation and brood-guard periods during 2010, 2011, and 2012 (Table 2.1). A small number of chicks were also sampled during the late brood-guard (n = 6 black-footed, n = 5 Laysan, 2010 only). Sampled adults were part of an ongoing tracking study of foraging behavior and each study bird was equipped with either a GPS datalogger or satellite PTT that weighed well below three percent of the birds' body mass, the recommended maximum tag weight for albatrosses. When the birds returned to the colony after a foraging trip, we removed the tracking device, collected stomach oil samples and measured mass and morphometrics (bill length, bill depth, tarsus length). Stomach oil was sampled through stomach intubation, using a sterile #5 Kendall catheter tube attached to a 35 mL plastic monoject syringe. Stomach intubation is a quick procedure (< 3 min.) that is less invasive than other methods of diet sampling, such as forced regurgitations (Karnovsky et al. 2012). Lipid analysis only requires a small amount of oil (1-5 mL) from each bird, substantially less than the volume of diet held by the stomach. Regardless, stomach oil has an extremely high caloric density and serves as an important source of energy and hydration for birds on the nest, so we supplemented the diet of sampled birds with a 35 mL blended mixture of market squid, Ensure® shake, and Pedialyte® solution following the recommendation of a marine wildlife veterinarian. Oil samples were kept frozen in 10 mL cryovials at 20 °C until analysis. Long-term USFWS banding records provided true age and minimum ages for our study birds, and birds were classified into Young (5-11), Adult (12-25), and Old (> 25) age classes. Sex was determined from either 1) a visual assignment (recorded when possible when pairs were seen together) or 2) a discriminant function analysis of morphometrics (see Conners et al. 2015).

2.2.3 Lipid Library of Potential Albatross Prey

Quantitative fatty acid analysis requires a comprehensive library of lipid signatures from all prey species potentially consumed by the predator. North Pacific albatrosses are opportunistic foragers and consume a wide variety of prey using flexible foraging tactics (Conners et al. 2015), therefore collecting a library of all potential prey species for lipid analysis would be both impractical and unfeasible. However, since the fatty acid composition of an organism depends on its feeding ecology, collecting species from a comprehensive array of functional groups regularly consumed by the predator should, in theory, be adequate to represent the range in lipids consumed by the predator. We identified twelve important functional groups of albatross prey, and collected species that would represent these groups (Table 2.2).

Twenty-four species of fish, squid, and crustaceans were collected from the North Pacific Transition Zone (NPTZ), a frontal zone heavily exploited by foraging albatross during the breeding season (Fernández et al. 2001, Kappes et al. 2015, Thorne et al. 2015), using a mid-water trawl, frame trawl, neuston tow, and an automated jigging machine on the M/V Oshoromaru (University of Hokkaido, Japan) in the summer of 2011 (Figure 2.1,Table 2.2). To represent prey from other regions that are important foraging grounds for albatrosses, five additional fish and squid species were collected from a Cobb trawl conducted by National

Marine Fisheries Service in 2012 in waters off the main Hawaiian islands, while one additional species of squid was collected from a demersal fishery off the Oregon-Washington coast in 2014 (Figure 2.1, Table 2.2). Fisheries-associated bait and target fish is an important source of food for albatross (Bisson 2008), so bait (Asian-sourced pacific saury and chub mackerel) was collected from POP Bait supply (Honolulu, HI), the main supplier to the Hawaiian longline fleet. Pacific sardines, sourced from the California Current, were purchased at a market in California as they represent another common bait species used in Hawaiian pelagic longline operations (Bisson 2008). As albatross are known to consume not just bait from fishery operations, but also the catch (Bisson 2008), we additionally purchased Pacific swordfish, sourced from the California Current. Flying fish eggs are a known important source of food for black-footed albatrosses (Harrison et al. 1983) and were collected opportunistically from the albatross breeding colony when found fresh. Albatrosses are known scavengers of marine mammal carcasses, so we included elephant seal blubber lipid data from a concurrent study (Goetsch et al., in preparation). Finally, a unique relationship between North Pacific albatrosses and pacific sunfish was recently described by Takuzo Abe et al. (2012) showing Laysan and black-footed albatrosses eating ecto-parasitic copepods (*P. pennella*) off the skin of ocean sunfish; thus we opportunistically collected *P.pennella* from a Pacific pomfret fished off the M/V Oshoromaru in the NPTZ. When possible, standard lengths of fish, and dorsal mantle lengths of squid were measured to the nearest 0.1 cm; body mass was measured to the nearest 0.1 g. Prey were identified to genus, or species when possible, at the National Marine Mammal Laboratory in Seattle, Washington. In total, thirty-five prey species, spanning all targeted functional groups, were collected for lipid analysis (Table 2.2). All samples were kept frozen at -20 ˚C in plastic bags until analysis.

2.2.4 Lipid analysis

2.2.4.1 *Lipid extraction*

Whole, individual prey samples were homogenized in the lab using scalpels, a blender and an industrial meat grinder. For large neon flying squid (*O. bartrammi, ~1.9 kg*), we isolated the mantle and tentacles only, because given their large size, it is highly unlikely a bird would consume whole individuals. Swordfish and marine mammal samples were also subsampled from the whole specimen (muscle only for swordfish and blubber only for elephant seals). To avoid prohibitive time and cost constraints, rather than analyzing all individuals separately (35 species, > 300 individual specimens) we combined individual prey specimens into species-specific homogenates, from which three 1.5 g subsamples were collected for lipid analysis. Using averaged prey signatures removes information on the variability of lipids between individuals within a species, however since within-species variability in fatty acid composition is small relative to between-species differences (Budge et al. 2002) we believe this method was adequate for the objective of our study. For most species, we collected and combined 15 individuals into our prey homogenate; however, for some difficult to obtain species, such as some mesopelagic gelatinous squids, we had fewer individuals (samples sizes in Table 2.2). Lipids were extracted and purified using chloroform:methanol:water (8:4:3 v/v/v) from prey homogenates following the modified Folch et al. 1957 method, while lipids from albatross stomach oil were extracted using the simplified Folch et al. 1957 method (Budge et al. 2006, Appendix 1. and Appendix 3, respectively).

2.2.4.2 *Isolating triacylglycerols and wax esters*

A preliminary assessment of the lipid classes found in albatross stomach oil found high levels of both triacylglycerols (TAG) and wax esters (Budge, *pers. comm*; also see Warham 1977, Connan and Cherel 2007) reflecting the dietary origin of albatross stomach oil and the high amounts of wax esters commonly found in marine organisms (Imber 1976). We isolated both TAG and wax lipid classes from prey and albatross lipid samples with preparative thin layer chromatography (TLC) by streaking each lipid sample at a concentration of 150 mg/mL [CHCl3] onto a silica-coated glass plate before placing the plate into a developing chamber of hexane:ethyl ether:acetic acid (85:15:1 v/v/v). Plates were developed and dried, then sprayed with 0.2% 2,7-dichlorofluoroscein in ethanol before viewing under UV light. Wax ester and triacylglycerol classes were identified in comparison with standards, scraped off the plate, then eluted with multiple chloroform rinses. Each lipid class per sample was weighed to the nearest mg to provide us with a ratio of TAG:wax ester per sample.

2.2.4.3 *Gas Chromatography*

In preparation for gas chromatography, an acid-catalyzed transesterification procedure converted triacylglyceride and wax ester samples to fatty acid methyl esters and free fatty alcohols (FAME and FAlc, respectively) using an acid catalyst of H_2SO_4/MeOH following Budge et al. 2006, Appendix 4. FAME and FAlc were quantified using temperature-programmed gas liquid chromatography on a Perkin Elmer Autosystem II Capillary FID linked to a computerized integration system (Varian Galaxie software). We used a DB-23 30 m Agilent column with a (50%-cyanopropyl)-methylpolysiloxane phase when analyzing FAME and a ZB-FFAP 30 m Phenomenex column with a nitroterephthalic acid modified polyethylene glycol phase when analyzing FAlc, both with an internal diameter of 0.25 mm and a film thickness of 0.25 µm. Due to low concentrations of FAlc, we used a splitless injection for both FAME and FAlc samples. Initial oven temperature of 60 °C was held for 2 minutes, then rose 45 °C per minute to 150 °C held for 1 minute, after which it rose 4 °C per minute to a final temperature of 240 °C held for 125 minutes. Helium was used as a carrier gas and the gas line was equipped with an oxygen-scrubber. Resulting chromatograms were individually assessed for correct peak identification and reintegrated when necessary. To create a single lipid signature for each sample, the FAME/FAlc constituents from each TAG and wax ester lipid class were weighted separately relative to the TAG:wax ester ratio, before combining into a single lipid signature for that sample. We report fatty acid and fatty alcohol constituents of each sample as weight percent of total.

2.2.4.4 *QFASA modeling*

We estimated albatross diet using the QFASA model developed by Iverson et al. (2004). Before running the QFASA model, we eliminated any FAME and FAlc constituents that were on average less than 0.1 % of the sample, unless they were greater than 0.2 % in any sample. After removing insignificant constituents, the FAME and FAlc remainder were renormalized and retained for diet modeling (Supplemental Table 1). Since albatross oil is dietary in origin we did not subset our suite of FAME/FAlc constituents to those considered ‘dietary’ (versus ‘structural’) as is common in studies using QFASA to estimate diet from tissue (blubber, adipose tissue) where lipids have been metabolically reconstituted. Final diet estimates modeled using QFASA were given as biomass consumed (% diet) of each prey in the diet of each individual albatross. To assess the importance of each prey and functional group of prey in albatross diets, we calculated percent frequency of occurrence (number of individuals with a prey species divided by the total number of birds) and percent pooled diet (proportion of a prey species in total diet when all individuals were combined).

2.2.5 Understanding prey-driven error in the QFASA model

Given that albatrosses are opportunistic, generalist predators, requiring a large and diverse library of prey lipids, we felt it important to understand similarities and dissimilarities of prey species according to their lipid composition. Non-metric multi-dimensional scaling (NMDS) and a hierarchical cluster analysis were used to visualize the distance among prey species relative to their FAME/FAlc constituents both at the species level and at the level of functional group. To more rigorously quantify the performance of the QFASA model specific to our library of prey lipids, we quantified error in QFASA diet estimations running known simulated “pseudo-diets” through the QFASA model. 16456 pseudo-diets were simulated at random from a modified dirichlet distribution, and for each simulated pseudo-diet, 50 diet estimations were modeled by the QFASA model. For each of the pseudo-diet simulations, model error was defined as the mean difference of the 50 QFASA estimations from the “true” pseudo-diet was calculated. Mean error of the QFASA estimates was calculated at the species level and at the functional group level.

2.2.6 Statistical analyses

Permutational multivariate analysis of variation (PERMANOVA), simper and hierarchical cluster analyses of lipid data were run in PRIMER statistical software. All other statistical analyses were conducted in R 3.1.1 (R Core Team 2014). Significance was set to $P \leq 0.05$ and marginal significance to $P \leq 0.10$.

After assessing the variability in error of the QFASA model specific to our prey library, we ran statistical analyses on diet composition by functional groupings rather than the full suite of prey species. For some analyses, functional groups were further subdivided by collection location. The response of multivariate diet compositions to intrinsic factors (species, sex) and extrinsic factors (breeding phase, year) were tested with PERMANOVAs. Multivariate response variables (% of each functional group in diet) were not transformed before analysis, because they were compositional in structure and therefore scaled between 0 and 1. Bray-Curtis distance was used to create dissimilarity matrices between all pairs of variables for use in subsequent analyses. Post-hoc simper analyses (Clarke 1993) examined the percentage contributions to Bray-Curtis dissimilarities in diet composition for tested factors (species, sex, breeding phase, and year) that were significant in per-MANOVA analyses. To further explore relationships between diet composition and tested factors, we used canonical analyses of principle components to visualize the strength of the association between each functional group of prey and factors of interest. Zero-inflated count models tested for the effect of year, breeding phase, sex and age on the proportion of fisheries-associated food in albatross diets.

Feeding strategies of Laysan and black-footed albatrosses were visualized using Amundson-Costello diagrams (Costello 1990). Prey-specific percentage abundances (i.e. each prey's percent contribution in only those stomachs that contained that particular prey) were plotted against frequency of occurrence of each prey. Prey items that clustered together with high prey-specific % abundance and high frequency of occurrence indicate specialism at the population level, whereas high prey-specific % abundance but low frequency of occurrence indicates specialism at the individual level. Generalist populations are represented by prey types with high frequency of occurrence and low to moderate prey-specific % abundances.

2.3 RESULTS

The overall lipid content and proportion of triacylglyceride and wax ester lipid classes from each prey species (n=34) and of stomach oil samples from albatrosses (n=95) are presented in Supplemental Table 1 along with their FA and FAlc compositions.

2.3.1 Qualitative assessment of prey similarity by lipid signatures

There was clear differentiation between some but not all functional groups using multi-dimensional scaling (Figure 2.3). Species from crustacean and fish egg functional groups clustered together and were relatively isolated, while species from the other functional groups, mostly mesopelagic squid and fish, showed varying degrees of overlap, mostly driven by dissimilarities between species classified under the same functional group (Figure 2.3). Jellyfish were most closely associated with crustaceans, whereas northern elephant seal blubber clustered with mesopelagic gelatinous squid collected from the North Pacific Transition Zone. Species within the same functional group but collected in different regions showed dissimilarities in lipid signatures as seen from the MDS plot. For example, squid collected around local Hawaiian waters clustered away from squid collected in the North Pacific Transition Zone. Large vertically-migrating muscular squid (i.e. *G. borealis*, *O.*

borealjaponicus) clustered close to small epipelagic (muscular) squid (i.e. *A. felis, B. anonychous*) and myctophid fish, while they clustered away from mesopelagic gelatinous squid (i.e. *Taonius sp*., *Galiteuthis sp*.). Asian-sourced Pacific saury (*C. saira*) clustered away from both adult and juvenile Pacific saury sourced in the North Pacific Transition Zone. Longline-associated prey as a functional group showed the greatest dissimilarity among group members, likely because species were classified as longline-associated prey for reasons unrelated to their own feeding ecology (Figure 2.3). The hierarchical cluster analysis showed similar relationships between functional groups as inferred from the MDS plot Figure 2.4).

2.3.2 Species and functional group error associated with QFASA modeling

The amount of error in diet estimations from the QFASA simulations varied substantially among functional groups of prey and also among species within the same functional group (Figure 2.5 – Figure 2.7). Crustaceans, flying fish eggs and jellyfish were ranked the highest in QFASA estimation accuracy (Figure 2.7). Mesopelagic gelatinous squid and small epipelagic fish ranked the next highest followed by longline-associated bait and target fish, and ectoparasitic copepods. Small, epipelagic squid were chronically overestimated while vertically-migrating muscular squid were chronically underestimated (Figure 2.5 – Figure 2.7). Most species of mesopelagic fish were only marginally overestimated and only when known pseudo-diet proportions were low, with the exception of *S. leucopsaurus* which had the largest species-specific error and was regularly underestimated, even at higher proportions in pseudo-diets (Figure 2.6). Plotting QFASA estimations against known “pseudo-diets” for each species showed that most prey species were spuriously overestimated when percentage contribution to the “pseudo-diet” for that species was low (< 10 %) (Figure 2.5), but accuracy in QFASA estimations for most, but not all, species increased with increasing percentage contribution to the “pseudo-diet” of that species (Figure 2.5).

2.3.3 Albatross Diet:

Detailed diet estimations, including frequency of occurrence and percent of pooled diet for black-footed and Laysan albatrosses are shown in Table 2.3 and Table 2.4. Breeding albatrosses from Tern Island consumed a broad diversity of prey across all functional groups, except ecto-parasitic copepods (both species) and small epipelagic fish (black-footed albatrosses only). Mesopelagic gelatinous squid dominated the diet for both species accounting for about approximately 30 % of the diet of each species across the breeding season (Table 2.3 and Table 2.4, Figure 2.8 - Figure 2.12). The vertically-migrating muscular squid functional group was the next largest component of diet for both species, however, the importance of this functional group was more significant in the incubation phase of the breeding cycle, especially for Laysan albatrosses. Flying fish eggs were a significantly large component in the diet of black-footed albatrosses (22 %) but only during the chick-brooding season. Consumption of flying fish eggs also occurred during incubation for black-footed albatrosses but to a much smaller degree (5 %). Only a single Laysan albatross diet estimation had flying fish eggs present, but they were the dominant prey item for this particular individual (69 % of the diet), indicating a rare but potentially important food item for this species. Mesopelagic fish (myctophids), fisheries-associated diet, crustaceans and small epipelagic squid were common in diet of both species, but were less dominant functional groups than mesopelagic gelatinous squid or vertically migrating muscular squid. Marine mammal blubber, small epipelagic fish and jellyfish were present, but rare, in albatross diet.

2.3.4 Effect of Species, Breeding Phase, Sex and Age on Diet Composition:

Overall diet composition was significantly different between Laysan and black-footed albatrosses for both phases of the breeding cycle (incubation: $t_{1,61} = 1.75$, $P = 0.002$; chick-brood: $t_{1,41} = 1.85$, $P = 0.005$). Although diet composition changed significantly between incubation and chick-brood breeding phases in black-footed albatrosses ($t_{1,51} = 1.74$, $P = 0.01$), it did not in Laysan albatrosses ($t_{1,51} = 0.94$, $P = 0.53$). Simper and CAP analyses highlighted which prey species drove significant differences in diet composition (Figure 2.13). Black-footed albatrosses had greater diet abundances of crustaceans, fish eggs, longline target fish (swordfish) and mesopelagic gelatinous squid collected from the California Current than Laysan albatrosses, which had higher abundances of all squid functional groups collected from the North Pacific Transition Zone as well as mesopelagic fish and longline bait. Chick-brooding black-footed albatrosses had higher abundances of crustaceans and fish eggs than did incubating birds, which ate more squid and mesopelagic fish (Figure 2.10 & Figure 2.12). Chick-brooding Laysan albatrosses had higher abundances of small epipelagic squids and longline bait while incubating birds consumed more muscular and mesopelagic gelatinous squid (Figure 2.11 & Figure 2.12).

Sex did not influence overall diet composition in either species (black-footed: $t_{1,46}$ = 0.77, P = 0.76 and Laysan: $t_{1,45}$ = 0.89, P = 0.60 , respectively). Age class did, however, significantly effect diet composition but only for Laysan albatrosses, where young birds had significantly different diet from both the adult and old age classes ($t_{1,28}$ = 1.28, P = 0.09; $t_{1,6}$ = 1.93, P = 0.03, respectively). Simper analyses indicated that older birds of both species had higher abundances of muscular squid and mesopelagic gelatinous squid than younger birds, while younger birds of both species had greater amounts of crustaceans, and mesopelagic fish in their diets (Table 2.5).

2.3.5 Fisheries-associated diet

The proportion of fisheries-associated prey in diet estimations was not different between the species (z = -0.85, P = 0.39), however, the two species differed significantly in their mode of exploitation (Figure 2.14). Black-footed albatrosses had significantly more longline-associated target fish (swordfish) in their diet than Laysan albatrosses (z = -2.79, P = 0.005), and Laysan albatrosses had significantly more longline-associated bait fish in their diet (z = 2.26, P = 0.02). Year, breeding phase, sex, and age were all nonsignificant effects and so were removed in final models.

2.3.6 Dietary specialization in albatrosses

Despite overall broad population-level diet, bar plots of raw diets (Figure 2.8 and Figure 2.9) and of diets grouped by functional group (Figure 2.10 and Figure 2.11) revealed that both species have some degree of individual dietary specialization with many individuals consuming over 60 % of a single functional group of prey (with one black-footed albatross consuming up to 93 % of mesopelagic gelatinous squid in a foraging trip during incubation). Using the 60 % cut-off, black-footed albatrosses had more individuals that had specialized diets than Laysan albatrosses, particularly so during the incubation, where many individuals specialized on mesopelagic gelatinous squid or mesopelagic fish. During the chick-brood phase, individual black-footed albatrosses specialized on a broader array of functional groups than during the incubation phase, including squid and fish but also flying fish eggs and longline-associated resources. Laysan albatrosses only showed a few individuals with specialized diets during incubation, with those individuals specializing on mesopelagic gelatinous and muscular squid. During chick-brood, Laysan albatrosses, like black-footed albatrosses, showed specialization on a broader array of functional groups with some individuals consuming over 60 % if squid, fish, longline-associated resources, flying fish eggs and jellyfish.

Amundson-Costello plots further enhanced our understanding of the dietary niche widths of the two species at an individual and population level (Figure 2.15). Not surprisingly, the most dominant functional group of prey in the diet of both species was mesopelagic gelatinous squid. Crustaceans and small epipelagic squid were as common in the diets of both species as mesopelagic gelatinous squid, but individual albatrosses did not specialize on these groups. Overall, the functional groups consumed by Laysan albatrosses clustered in the ‘high occurrence / low abundance’ sector of the plot, suggesting overall generalization at the population and individual levels. For black-footed albatrosses, however, many functional groups clustered at the ‘low occurrence / high abundance’ sector of the plot, suggesting a population with a greater degree of individual dietary specialization.

2.4 DISCUSSION

2.4.1 Incidence of fisheries-associated resources in albatross diet

Fisheries-associated prey occurred in the diets of Laysan and black-footed albatrosses across both breeding stages, but neither species appeared to rely on fisheries-related food as a dominant or primary food source. However, although the occurrence was low, it was not insignificant (at ~ 10 % of population diet for both species). Furthermore, the diet of a few individuals consisted almost entirely of fisheries-associated resources (i.e., 87 % of diet of one Laysan albatross consisted of longline bait) indicating that some individuals might specialize on fisheries resources. This result suggests that more long-term monitoring of diet variability within individual albatrosses breeding in the northwestern Hawaiian Islands to understand individual variability in fisheries reliance and whether specialization on fisheries resources is a short or long term strategy within individuals. Given the skill required for gleaning bait off longline hooks (Bisson 2008), it is reasonable to think that once an individual develops this skill, it is maintained by continued exploitation of lipid-rich fish species used as longline bait. Patrick and Weimerskirch 2014a described a relationship between personality and foraging strategy in albatrosses, which suggests an underlying genetic structure to different foraging strategies. If different foraging strategies impose different risks or lead to birds with poorer body conditions (Votier et al. 2010), this could have important implications for management strategies of populations.

The similarity in the importance of fisheries-associated prey in the diet of Laysan and black-footed albatrosses was unexpected given disproportionally higher bycatch rates of black-footed albatrosses documented by U.S. fisheries observer programs (Arata et al. 2009). These similar rates of fisheries exploitation might be specific to the colonies breeding at Tern Island. Black-footed albatrosses breeding on Tern Island have smaller foraging ranges than Laysan albatrosses, at least during the chick-brood season (Conners et al. 2015, Kappes et al. 2015), and as a result might overlap less with fisheries than birds from other colonies. Furthermore our diet sampling occurred across only a few breeding seasons and fishery dependence is likely to fluctuate across years, as seen in inter-annual variability in bycatch rates (Votier et al. 2008). Long-term monitoring of albatross diets from breeding colonies in the northwestern Hawaiian Islands is critical to understand the dynamics of inter-annual variability in fisheries dependence for Hawaiian-breeding albatrosses. Boluses, regurgitated by fledgling albatrosses, are regularly collected from albatross colonies in the northwestern Hawaiian Islands to monitor diet variation. Although useful for understanding squid diversity in albatross diet, boluses do not retain any tracer of fishery resources or other soft-bodied prey.

Distributions of squid, the dominant food of albatrosses, are strictly dictated by sea-surfaces temperatures, and squid show species-specific temperature preferences for feeding and spawning grounds (Ichii et al. 2009, 2011, Vijai et al. 2014). Given the anomalously warm sea-surface temperatures in the central and eastern North Pacific over the last few years (Bond et al. 2015), the distributions and ranges of squid occurrence are predicted to contract and shift northward if temperature anomalies persist (Alabia et al. 2015). How albatrosses respond to changing squid distributions is unknown. Foreseeably, they could shift foraging ranges to track squid distributions during part of the year, however, during the chick-brood phase of the breeding season, foraging ranges are highly constrained, leaving albatrosses with limited options. Here, albatrosses might respond with an increased dependency on non-cephalopod resources, such as fisheries-associated diet. Natural resource managers that monitor Laysan and black-footed albatross populations should develop consistent and long-term monitoring programs that track both natural (i.e. squid) and anthropogenic (i.e. fisheries-associated resources) contributions to albatross diets.

Despite similar overall exploitation of fisheries-associated resources, diet differences between Laysan and black-footed albatrosses indicate that the species use different feeding strategies when they interact with fishing vessels. Fisheries-associated resources in black-footed albatross diets were solely limited to swordfish meat, indicating this species predominately scavenges target fish, while Laysan albatrosses more heavily exploited baitfish. These results are congruent with direct observations of feeding behavior of the two species at swordfish and tuna fishing vessels (Bisson 2008), validating the accuracy of QFASA in estimating fisheries diet in albatross to some degree. Notably, behavioral differences at fisheries vessels might have health consequences: black-footed albatrosses have 400 % higher mercury body burdens than Laysan albatrosses (Finkelstein et al. 2006). Although Finklestein and colleagues convincingly linked species differences in mercury loads to habitat differences rather than diet, our results suggest that the greater consumption of swordfish meat in black-footed albatrosses may also contribute to higher mercury loads, given the remarkably high levels of mercury in swordfish meat compared to other fish species (USFDA 2015).

2.4.2 Deep, mesopelagic layer feeds surface-scavenging albatross

Consistent with recent studies of squid beaks collected from Laysan and black-footed albatross stomachs (Walker et al. 2012, Pitman 2004), our results also indicate that breeding North Pacific albatrosses primarily scavenge dead mesopelagic gelatinous squid that float to the ocean surface. Furthermore, relative abundances of squid species estimated from QFASA are congruent with Walker et al. (2012), further validating QFASA as a viable method to characterize the diets of North Pacific albatrosses. The present study and Walker et al. (2012) both highlight Cranchiidae and Histioteuthidae to be the most important squid families in North Pacific albatross diet. Our results also agree in the differences in squid composition between the two species, where both studies found higher abundances of Gonatidae and Cranchiidae, but lower abundances of Histioteuthidae, in Laysan albatross diet relative to that of black-footed albatrosses. Between-species diet differences in squid composition is likely a function of the distinct at-sea segregation between these two species, where Laysan albatrosses forage in colder waters of higher latitudes than black-footed albatrosses during the breeding season (Kappes et al. 2010, Kappes et al. 2015).

Diet estimations from QFASA corroborate previous studies describing the squid component of North Pacific albatross diet, but additionally and importantly, broaden these conclusions by highlighting other functional groups exploited by albatross, such as mesopelagic fish, crustaceans, fish eggs and longline-associated resources. Mesopelagic fish (myctophids) were relatively important in albatross diet (> 10 %), and particularly so for incubating black-footed albatrosses in which a subset of individuals showed high dietary specialization on this functional group (up to 77 % of the diet of one individual during incubation). A previous study of the fine-scale behavior of Laysan and black-footed albatrosses described how both species increase “sit-and-wait” foraging behavior on moonless nights when the deep scattering layer is closer to the surface (Chapter 1, Conners et al. 2015). Mesopelagic fish and red pelagic shrimp in the diet might be captured by this “sit-and-wait” foraging strategy by birds at night, however, there are observations of black-footed albatrosses eating red pelagic shrimp in daylight (Miller 1940), so interpretations about nocturnal foraging from diet composition should be cautious. Deploying video-recording cameras on free-ranging albatrosses to collect direct behavioral observations of foraging albatross across day and night would be invaluable to clarify our understanding of albatross foraging behavior and feeding ecology.

2.4.3 Greater behavioral and dietary flexibility in black-footed albatrosses

Diet composition changed significantly in black-footed albatrosses from the incubation to the chick-brood breeding phase, however, the diet of Laysan albatrosses remained consistent across the breeding season. The two species showed similar diet compositions during incubation, feeding primarily on mesopelagic squid and fish. During the chick-brood, however, black-footed albatrosses reduced their consumption of fish and squid while increasing in the consumption of flying fish eggs and crustaceans. Flying fish eggs were previously thought to be the dominant food of black-footed albatrosses during the breeding season (Harrison et al. 1983, Tickell 2000), but our results suggest that while they are an important component of chick-brood diet, mesopelagic gelatinous squid remains the most important functional group. Although Laysan albatrosses consumed similar proportions of prey across the breeding season, they fed on more vertically-migrating muscular squid (Gonatid species, in particular) during the incubation. Feeding ranges of incubating Laysan albatrosses extend into the cold waters of the North Pacific Transition Zone and subarctic gyre, which overlaps with distributions of cold water Gonatid species (Watanabe et al. 2006).

Consistency in Laysan albatross diet across the breeding season is concomitant with recent findings of Thorne et al. 2015 and Conners et al. 2015 (Chapter 1) that indicate Laysan albatrosses have less flexibility in foraging behavior than black-footed albatrosses. Thorne et al. 2015 further linked less flexibility in foraging behavior with reduced reproductive success in years of “poor” environmental conditions, highlighting potential demographic consequences of these behavioral differences. While Laysan albatrosses are generalist foragers in the context of our twelve defined functional groups, more than 60 % of their diet is composed of squid, classifying this species as a squid specialist. Thus, while black-footed albatross populations are currently considered more vulnerable to fishery bycatch than Laysan albatrosses (Lewison et al. 2004, Véran et al. 2007), their behavioral and dietary flexibility might impart greater adaptable to warming ocean temperatures than Laysan albatrosses if prey distributions shift with a changing climate (Hazen et al 2011, Alabia 2015). When prioritizing conservation actions for these species, managers should consider a suite of threats, including dependency on fisheries food subsidies, adult mortality from fisheries bycatch, loss of breeding colonies from sea level rise, and changing prey distributions due to climate change.

2.4.4 Older albatrosses consume more squid than younger birds

Dietary niche separation of age classes occurs in a number of seabird species, typically with young or immature age classes foraging at lower trophic levels than adults (Forero et al. 2005, Votier et al. 2011) reflecting an ‘ontogenetic niche shift’ (Werner and Gilliam 1984), although this is not always the case (Campioni et al. 2015). In our study, older birds consumed more mesopelagic gelatinous squid and vertically-migrating muscular squid, suggesting that learning and experience are important to find and exploit this prey type. Most squid species consumed by North Pacific albatrosses are only available to scavenging birds after the squids spawn and subsequently die (Pitman et al 2004, Walker et al 2012) since they are either too large to capture alive (i.e. adult G. borealis) or are a species that do not inhabit surface waters (i.e. Cranchiidae spp.). Thus, albatrosses are most likely consuming these squid after spawning events when spent individuals die and subsequently float to the surface. Using memory and experience to time their arrival in waters where squid spawning events occur might provide older albatrosses a selective advantage to exploit these prey. Age is known to influence the post-breeding distributions of North Pacific albatrosses with older birds having smaller home ranges, indicating that older birds need to search less than younger birds for prey (Chapter Three). Squid, however, are not the most lipid-rich functional group of prey consumed by albatross (Supplementary Table 1), so it is surprising that lipid-rich crustaceans and myctophids were more abundant in the diets of younger birds. Possibly, given the large biomass of mesopelagic squid, spawning events provide dense aggregations of moribund squid carcasses at the surface of the ocean, so if an individual knowns how to find these patches, the low lipid contents of squid might pay off in large amounts consumed.

2.4.5 Estimating diet with QFASA: the good, the bad, and the ugly

By quantifying the species-specific error in QFASA and comparing our diet estimates with direct observations of albatross diet from previous studies (Walker et al. 2012, Pitman et al. 2004, Bisson 2008, Henry 2011, Gould 1997, Harrison 1983), we show that QFASA, overall, accurately estimated the diet of North Pacific albatrosses. The overall accuracy of our diet estimations was likely a consequence of 1) modeling not just one, but two, lipid classes in QFASA, 2) not requiring a calibration coefficient to account for predator metabolism because albatross oil is dietary in origin, and most importantly, 3) collecting a large and comprehensive prey library of lipids representing prey consumed by North Pacific albatrosses across their range.

As seen in species-specific plots of ‘true’ pseudo-diet plotted against QFASA estimated diet (Figure 2.5), the majority of error in QFASA estimations came from underestimating species in mid ranges of % diet and overestimating species in low ranges of % diet. Error biased towards some functional groups over others reflected the particular trophic structure of our specific prey library, with most error occurring in species that co-occur and feed on each other in the mesopelagic zone, and less error occurring in functional groups unrelated (trophically) to each other (i.e. flying fish eggs). Some species were particularly problematic. For examples, northern lanternfish, *S. leucopsaurus,* is a midwater myctophid that dominates the biomass of midwater fishes in some regions of the Pacific and as such is preyed on by a multitude of predators, from fish and cephalopod to marine mammal and seabirds (Beamish et al. 1999). This species, however, was poorly estimated in our model, being chronically under-estimated. This may be due to the likelihood that, given its abundance, it is a common food of other species collected in our prey library and therefore its lipid signature might be similar to many predators in our library. This species was never estimated in any amount in the diet of either albatross species, but due to the chronic under-estimation associated with this species, we do not know whether it truly was not in the diet of albatross or if it was never estimated in diet due to modeling error. However, Walker et al (2012) found only trace amounts of this myctophid in the stomach contents of by-caught Laysan albatrosses and only in Alaskan-caught birds, with none in Hawaiian-caught birds – an observation which provides us with some measure of confidence in our QFASA estimation for this prey species despite the quantified error from simulations. This example highlights the importance of interpreting results of QFASA in combination with other methods of diet analysis such as stomach content analysis or DNA barcoding.

We stress the importance of estimating the performance of QFASA specific to each implementation, because each predator is going to have a different suite of prey lipids which will orchestrate their own unique set of error. Estimating error specific to each prey species in a given prey library greatly facilitates interpretation of QFASA results – as seen in our study, some species were estimated very well, while others very poorly; ultimately leading us to group prey by functional group for statistical analyses. Overall, estimating albatross diets with QFASA proved to be a highly effective method that provided diet estimations of these species across multiple stages of the breeding season for the first time. Additionally, QFASA proved a tractable method for estimating the importance of fisheries-associated resources in the diet of albatrosses, which could be an important management tool for future conservation efforts.

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Table 2.1. Sample sizes of albatross stomach oil by species breeding phase and year.

Species	n	Age	Breeding	2009/2010	2010/2011	2011/2012
Black-footed	53	Adult	Incubation	13	17	2
			Chick-Brood	12	0	4
		Chick	Late Brood	5	0	0
			Totals	30	17	6
Laysan albatrosses	53	Adult	Incubation	14	15	2
			Chick-Brood	15	0	2
		Chick	Late Brood	5	0	0
			Totals	34	15	4

Table 2.2 Species collected for the lipid prey library to be used in QFASA estimations of albatross diet. Thirty-eight species of twelve functional groups were collected across the North Pacific from six different locations.

	Code†	Site*	Scientific Name	Common Name	n	Length (cm)	Mass (g)
1	SES	NPTZ	*Abrialopsis felis*	-	14	4.51 ± 0.72	4.37 ± 1.11
2	SES	NPTZ	*Berryteuthis anonychous*	Minimal armhook squid	6	9.31 ± 0.48	25.47 ± 4.5
3	SES	HA-LOC	*Hyaloteuthis pelagica*	Glassy flying squid	15	5.59 ± 1.01	5.71 ± 3.74
4	SES	HA-LOC	*Abraliopsis pacifica*	-	4	4.98 ± 1.05	18.35 ± 2.34
5	CRS	NPTZ	*Acanthephyra purpurea*	Red pelagic shrimp	14	~10	8.77 ± 2.42
6	CRS	NPTZ	*Boreomysis kinkaidi*	Pelagic mysid	6	~4	0.62
7	CRS	NPTZ	*Calanus spp.*	Copepod	> 20	-	-
8	CRS	NPTZ	*Euphausiia pacifica*	North Pacific krill	> 20	-	-
9	MYC	NPTZ	*Diaphus theta*	California headlightfish	15	7.54 ± 0.60	8.43 ± 2.1
10	MYC	NPTZ	*Lampanyctus jordani*	Brokenline lanternfish	15	9.1 ± 0.86	10.01 ± 2.84
11	MYC	NPTZ	*Lampadena urophaus*	Sunbeam lampfish	2	10.6 ± 0.28	16.25 ± 7.43
13	MYC	NPTZ	*Stenobrachius leucopsaurus*	Northern lampfish	21	9.92 ± 0.34	14.65 ± 1.59
14	MYC	NPTZ	*Tarletonbeania taylori*	-	14	4.29 ± 0.23	2.48 ± 0.35
15	MSQ	NPTZ	*Chiroteuthis spp.*	-	2	19.25 ± 14.64	48.65 ± 38.68
16	MSQ	NPTZ	*Galliteuthis phyllura*	-	3	43.27 ± 11.70	86.83 ± 61.15
17	MSQ	NPTZ	*Octopoteuthis deletron*	Eight armed squid	3	14.2 ± 0.70	128.2 ± 7.26
18	MSQ	NPTZ	*Taonius spp.*	-	2	38.8 ± 7.50	168.45 ± 43.77
19	MSQ	CC-GOA	*Stigmatoteuthis dofleini*	-	1	-	565
20	MSQ	HA-LOC	*Grimalditeuthis bonplandi*	-	1	16.5	-
21	VSQ	NPTZ	*Gonatus berryi*	Berry armhook squid	1	19.70	102.90
22	VSQ	NPTZ	*Ommastrephes bartrammi*	Neon flying squid	9	190.12 ± 60.10	1901.3 ± 601.0
23	VSQ	NPTZ	*Gonatopsis borealis*[1]	Octopus squid	15	23.5 ± 2.26	429.84 ± 129.17
24	VSQ	NPTZ	*G. borealis*[2]	Octopus squid	5	15.28 ± 2.02	103.61 ± 23.83
25	VSQ	NPTZ	*O. borealjaponica*[2]	Boreal clubhook squid	10	21.94 ± 2.86	264.07 ± 95.04
26	VSQ	HA-LOC	*Stenoteuthis oualeniensis*	Purpleback flying squid	15	12.86 ± 1.15	106.59 ± 38.73

Table 2.2 Continued:

	Code†	Site*	Scientific Name	Common Name	n	Length (cm)	Mass (g)
27	SEF	NPTZ	*Cololabus saira*[2]	Pacific saury	15	10.8 ± 0.93	6.8 ± 1.6
28	SEF	HA-LOC	*Exocotidae sp.*	Flying Fish	1	15.5	57.84
29	LLB	NPTZ	*C. saira*[1]	Pacific saury	2	25.6 ± 2.69	99.75 ± 22.00
30	LLB	ASIA	*C. saira*[1]	Pacific saury	5	26.18 ± 0.70	79.62 ± 5.82
31	LLB	ASIA	*Scomber japonicus*	Chub mackerel	5	20.14 ± 1.04	122.02 ± 46.66
32	LLB	CC	*Sardinops sagax*	Pacific sardine	3	18.93 ± 0.75	112.55 ± 7.25
33	LLT	CC	*Xiphius Gladius*	Pacific swordfish	3	-	-
34	BLB	CC-COL	*Mirounga angustirostris*	Northern elephant seal	45	-	-
35	FFE	HA-LOC	*Exocotidae sp*	Flying Fish Eggs	3	-	-
36	JLY	NPTZ	*unkown pelagic disc jellyfish*	Jellyfish sp.	10	-	-
37	JLY	CC	*Vellela vellela*†††	By-the-wind sailors	15	7.43 ± 0.59	6.14 ± 1.37
38	PAR	NPTZ	*Pennella spp.*	-	1	15.7	2.2

† Functional Group Code: SES: Small Epipelagic Squid; CRS: Crustacean; MYC: Mesopelagic Fish (myctophids); MSQ: Mesopelagic Gelatinous Squid; VSQ: Vertically-Migrating Muscular Squid; SEF: Small Epipelagic Fish; LLB: Longline Fishery Bait Fish; LLT: Longline Fishery Target Fish; BLB: Marine Mammal Blubber; FFE: Flying Fish Eggs; JLY: Cnidarian; PAR: Ectoparasitic Copepod.

*Collection Site Code: NPTZ: North Pacific Transition Zone M/V Oshoromaru ; HA-LOC: Local Hawaiian waters Cobb Trawl; CC: California Current; CC-GOA: CC-COL: Ano Nuevo State Reserve; blubber biopsy from Goetsch C. manuscript in prep. ; ASIA: Asian-sourced bait from long-line supplier

†† Samples were combined in order to have a large enough lipid sample for analysis

††† Were not able to extract measurable lipid from this species

[1] Adult specimen

[2] Juvenile specimen

Table 2.3 Percent frequency of occurrence (% FO) and percent of pooled diet (% pooled) of prey items identified to lowest taxon in breeding black-footed albatrosses from Tern Island, 2009-2012.

		Black-footed Albatrosses			
		Incubation		Chick - Brood	
		% FO	% Pooled	% FO	% Pooled
Crustaceans		**75**	**6.54**	**76**	**14.83**
ACANTHEPHYRA					
	Acanthephyra purpurea	75	5.7	67	13.0
MYSIDAE					
	Boreomysis kinkaidi	47	0.9	10	0.3
EUPHAUSIIDAE					
	Euphausiia pacifica	0	0	0	0
CALANIDAE					
	Calanus sp.	0	0	0	0
Ectoparasitic Copepod		**0**	**0**	**0**	**0**
PENNELLIDAE					
	Pennella pennella	0	0	0	0
Mesopelagic Fish		**31**	**13.93**	**24**	**8.25**
MYCTOPHIDAE					
	Diaphus theta	13	5.8	5	4.1
	Lampanyctus jordani	13	2.6	14	2.5
	Lampadena urophaus	22	5.5	14	1.7
	Stenobrachius leucopsaurus[3]	0	0	0	0
	Tarletonbeania taylori	0	0	0	0
Small, Epipelagic Fish		**16**	**0.97**	**14**	**1.03**
SCOMBERESOCIDAE					
	Cololabis saira	0	0	0	0
EXOCOETIDAE					
	Exocoetus sp.	0	0	0	0
Longline-Associated Bait Fish		**16**	**0.97**	**14**	**1.03**
SCOMBERESOCIDAE					
	Cololabis saira[1,3]	13	0.9	5	0.7
	Cololabis saira[1]	3	0.1	5	0.3
SCOMBRIDAE					
	Scomber japonicus	0	0	0	0
CLUPEIDAE					
	Sardinops sargax	0	0	0	0
Longline-Associated Target Fish		**28**	**6.08**	**19**	**9.74**
XIPHIIDAE					
	Xiphias gladius	28	6.1	19	9.7
Flying Fish Egg Mass		**16**	**5.37**	**43**	**22.39**
EXOCOETIDAE					
	Exocoetus sp.	16	5.4	43	22.4

Table 2.3 Continued:

	Black-footed Albatrosses			
	Incubation		Chick-Brood	
	% FO	% Pooled	% FO	% Pooled
Small, Epipelagic Squid	**63**	**10.67**	**43**	**3.22**
ENOPLOTEUTHIDAE				
Abrialopsis felis	6	0.1	14	0.3
Abrialopsis pacifica	0	0	0	0
GONATIDAE				
Berryteuthis anonychous	31	2.5	19	1.2
OMMASTREPHIDAE				
Hyaloteuthis pelagica	31	8.1	14	1.7
Mesopelagic Gelatinous Squid	**94**	**37.37**	**81**	**29.46**
CHIROTEUTHIDAE				
Chiroteuthis sp.	28	2.9	24	3.3
Grimalditeuthis bonplandi	9	3.8	5	0.8
CRANCHIIDAE				
Galliteuthis sp.	25	5.3	10	3.4
Taonius sp.	50	13.4	33	6.2
OCTOPOTEUTHIDAE				
Octopoteuthis deletron	0	0	0	0
HISTIOTEUTHIDAE				
Stigmatoteuthis dofleini	9	7.8	29	13.4
Vertically-Migrating Muscular Squid	**41**	**16.58**	**29**	**10.33**
GONATIDAE				
Gonatus berryi	59	4.2	33	2.3
Gonatus borealis[1]	25	6.6	10	1.8
Gonatus borealis[2]	0	0	0	0
ONYCHOTEUTHIDAE				
Onychoteuthis borealjaponicus	0	0	5	0.8
OMMASTREPHIDAE				
Sthenoteuthis oualensis	34	10.0	24	7.1
Ommastrephes bartrammi	0	0	5	0.6
Marine Mammal	**9**	**2.28**	**5**	**0.74**
PHOCIDAE				
Mirounga angustirostris	9	2.3	5	0.7
Cnidarian	**3**	**0.20**	**0**	**0**
Unidentified cnidarian	3	0.2	0	0

[1] Adult specimen

[2] Juvenile specimen

[3] Asian-sourced

Table 2.4 . Percent frequency of occurrence (% FO) and percent of pooled diet (% pooled) of prey items identified to lowest taxon in breeding Laysan albatrosses from Tern Island, 2009-2012.

		Laysan Albatrosses			
		Incubation		Chick - Brood	
		% FO	% Pooled	% FO	% Pooled
Crustaceans		**94**	**9.27**	**73**	**8.66**
ACANTHEPHYRA					
	Acanthephyra purpurea	84	6.5	73	7.8
MYSIDAE					
	Boreomysis kinkaidi	74	2.5	36	0.9
EUPHAUSIIDAE					
	Euphausiia pacifica	3	0.3	0	0
CALANIDAE					
	Calanus sp.	0	0	0	0
Ectoparasitic Copepod		**0**	**0**	**0**	**0**
PENNELLIDAE					
	Pennella pennella	0	0	0	0
Mesopelagic Fish		**52**	**13.18**	**59**	**14.02**
MYCTOPHIDAE					
	Diaphus theta	0	0	5	2.3
	Lampanyctus jordani	26	7	27	7.6
	Lampadena urophaus	39	5.6	36	4
	Stenobrachius leucopsaurus[3]	0	0	0	0
	Tarletonbeania taylori	6	0.6	5	0.1
Small, Epipelagic Fish		**16**	**2.77**	**14**	**0.71**
SCOMBERESOCIDAE					
	Cololabis saira[2]	16	2.8	14	0.7
EXOCOETIDAE					
	Exocoetus sp.	0	0	0	0
Longline-Associated Bait Fish		**42**	**4.10**	**23**	**5.65**
SCOMBERESOCIDAE					
	Cololabis saira[1,3]	32	3.3	18	1
	Cololabis saira[1]	10	0.7	9	4.5
SCOMBRIDAE					
	Scomber japonicus	0	0	0	0
CLUPEIDAE					
	Sardinops sargax	6	0.1	5	0.2
Longline-Associated Target Fish		**10**	**3.20**	**14**	**3.18**
XIPHIIDAE		0	0	5	3.2
	Xiphias gladius	10	3.2	14	3.2
Flying Fish Egg Mass		**0**	**0**	**5**	**3.20**
EXOCOETIDAE					
	Exocoetus sp.	0	0	5	3.2

Table 2.4 Continued:

		Laysan Albatrosses			
		Incubation		Chick-Brood	
		% FO	% Pooled	% FO	% Pooled
Small, Epipelagic Squid		**74**	**12.31**	**86**	**13.14**
ENOPLOTEUTHIDAE					
	Abrialopsis felis	6	0.3	5	0.1
	Abrialopsis pacifica	0	0	5	0.2
GONATIDAE					
	Berryteuthis anonychous	61	10.6	64	8.1
OMMASTREPHIDAE					
	Hyaloteuthis pelagica	23	1.4	23	4.6
Mesopelagic Gelatinous Squid		**97**	**30.55**	**91**	**33.07**
CHIROTEUTHIDAE					
	Chiroteuthis sp.	29	4.5	23	3.9
	Grimalditeuthis bonplandi	3	1	9	3.4
CRANCHIIDAE					
	Galliteuthis sp.	45	10.3	41	8.5
	Taonius sp.	29	3.7	23	7.8
OCTOPOTEUTHIDAE					
	Octopoteuthis deletron	6	0.6	5	1.3
HISTIOTEUTHIDAE					
	Stigmatoteuthis dofleini	6	3.2	9	3.1
Vertically-Migrating Muscular Squid		**55**	**23.81**	**50**	**10.55**
GONATIDAE					
	Gonatus berryi	90	7.2	64	5.1
	Gonatus borealis[1]	45	18	27	5.6
	Gonatus borealis[2]	3	0.5	5	0.5
ONYCHOTEUTHIDAE					
	Onychoteuthis borealjaponicus	3	0.4	0	0
OMMASTREPHIDAE					
	Sthenoteuthis oualensis	32	4.9	27	4.1
	Ommastrephes bartrammi	0	0	5	0.4
Marine Mammal		**3**	**0.68**	**23**	**4.64**
PHOCIDAE					
	Mirounga angustirostris	3	0.7	23	4.6
Cnidarian		**3**	**0.13**	**5**	**3.17**
	Unidentified cnidarian	3	0.1	5	3.2

[1] Adult specimen

[2] Juvenile specimen

[3] Asian-sourced

Table 2.5 Results from SIMPER analyses indicating the top six functional groups that contributed the most to the dissimilarity between age classes in Laysan and black-footed albatrosses

Arrows indicate the direction of the age trend for each functional group of prey. Average porportions of diet are given for each age class, and light to dark grey shading is relative to the importance of that prey in each age class (darker = larger % in diet). * indicates prey that showed the same trend in both Young-to-Adult and Adult-to-Old comparisons. Percent contribution to dissimilarity between diet compositions of age classes are given for Young/Old and Adult/Old.

	Prey Species	*Age Trend*	***Young***	***Adult***	***Old***	*% contr Yng/Old*	*% contr Adt/Old*
Laysan	Muscular Squid (NPTZ)*	→ →	0	12	34	25.55	24.91
	Crustacean*	← ←	25	8	4	16.53	5.79
	Mesopelagic Fish	-	21	11	17	15.43	15.39
	Mesopel. Gelat. Squid (NPTZ)*	→ →	17	28	33	14.88	17.59
	Marine Mammal*	← ←	21	4	2	13.89	3.44
	Small, Epipelagic Squid (NPTZ)	-	12	4	6	8.18	6.81
Black-footed	Mesopel. Gelat. Squid (NPTZ)*	→ →	19	24	26	15.24	16.25
	Muscular Squid (tropical)	-	8	7	20	14.68	7.71
	Mesopelagic Fish*	← ←	16	10	3	11.35	13.98
	Marine Mammal	-	4	3	16	10.86	11.76
	Muscular Squid (NPTZ)*	→ →	1	8	15	9.93	4.99
	Longline Target	-	9	6	8	8.06	7.81

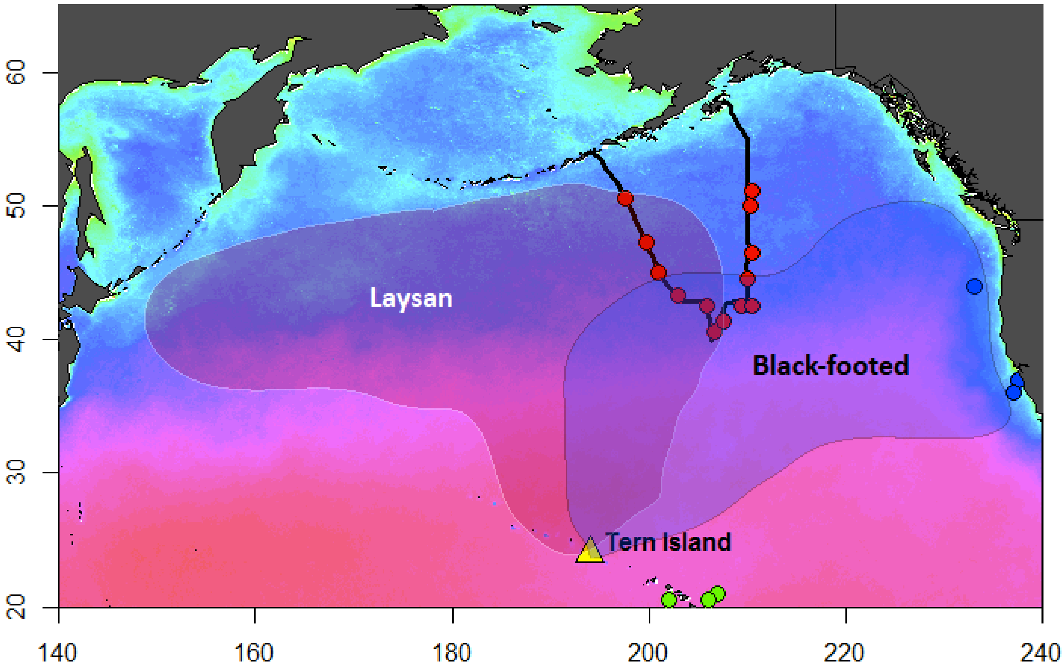


Figure 2.1 Collection sites across the North Pacific for albatross prey specimens

The track of the M/V Oshoromaru is represented by the thick black trackline, and red circles represent the locations of midwater trawls and squid jigging in the North Pacific Transition Zone and Subarctic Gyre. Blue and green circles represent generalized locations where samples were collected in the California Current and in local waters of the main Hawaiian Islands, respectively.

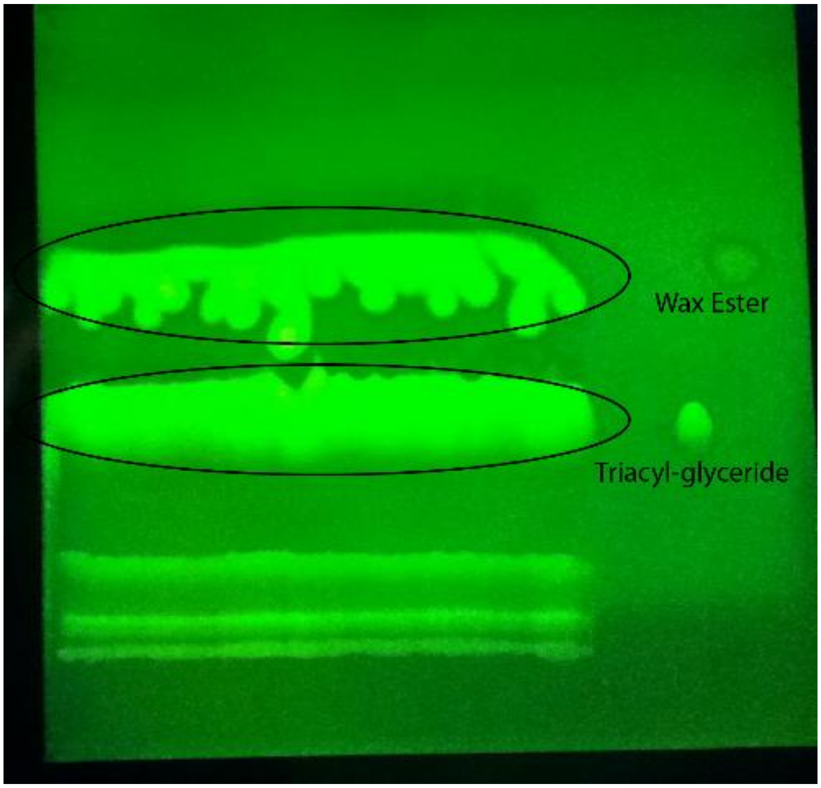


Figure 2.2 Lipid classes in albatross stomach oil

One example of the separation of wax ester and triacylglyceride lipid classes in a sample of albatross stomach oil using the thin layer chromatography technique.

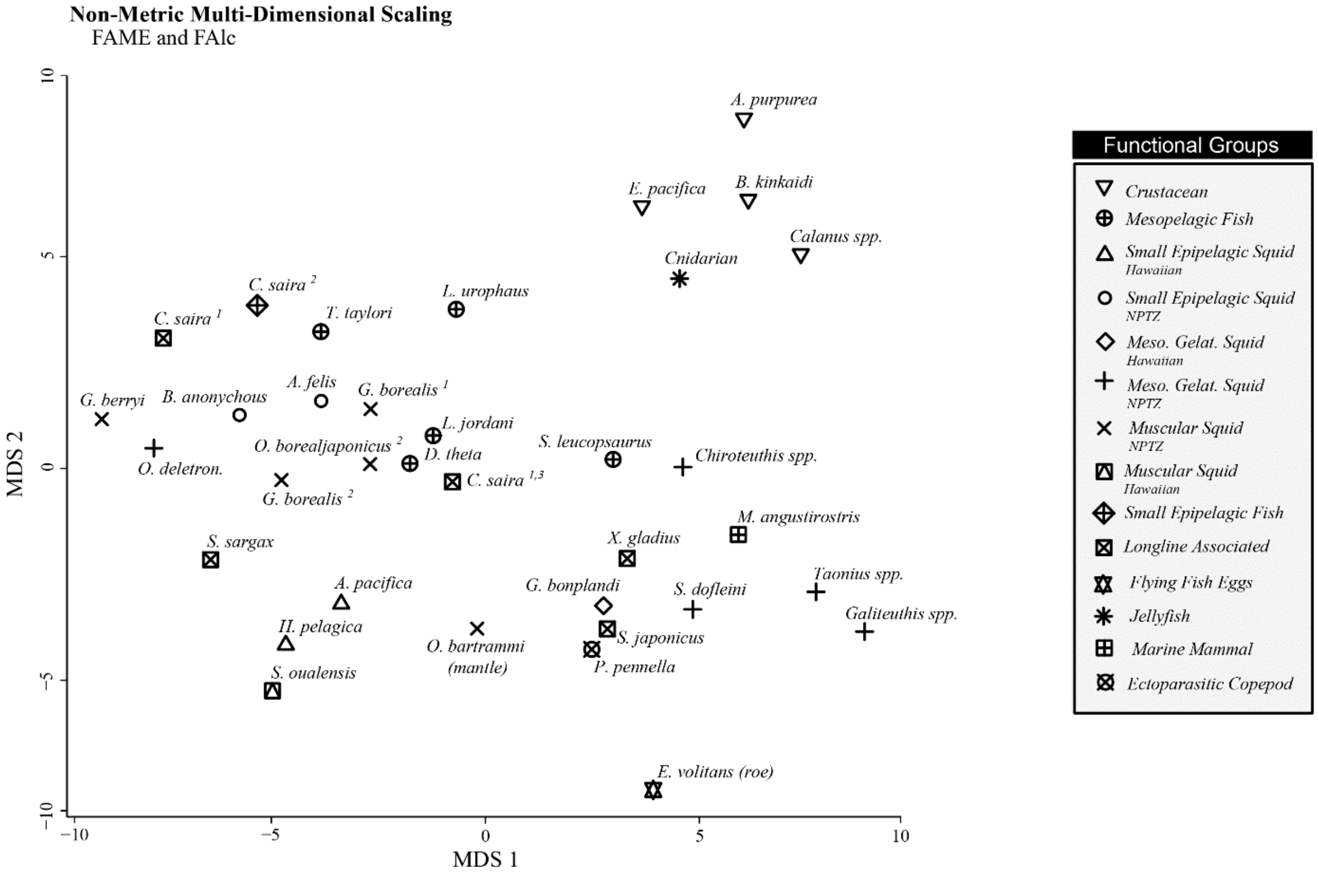


Figure 2.3 . Plot of MDS 1 and MDS 2 scores derived from non-metric multi-dimensional scaling analysis of raw FAME and FAlc values from all species.

Species-specific FAME/FAlc values represent the mean of the species-specific homogenate subsamples. Thirty-five species from fourteen functional groups are represented: ‘Small Epipelagic Squid’, ‘Muscular Squid’, and ‘Mesopelagic Squid’ were further grouped by location of specimen collection (i.e. NPTZ versus Hawaii). [1] adult specimens; [2] juvenile specimens; [3] sourced from Asia

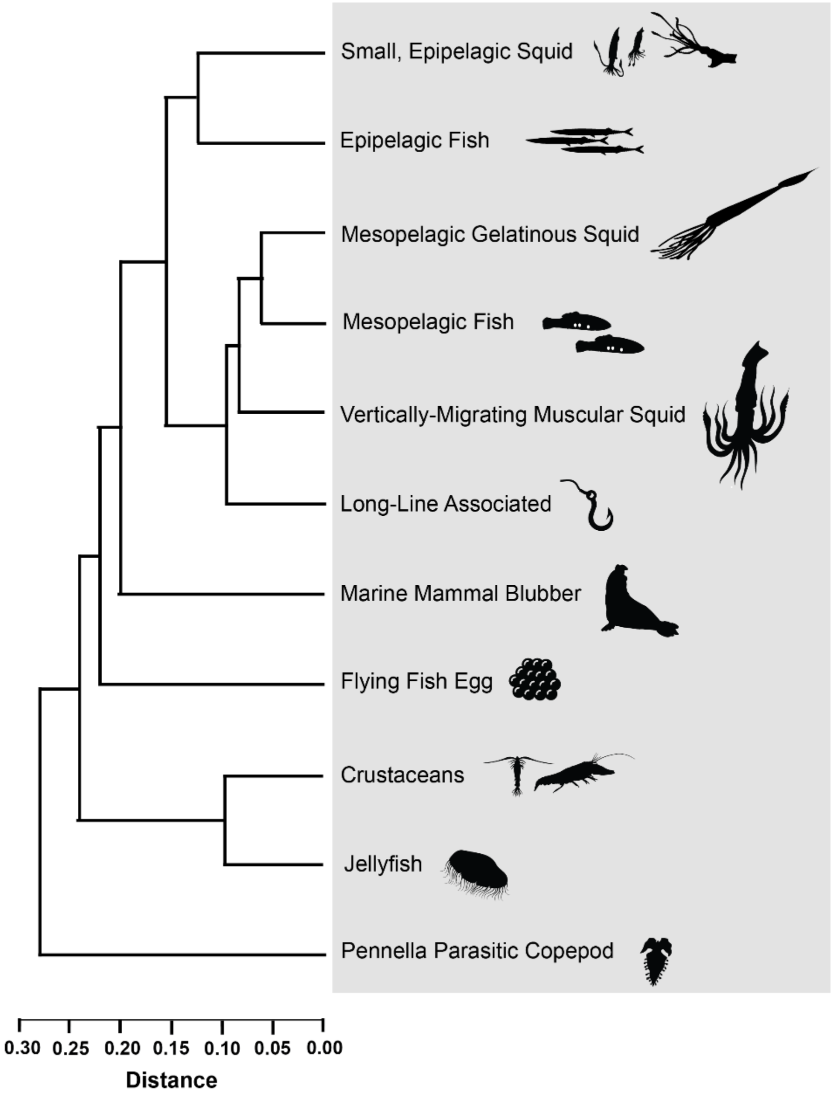


Figure 2.4 A hierarchical clustering analysis on the FAME/FAlc values of prey species using Euclidean distance shows relationships among functional groups of prey based on lipid constituents.

Fish and squid that inhabit the epipelagic zone clustered separately from fish and squid of the mesopelagic. Elephant seal blubber clustered with mesopelagic squid and fish species reflecting their feeding ecology. Fisheries-associated diet also clustered with mesopelagic organisms, but that is likely because species of that particular functional group were classified for reasons outside of their own feeding ecology. Crustaceans and jellyfish clustered together, while flying fish eggs and ectoparasites did not cluster with any other functional group.

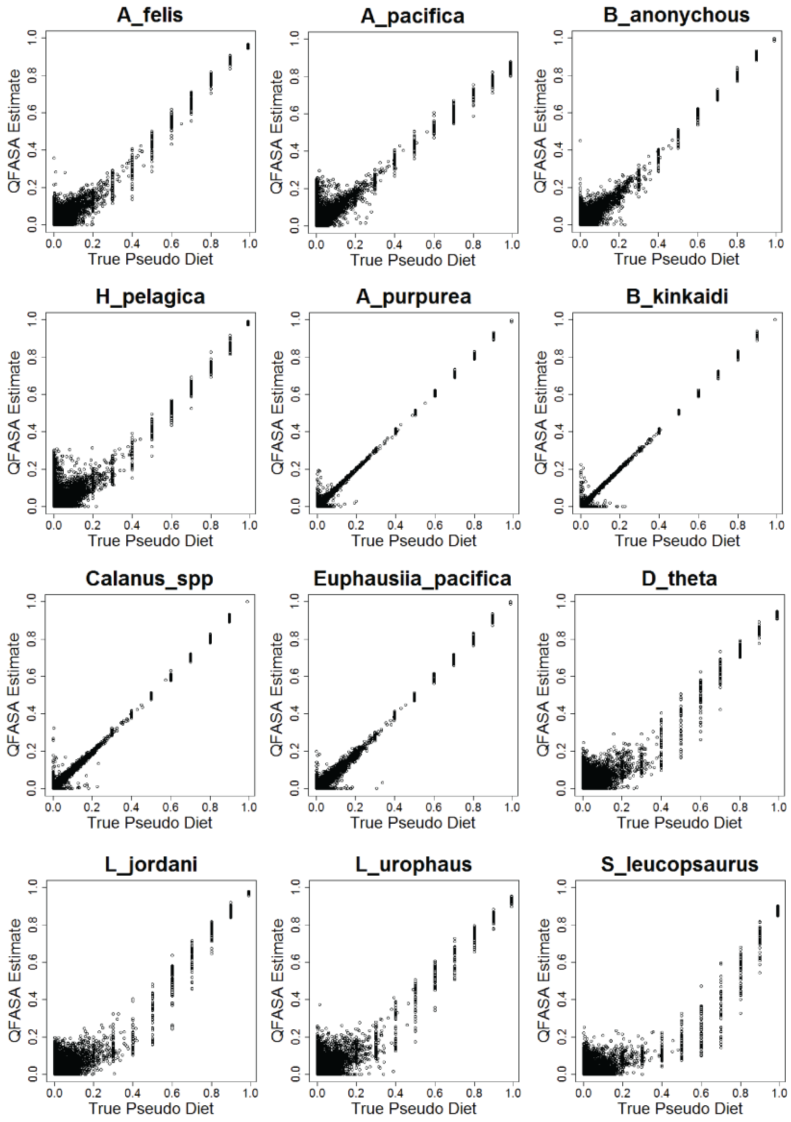


Figure 2.5 Species-specific accuracy of QFASA estimates.

QFASA diet estimates were plotted as a response to “true” known pseudo-diets for all prey species in our prey library. Dirichlet distributions that were used to construct 16456 simulated pseudodiets. Species with the highest estimation accuracy had a near 1:1 linear relationship (i.e. A. purpurea) between known pseudodiets and QFASA estimations. Species that were not estimated accurately had curvilinear relationships between known and estimated diet, usually showing underestimation in mid-values (i.e. S. leucopsaurus). Even the most accurately estimated prey species had some spurious over- and under- estimations at very low known pseudo-diet values.

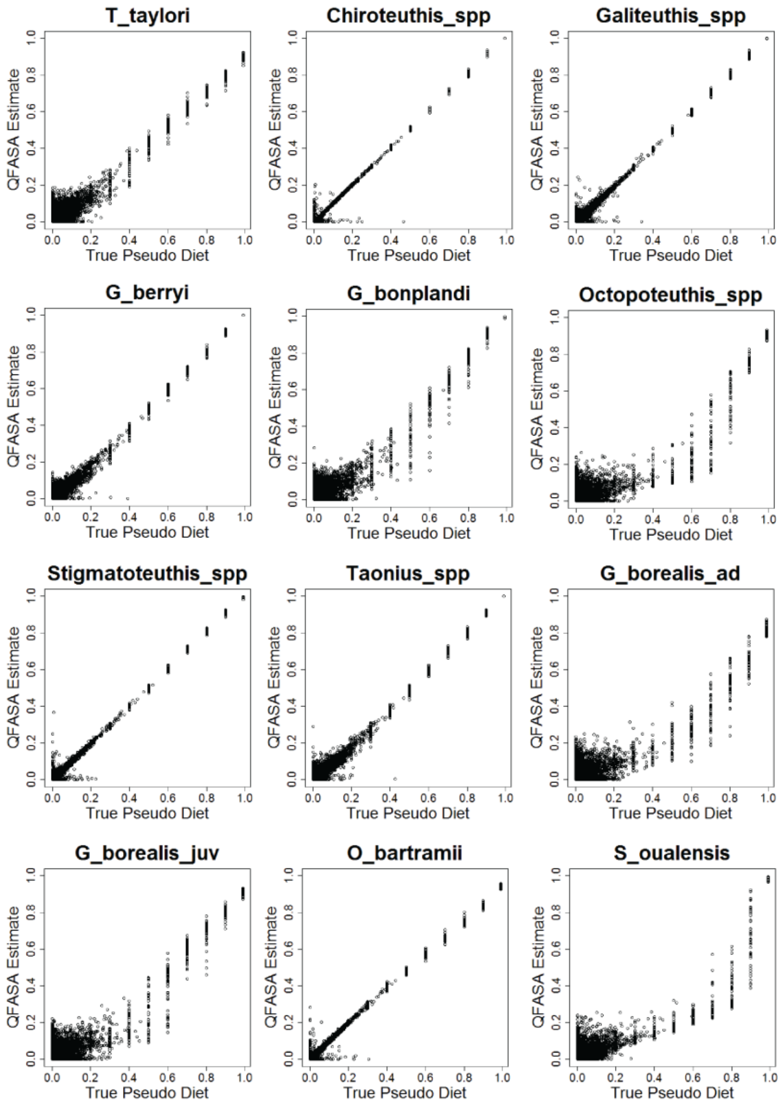
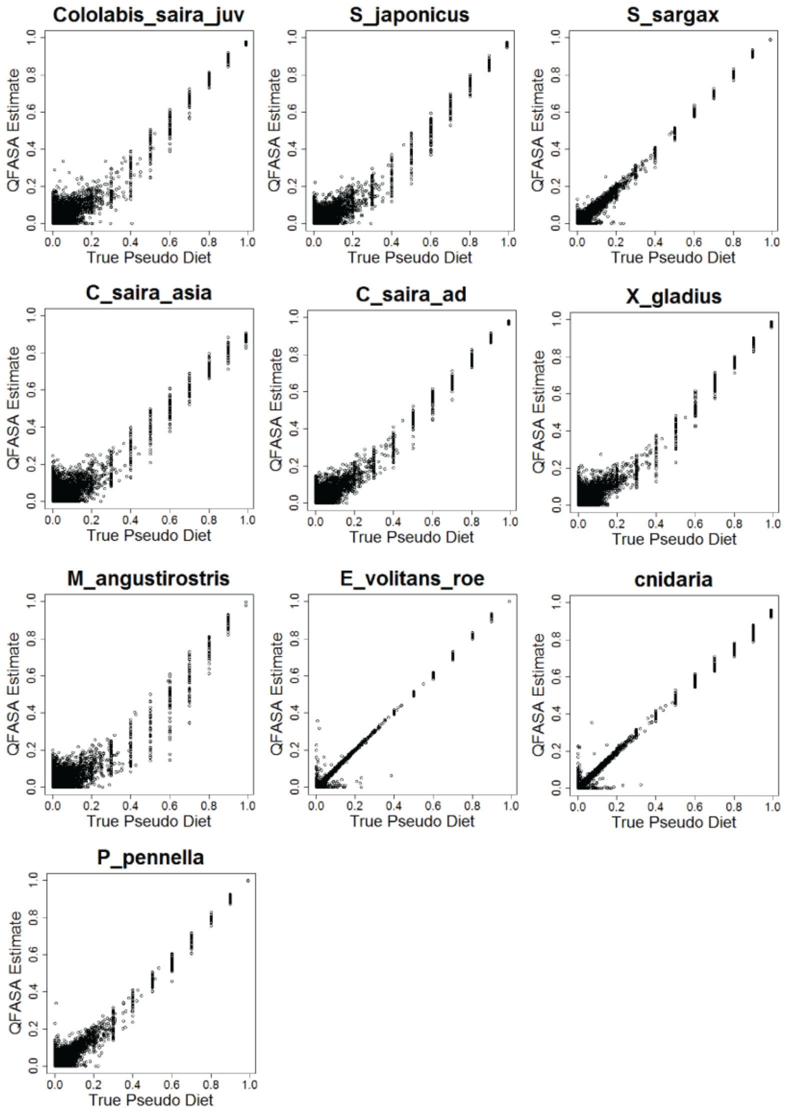


Figure 2.5 CONTINUED. Species-specific accuracy of QFASA estimates.

QFASA diet estimates were plotted as a response to “true” known pseudo-diets for all prey species in our prey library. Dirichlet distributions that were used to construct 16456 simulated pseudodiets. Species with the highest estimation accuracy had a near 1:1 linear relationship (i.e. A. purpurea) between known pseudodiets and QFASA estimations. Species that were not estimated accurately had curvilinear relationships between known and estimated diet, usually showing underestimation in mid-values (i.e. S. leucopsaurus). Even the most accurately estimated prey species had some spurious over- and under- estimations at very low known pseudo-diet values.



Cololabis_saira_juv

S_japonicus

S_sargax

C_saira_asia

C_saira_ad

X_gladius

M_angustirostris

E_volitans_roe

cnidaria

P_pennella

Figure 2.5 CONTINUED. Species-specific accuracy of QFASA estimates. QFASA diet estimates were plotted as a response to “true” known pseudo-diets for all prey species in our prey library. Dirichlet distributions that were used to construct 16456 simulated pseudodiets. Species with the highest estimation accuracy had a near 1:1 linear relationship (i.e. A. purpurea) between known pseudodiets and QFASA estimations. Species that were not estimated accurately had curvilinear relationships between known and estimated diet, usually showing underestimation in mid-values (i.e. S. leucopsaurus). Even the most accurately estimated prey species had some spurious over- and under- estimations at very low known pseudo-diet values

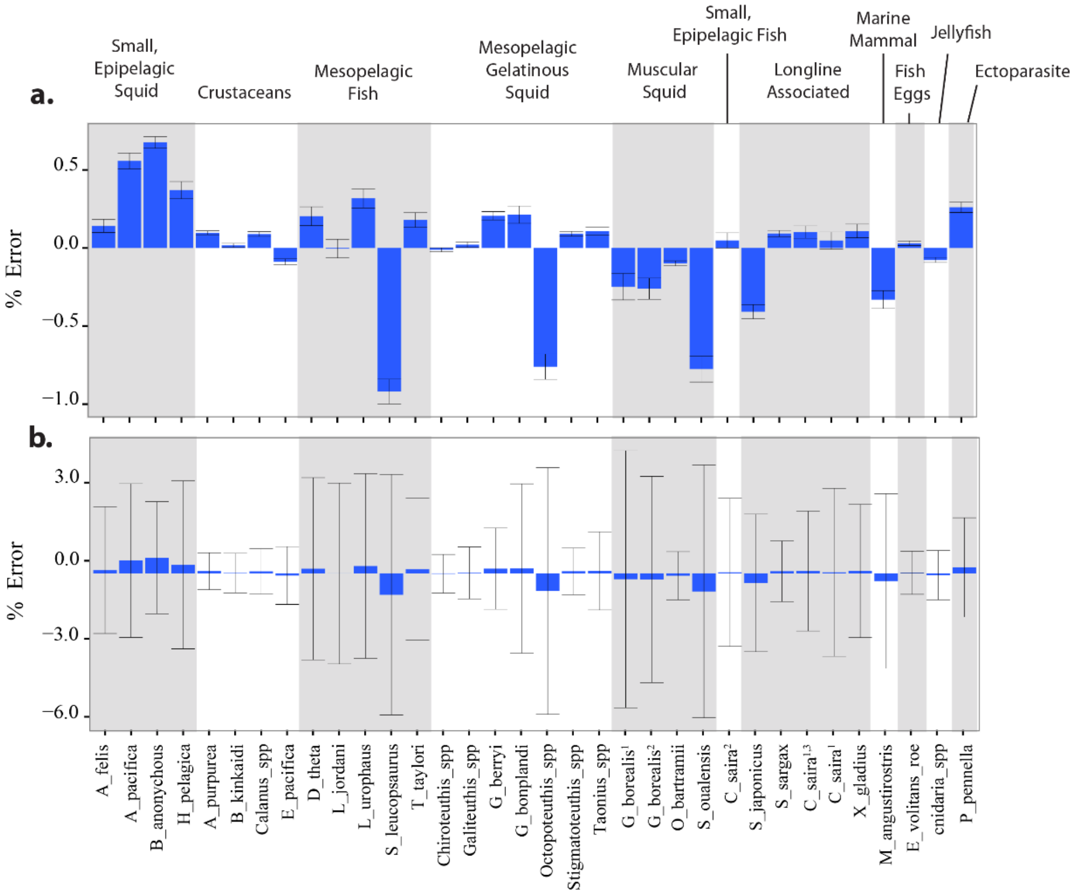


Figure 2.6 Summarized species-specific error in QFASA diet estimations.

a) Species-specific bar plots represent mean error (% QFASA estimate - % True “pseudo-diet”) with 95 % confidence intervals. B) Barplots representing mean error with standard deviations.

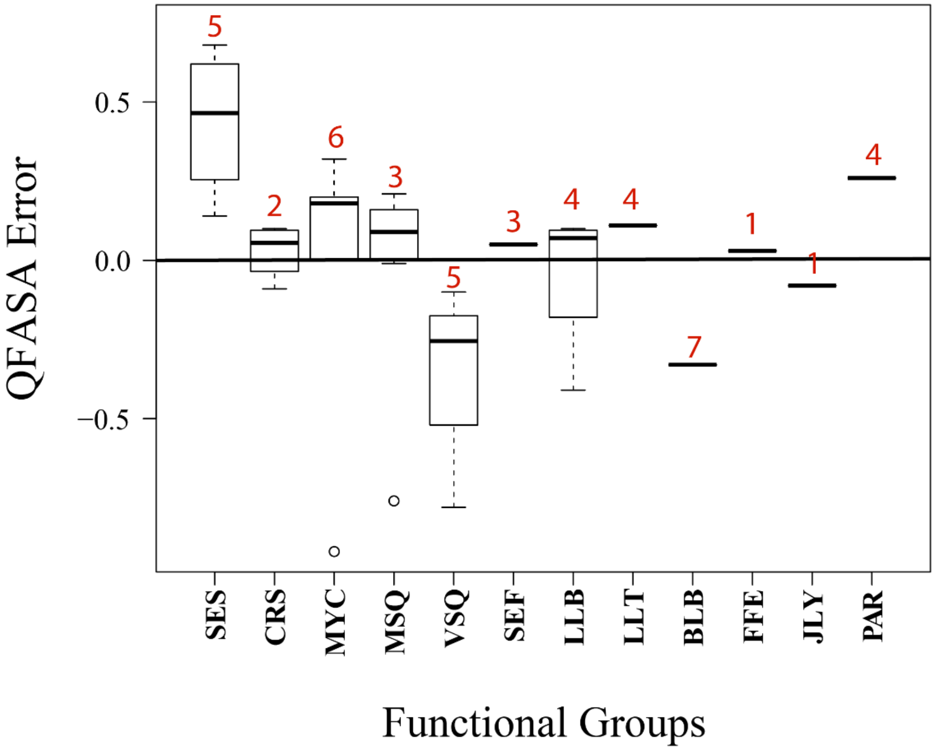
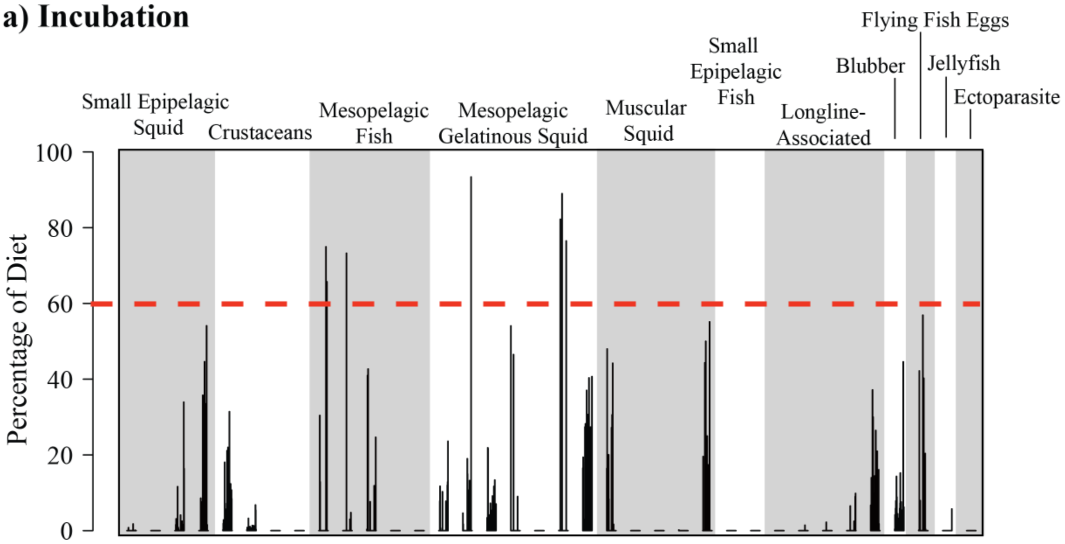


Figure 2.7 Summarized error in QFASA diet estimations by functional groups

Red numbers indicate accuracy ranking, which considered both mean error and magnitude of variance in error for all species within the functional group. The lower the ranking the higher the accuracy. SES = small, epipelagic squid; CRS = crustaceans; MYC = mesopelagic fish; MSQ = mesopelagic gelatinous squid; VSQ = vertically-migrating, muscular squid; SEF = small, epipelagic fish; LLB = longline bait; LLT = longline target fish; BLB = marine mammal blubber; FFE = flying fish eggs; JLY = jellyfish; PAR = ectoparasitic copepod.

a) Incubation



b) Chick-brood

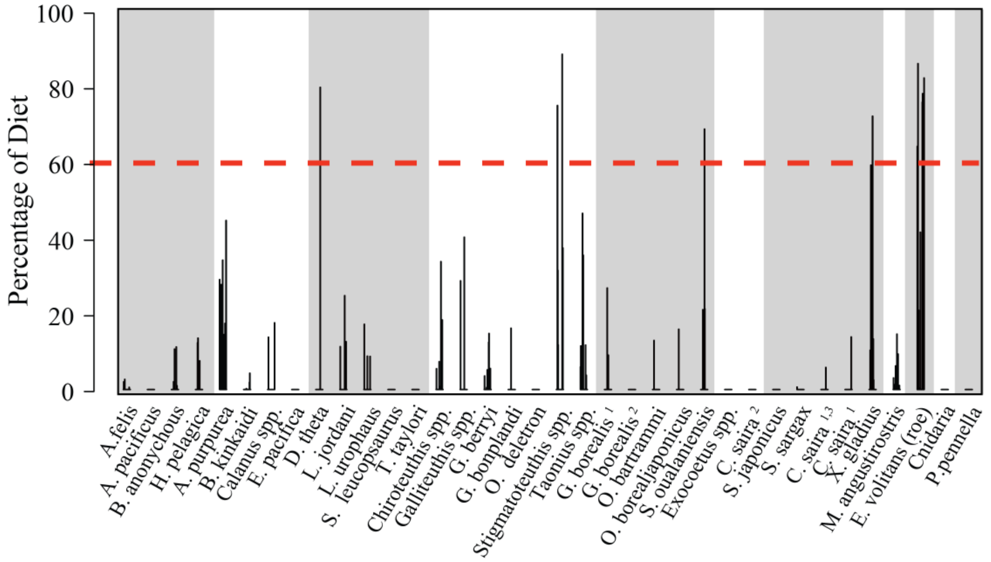
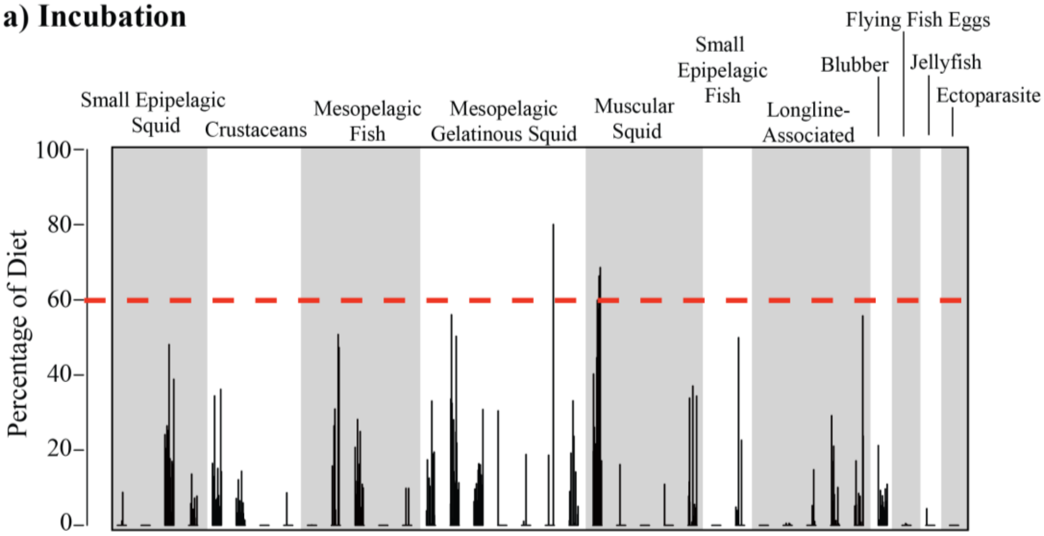


Figure 2.8 Side-by-side barplots of raw diet estimations from QFASA modeling for black-footed albatross stomach oil samples from a) incubation and b) chick-brood.

Each bar represents the proportion of diet made up of that particular prey species for a single individual. Functional groups of prey are grouped together and highlighted with alternating grey shading. The red dotted line at 60 % of the diet represents a threshold above which an individual was classified as having a specialized diet

a) Incubation



b) Chick-brood

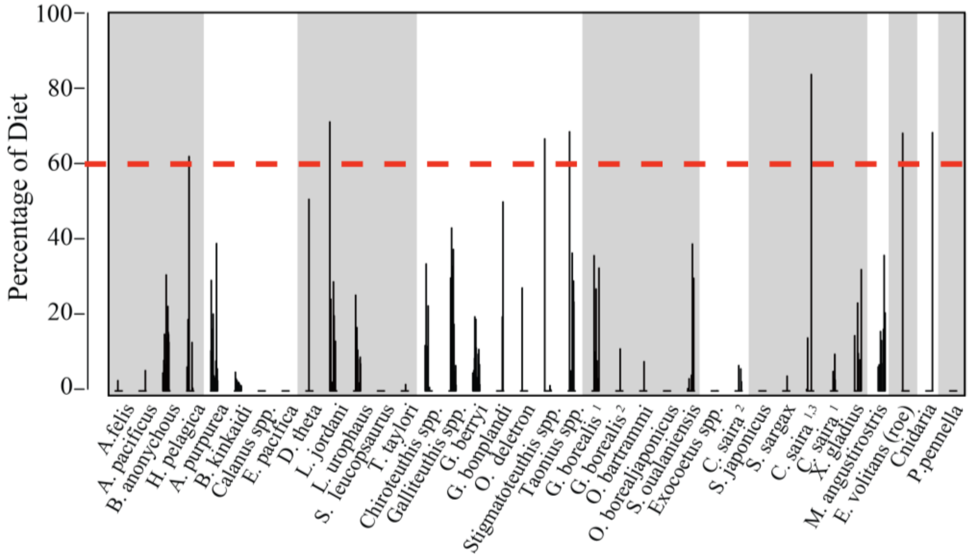


Figure 2.9 Side-by-side barplots of raw diet estimations from QFASA modeling for Laysan albatross stomach oil samples from a) incubation and b) chick-brood.

Each bar represents the proportion of diet made up of that particular prey species for a single individual. Functional groups of prey are grouped together and highlighted with alternating grey shading. The red dotted line at 60 % of the diet represents a threshold above which an individual was classified as having a specialized diet

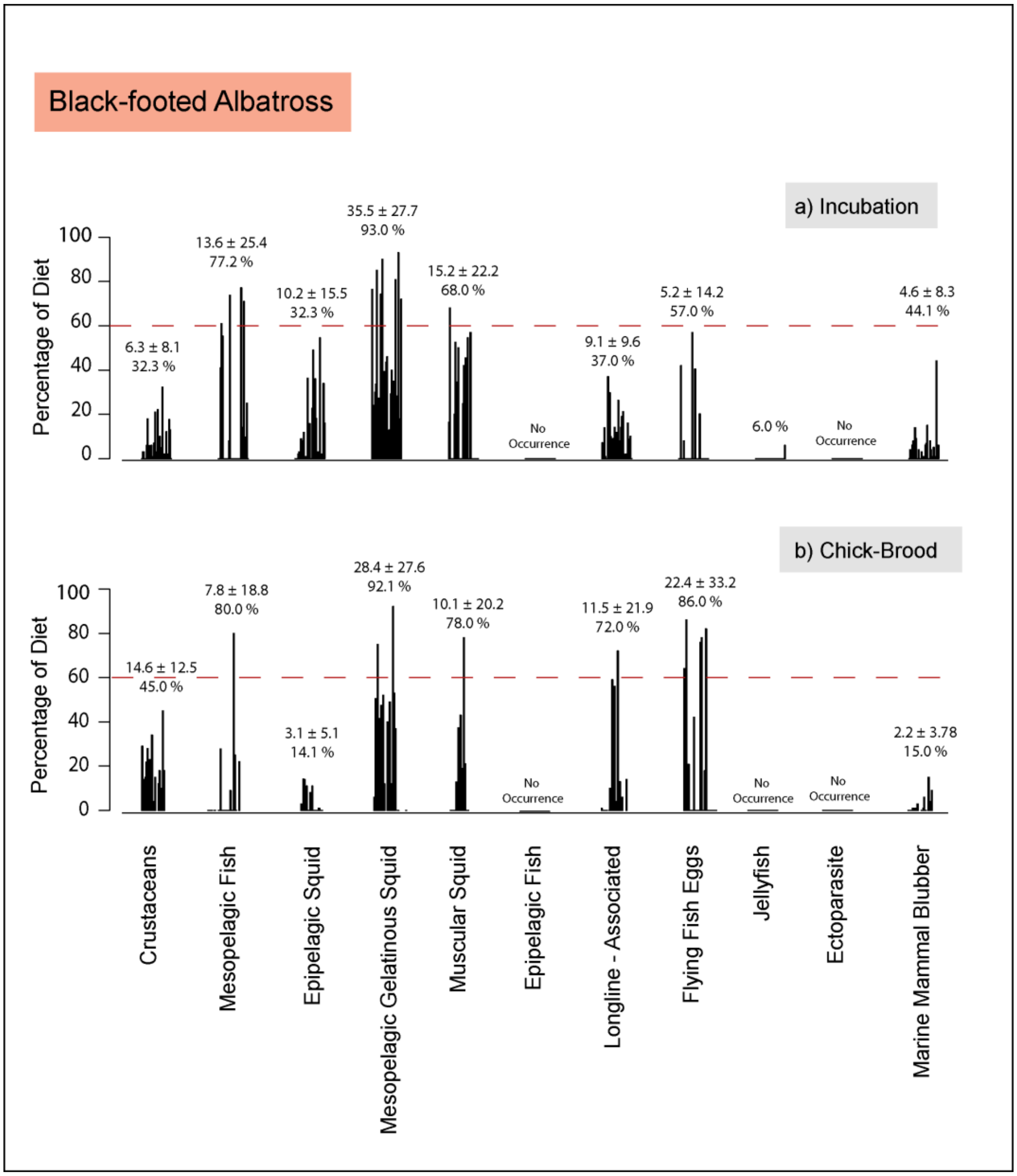


Figure 2.10 Side-by-side barplots of QFASA diet estimations grouped by functional group for black-footed albatross stomach oil samples from a) incubation and b) chick-brood

Each bar represents the proportion of diet made up of that particular prey species for a single individual. Functional groups of prey are grouped together and highlighted with alternating grey shading. The red dotted line at 60 % of the diet represents a threshold above which an individual was classified as having a specialized diet. Means ± standard deviations as well as maximums are given above each functional group.

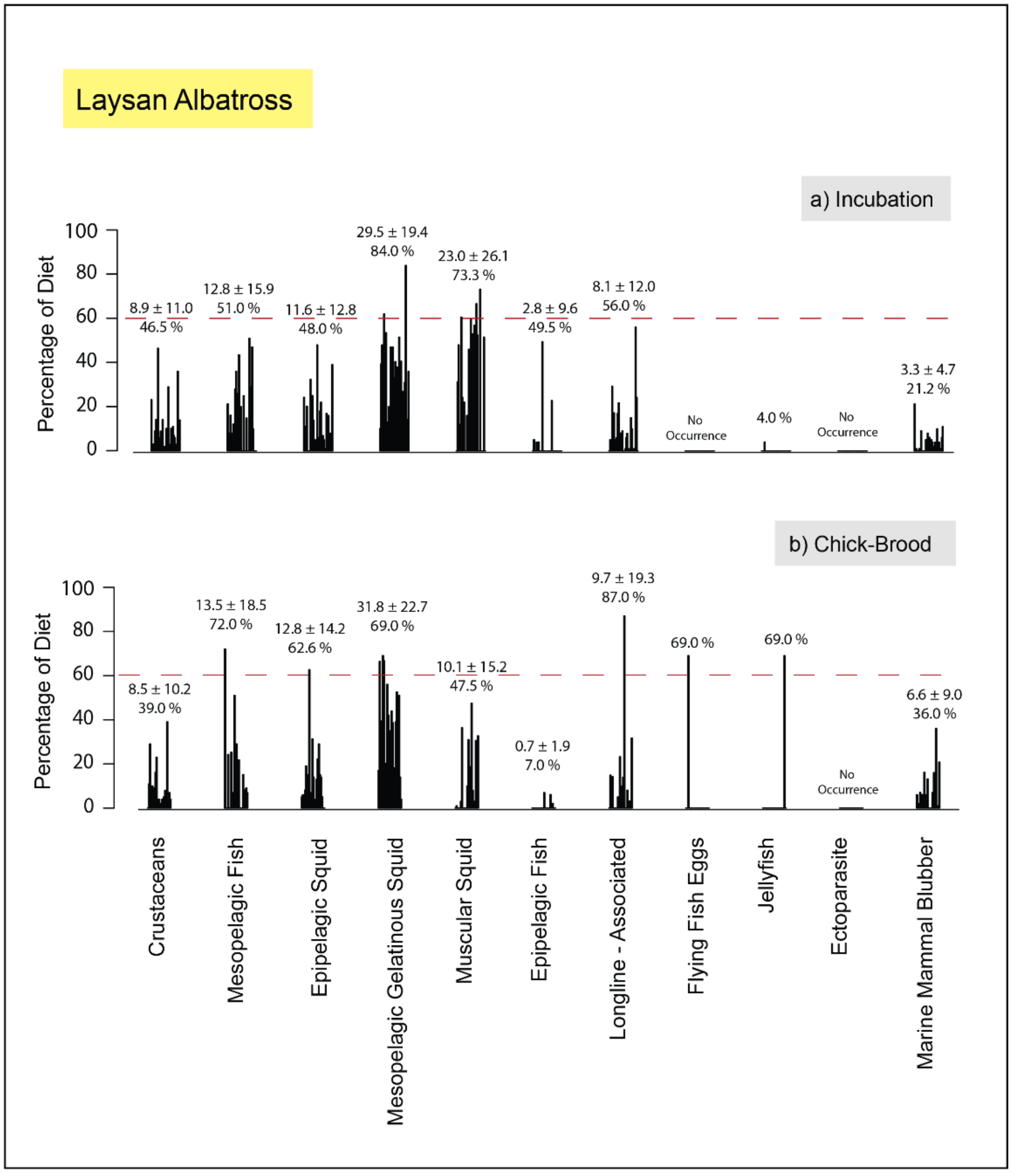


Figure 2.11 Side-by-side barplots of QFASA diet estimations grouped by functional group for Laysan albatross stomach oil samples from a) incubation and b) chick-brood.

Each bar represents the proportion of diet made up of that particular prey species for a single individual. Functional groups of prey are grouped together and highlighted with alternating grey shading. The red dotted line at 60 % of the diet represents a threshold above which an individual was classified as having a specialized diet. Means ± standard deviations as well as maximums are given above each functional group

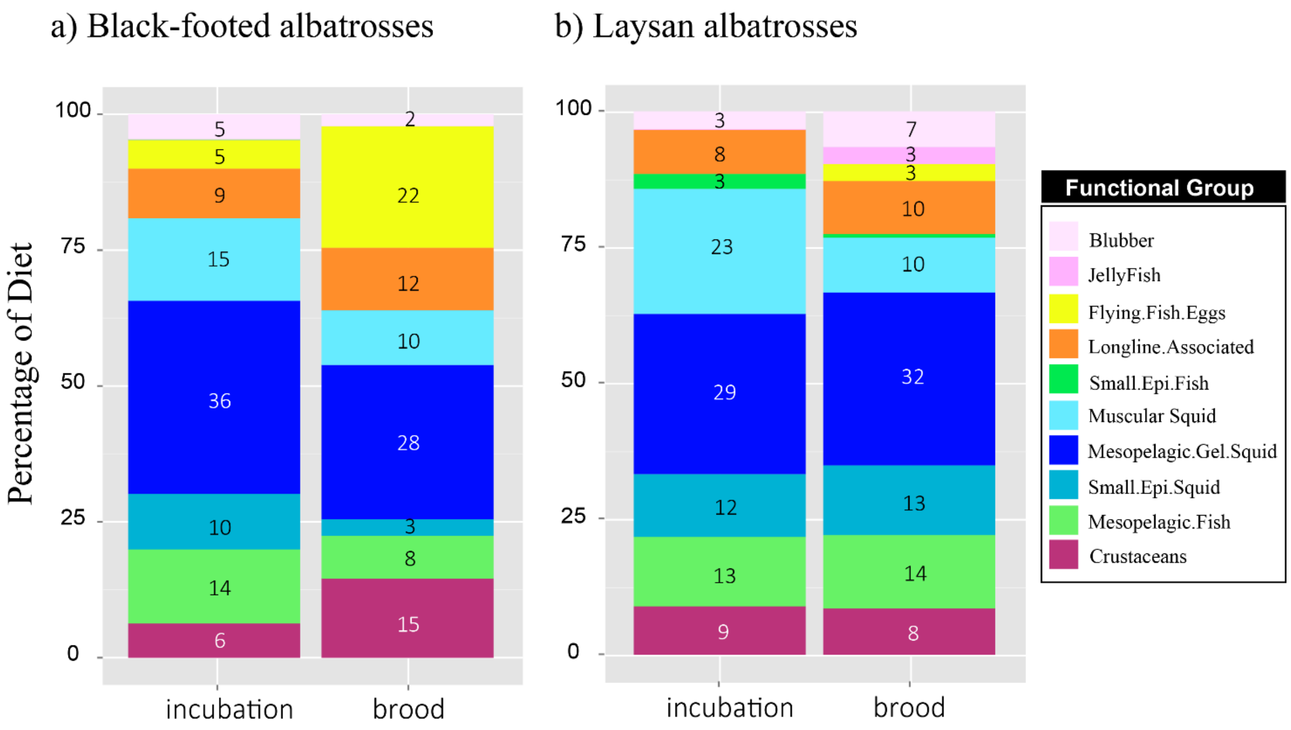


Figure 2.12 Diet Composition of a) black-footed and b) Laysan albatrosses across the incubation and chick-brood breeding phases.

The percentages of diet for each functional group pooled across all individuals are given as numbers within each box. Diversity of diet (measured by Simpson's D index) increased from incubation to chick-brood in both species, however the magnitude of this increase was larger in black-footed albatrosses (a .47 increase in black-footeds versus a .39 increase in Laysan). Fish eggs and crustaceans became important items in black-footed albatross diet in the chick-brood, while squid and mesopelagic fish reduced from 75 % of ther diet to 49 %. Squid and mesopelagic fish remained important across incubation and chick-brood for Laysan albatrosses (77 % and 69 %, respectively), however, vertically-migrating squid was substantially more important in incubation diet. Longline diet increased during the chick-brood for both species, although the increase was small and breeding phase was not a significant effect in zero-inflated binary models measuring the proportion of longline-associated resources in albatross diet.

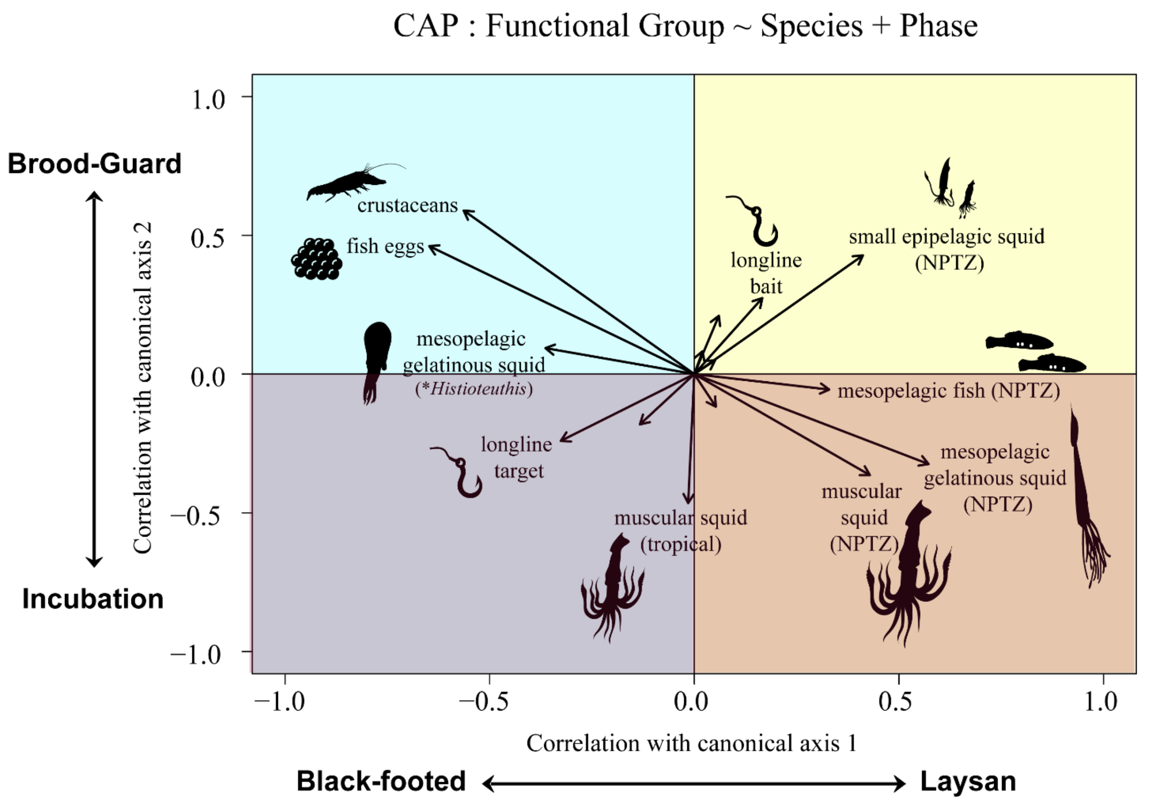


Figure 2.13 A canonical analysis of principal components shows which functional groups of prey drive the major differences in diet composition between species and breeding phase.

Canonical axis 1 represents differences between Laysan and black-footed albatrosses while axis 2 represents differences between the incubation and chick-brood phases. Lengths and directions of arrows represent the strength and sign of the correlation of functional groups with the two canonical axes.

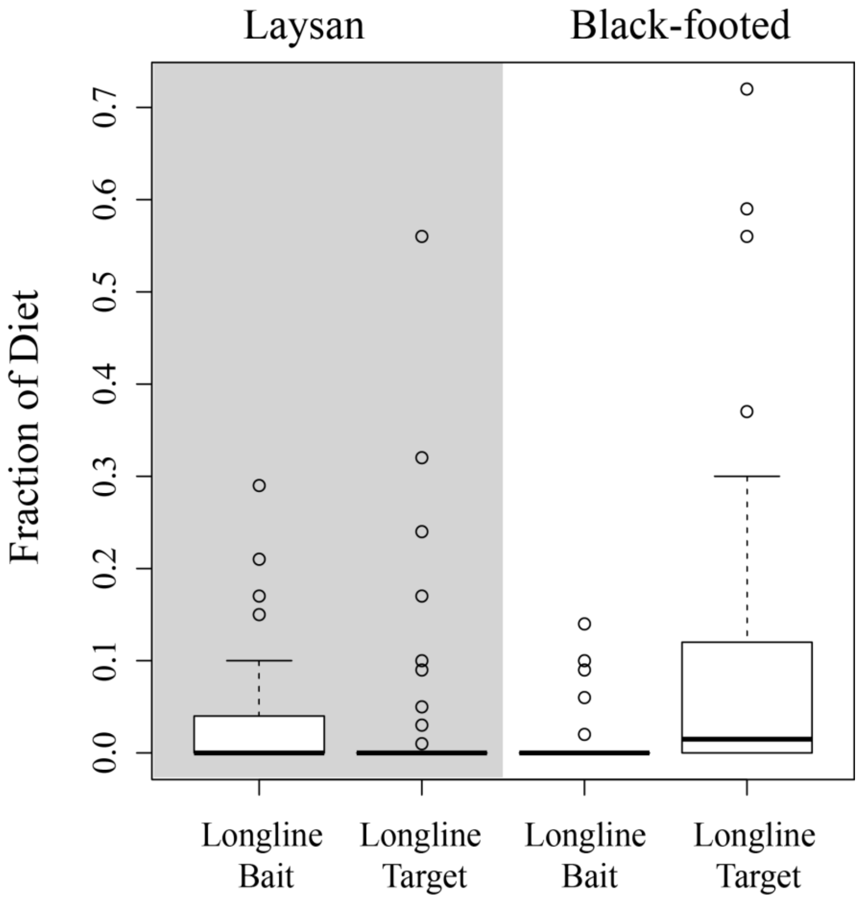


Figure 2.14 Laysan and black-footed albatrosses use different strategies to exploit fisheries resources.

Laysan albatrosses consume mostly longline bait fish while black-footed albatrosses consume more longline target fish (swordfish).

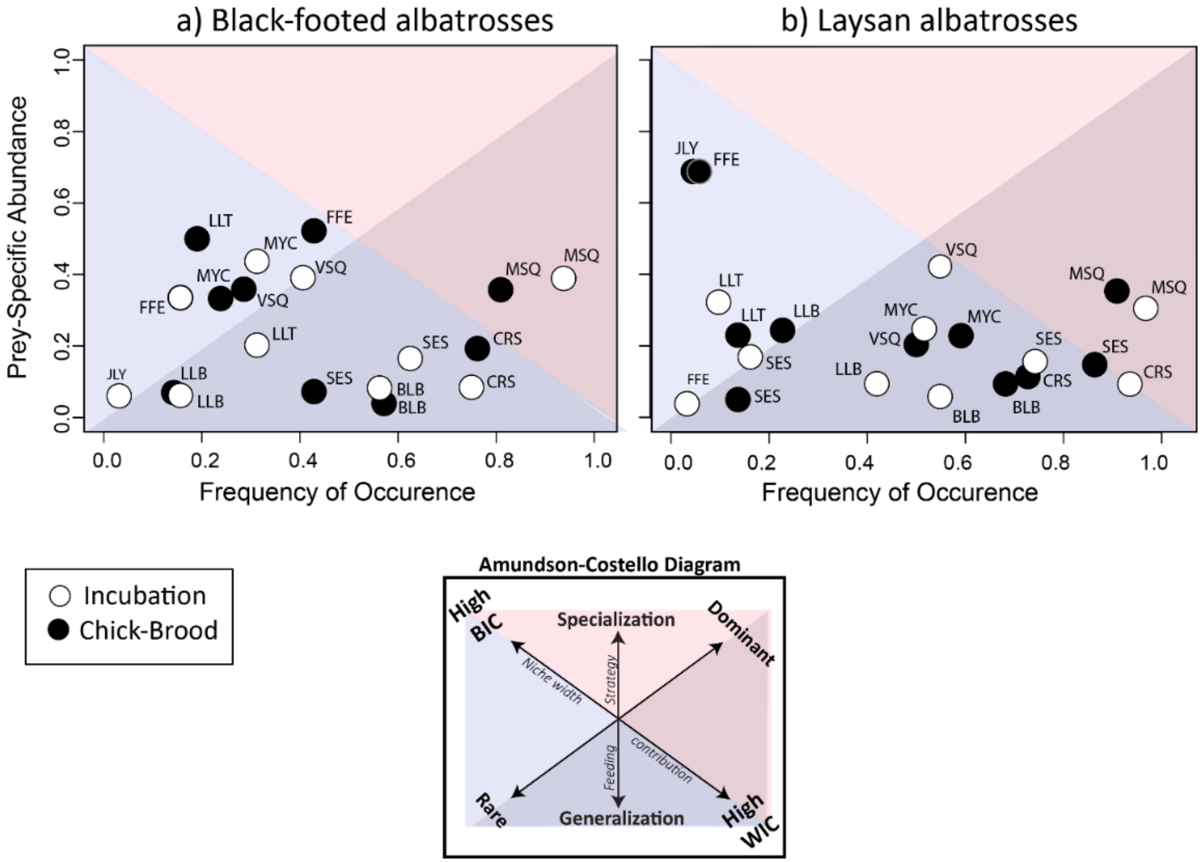


Figure 2.15 Amundson-Costello plots showing feeding strategies of a) black-footed and b) Laysan albatrosses.

Each data point represents each functional group of prey. Dark circles represent diet from the chick-brood while open circles represent incubation diet. If functional groups fall in the lower right sector of the diagram, the population utilizes a generalist feeding strategy, while functional groups clustering towards the upper right sector indicate a generalist population composed of individual specialists. SES = small, epipelagic squid; CRS = crustaceans; MYC = mesopelagic fish; MSQ = mesopelagic gelatinous squid; VSQ = vertically-migrating, muscular squid; SEF = small, epipelagic fish; LLB = longline bait; LLT = longline target fish; BLB = marine mammal blubber; FFE = flying fish eggs; JLY = jellyfish; PAR = ectoparasitic copepod

3 CHAPTER THREE

Flight feather molt, age and sex influence the post-breeding migrations of two long-lived seabird species.

Melinda Conners, Michael Sumner, Michelle Kappes, Daniel Costa, Scott Shaffer

ABSTRACT

Balancing the allocation of energy between reproduction and self-maintenance is a fundamental trade-off in biology. To gain reproductive fitness organisms must successfully bear viable offspring, but at what cost to one's survival and future breeding efforts? Long lived species act as "prudent parents" and only invest in reproduction if it comes at minimal cost to their own survival probability. For birds, the replacement of flight feathers, critical for survival, requires the largest investment of energy next to reproduction, and these activities generally do not overlap in time. For large gliding oceanic birds, such as albatross, a complete replacement of flight feathers and a successful breeding season sometimes do not fit within the annual cycle. To negotiate the mutually exclusive time and energy constraints of molt and breeding, Laysan and black-footed albatrosses have developed a unique molting strategy in which birds can complete a full flight feather molt in discrete units across two post-breeding seasons using a combination of different large-scale molt sequences. These species are neither strictly annual nor strictly biennial breeders, and breeding frequency is influenced heavily by large-scale molt patterns. Here, we used a long-term tracking study to investigate how intrinsic characteristics of birds (molt extent, sex and age) impact the activity and habitat use of Laysan and black-footed albatrosses during the post-breeding season. We also measured the degree of site fidelity across the breeding season with a focus on the molting months. We found that molt extent (as classified as 'large', 'medium', or 'small') impacted activity level, but not habitat, with birds with largest molt extents having the most significant reduction in space use that began earlier in the post-breeding season than other birds. Molt extent did not impact habitat use, likely because albatrosses showed a large degree of site fidelity to their molting grounds between years. Age influenced home range size, with sizes decreasing with age, most likely reflecting that birds accumulate memory and experience over time, thereby reducing searching effort when pursuing suitable feeding grounds. While the productive passes of the Aleutian Island archipelago and the California

Current upwelling region were important habitats for molting albatrosses, many albatrosses spent the molting months in pelagic areas of the Transition Zone Chlorophyll Front, suggesting offshore oceanic zones can also have productivity levels high enough to support birds that switch to a high residency behavioral pattern due to feather molt. Sex had a stronger influence on post-breeding habitat of birds for both species, and these differences were more apparent in the pre-breeding stages of the late post-breeding migrations. While environmental factors certainly influence behavior of albatross spatial and activity levels at multiple scales, we show that the intrinsic factors of molt extent, sex and age play a large role in dictating the spatial patterns of post-breeding albatross and need to be considered in studies of this critical phase of the annual cycle.

3.1 BACKGROUND

Balancing the allocation of energy between reproduction and self-maintenance is a fundamental trade-off faced by all living organisms (Lack 1968, Stearns 1992). To gain reproductive fitness organisms must successfully bear viable offspring, but at what cost to one's survival and future breeding efforts? Species-, population-, and sex- and age- specific life history strategies negotiate this conflict, shaped by phylogenetic history, morphology and physiology, as well as the availability and predictability of food at both regional and local scales (Suryan et al. 2009, Froy et al. 2013, Schultner et al. 2013, Weimerskirch et al. 2015). The broadest classification of reproductive life history strategies separates species or populations into 'fast-living' and 'slow-living' – the so-called r/K gradient (Pianka 1970, Gaillard et al. 1989) – where those species that are 'fast-living' (*r-selected*) sacrifice longevity for early maturation and high annual fecundity, amassing large bursts of reproductive output early in life before a quick senescence. 'Slow-living' species (*K-selected*), on the other hand, invest heavily in self-maintenance, have low annual fecundity, and gradually accrue reproductive investment over longer lifespans.

Seabirds that rely exclusively on the marine environment for food tend to be on the slow end of the fast-slow life history gradient in birds (Weimerskirch 2002); a characteristic tied to larger size and a reliance upon the marine environment, which, in general, has patchier and less predictable resources than the terrestrial environment (Ashmole 1971, Weimerskirch 2002). Within seabirds, the Diomedeidae family of albatrosses represents an extreme case of the ‘slow-living’ demographic tactic: they have a delayed age at first breeding (5-12 years old), low annual fecundity rates (< 1 offspring per nest), and high survival paired with late breeding ages (Tickell 2000, Weimerskirch 2002). Low annual reproductive rates are a consequence of single egg clutches and of notably slow growth rates of chicks characteristic to all Diomedeidae (3.8 months in grey-headed albatrosses to 9.3 months in wandering albatrosses, Tickell 2000). Prolonged chick-rearing periods, resulting from slow growth rates, partially contribute to the biennial breeding patterns of some albatross species. Slow growth rates, in particular, are thought to be a consequence of foraging in resource-limited pelagic environments with long transport times for parents to return from foraging hotspots to nests (Ashmole 1971, Ainley 1977, Jouventin and Dobson 2002). To offset this challenge, many albatrosses species utilize efficient, low energy flight, to seek productive regions far from their nest rather than relying on food conditions near the colony (Ainley 1977, Weimerskirch et al. 1997)

Given the importance of efficient flight for survival and reproduction, it is not surprising that albatrosses allocate a significant amount of energy to the annual maintenance (through replacement) of flight feathers. Even a moderate amount of wear in flight feathers can reduce flight efficiency (Hedenström and Sunada 1999) with measureable impacts on current and future reproduction (Weimerskirch 1991, Langston and Rohwer 1996). However, this obligatory act of self-maintenance requires a considerable investment of energy and time (Murphy 1996), especially for albatrosses that, as a group, have the largest wingspans of all seabirds. Considering the time and energy demands of both molting and breeding, these activities generally do not overlap in time and are considered “incompatible” for most bird species (Payne et al. 1972, Walsberg 1983, Edwards 2008, Alonso et al. 2009). As a response to the temporal and energetic constraint of breeding, albatrosses have developed a unique molting strategy in which birds can complete a full flight feather molt in discrete units across two or more post-breeding seasons using a combination of different large-scale molt sequences. Large-scale molt patterns vary among species, and are shaped by size, by differences in the availability and abundance of resources in different habitats, and by the duration of post-breeding intervals (Weimerskirch 1991, Edwards 2008, Alonso et al. 2009).

Many albatross species breed biennially, while others breed each consecutive year. The smaller albatross species are typically annual breeders, with higher breeding frequencies facilitated, in part, by shorter chick-rearing and molt durations (Weimerskirch 2002, but see Weimerskirch et al. 2015). Laysan and black-footed albatrosses (*Phoebastria immutabilis* and *P. nigripes*, respectively) that breed throughout the northwestern Hawaiian Islands and are on the smaller end of the albatross size spectrum but fall somewhere between annual and biennial breeders, with, on average, approximately 35% of the population skipping breeding in any given year, although this varies among years and colonies (Arata et al. 2009). Importantly, breeding frequency in both species is heavily influenced by flight feather molt pattern (Viggiano 2001, Edwards 2008).

Laysan and black-footed albatrosses can complete a flight feather molt in two consecutive post-breeding seasons using one of two different molt sequence patterns: 1) a large molt series followed by a small molt series, or 2) two consecutive medium molts (Edwards and Rohwer 2005) (see Figure 3.1a). Birds that complete a flight feather molt with the medium-medium sequence can functionally breed annually, since the combined duration of a medium molt and a full breeding cycle fit within a single annual cycle and do not overlap (Edwards 2008). However, birds utilizing the large-small molt sequence are limited to biennial breeding because the large molt is long in duration and overlaps in time with the chick-rearing season (Edwards 2008). Having multiple molting pattern options allows North Pacific albatrosses flexibility in molt-reproductive strategies, so that they can adjust their strategy if they fail a breeding season and initiate a larger molt. However, the variability of breeding frequency and molt patterns within an individual's lifetime is not well known, and it is possible some individuals consistently breed biennially with the large-small molt pattern, while others are consistently annual breeders (see Weimerskirch et al. 2015).

While albatrosses do not undergo catastrophic molts that would render them completely flightless, albatrosses actively replacing flight feathers do experience reduced flight capabilities, evident in large mortality events of molting birds during storms (Kinsky 1968). Not surprisingly, Laysan and black-footed albatrosses show an overall population-level reduction in flight activity for approximately 40 days during the post-breeding season when birds are known to molt (Gutowsky et al. 2014). However, birds undergoing different molt extents experience different physical and energetic constraints that must have variable impacts on optimal foraging strategies – which would be seen in different activity levels and habitat use among birds classified by molt extent. Individuals replacing the most flight feathers would theoretically have the greatest wing loading, and might seek out areas with stronger wind conditions and/or regions with predictable oceanographic features that concentrate prey at the surface, enabling efficient use of the “sit-and-wait” drifting foraging strategy (Weimerskirch et al. 2007, Louzao et al. 2014, Conners et al. 2015).

Across the breeding season, Laysan and black-footed albatrosses have large foraging ranges and spend extensive time foraging in flight (Fernández and Anderson 2000, Hyrenbach et al. 2002, Kappes et al. 2015), but the reduced flight efficiency during the flight feather molt (post-breeding season) likely forces albatrosses to switch tactics to a less mobile, higher residency strategy. Indeed, the idea of albatross “molting grounds” in the productive passes of the Aleutian Island was first suggested by Suryan and Fischer (2010) after encountering an unusually high occurrence of albatross with extremely worn feathers in these passes. Here, they speculated that the Aleutian Island ecosystem, and specifically certain passes that have extremely high levels of summertime productivity, were potentially of critical importance for albatrosses undergoing the most extensive flight feather molts. Vigorous tidal mixing in the archipelago combined with steep and variable bathymetry results in seasonally enriched surface waters, as well as surface convergences that concentrate food, consequently attracting a high biomass of seabirds and marine mammals (Hunt and Stabeno 2005). Beyond a high abundance of predators in general, these passes might be supporting a large proportion of albatrosses that have enhanced vulnerabilities to changing wind conditions and local food availability due to an extensive molt of flight feathers.

Post-breeding distributions of North Pacific albatrosses have been thoroughly mapped from ship-based observations and tracking studies (Shuntov 1974, Hyrenbach and Dotson 2001, 2003, Hyrenbach et al. 2006, Fischer et al. 2009, Suryan and Fischer 2010, Kuletz et al. 2014). However, colony-based tracking studies of these species are uncommon and valuable in their potential to link post-breeding distributions with breeding colony and individual characteristics such as breeding history and molt status, as well as sex and age. The same ship-based tracking study that identified a high frequency of Laysan and black-footed albatrosses undergoing extensive primary molts in the Aleutians also encountered a male bias in birds captured off the ship (Fischer et al. 2009), although it was not possible in that study to determine if the sex-bias was due to different distributions of the sexes or to a male-bias in vessel attraction. At-sea segregation of males and females is not uncommon among seabird species, even in sexually monomorphic species. If there are dense aggregations of post-breeding albatrosses with restricted ranges during active flight feather molt, intraspecific competitive forces might shape distributions based on sex or age structure. For long-lived species such as albatrosses, age can influence both competitive ability and space use. Older birds, with accumulated memories of foraging experience likely spend less time searching for profitable areas. However, as individuals age, interactions between their energy supplies and competitive ability might result in habitat segregation between older and younger individuals, as seen in wandering albatrosses (Lecomte et al. 2010).

Here, we investigate space use, measured by activity and habitat, of Laysan and black-footed albatrosses from Tern Island across the post-breeding migration, when activities related to self-maintenance are paramount and manifest in two discrete stages: flight feather replacement through molt and the regaining of body condition to prepare for the breeding season. We hypothesize that: 1) birds will be least active during core molting months and activity will be most reduced in birds undergoing the largest molt extent; 2) the habitat used by post-breeding albatrosses will be least pelagic during molting months, and this will be most notable for birds undergoing the largest molt extent; 3) the degree of site fidelity will be greatest during the molting months; and 4) there will be sex and age effects in habitat-use of post-breeding migrations due to niche partitioning.

3.2 METHODS

3.2.1 Tracking methods

To understand the post-breeding migration behavior of Laysan and black-footed albatrosses, we deployed 166 geolocation data-loggers of three models (LTD2400, LAT2500 (Lotek Wireless) & MK19 (British Antarctic Survey)) on individual albatrosses over eight seasons (2004-2006, 2008- 2012) at Tern Island in the northwestern Hawaiian Islands (23.870°N, 166.284°W) (Table 1). Geo-locators were attached to plastic auxiliary leg bands with cable ties and epoxy and weighed between 2.5 - 5 g – less than 1 % of the birds mass – well under than the weight threshold recommended for gliding seabirds such as albatross (Phillips et al. 2003). Most individuals were followed for a single post-breeding trip, however, nine individuals were tracked for two or more continuous years, capturing multiple post-breeding trips.

Birds were weighed and measured at the time of tag deployment. Sexes were identified through molecular DNA analysis, visual identification, or a discriminant function analysis using morphometrics (see Shaffer et al. 2001, Conners et al. 2015). Ages of tracked birds (known age and minimum age) were obtained from a long-term banding program conducted by the U.S. Fish & Wildlife Service since the 1970s. For some statistical analyses (Per-MANOVAs, canonical analyses of principal components) we grouped birds by age-class (‘Younger’, ‘Older’). Given that black-footed albatrosses have younger mean ages at first breeding than Laysan albatrosses (Fisher 1975, Viggiano 2001), we used a younger age-class threshold for this species than for Laysan albatrosses: ‘Older’ black-footed albatrosses were birds > 20 years of age, while ‘Older’ Laysan albatrosses were birds > 25 years of age.

We recovered 95% of deployed data-loggers but due to tag failure (1.8 % of LTD2400 tags, 13.2 % of LAT2500 tags, and 9.3 % of MK19 tags), the final sample size of post-breeding trips for analysis was 143 (86% of tags deployed). Tag recovery was high, even among birds that skipped breeding efforts, because breeding-age albatrosses typically visit their breeding colonies early in the nesting season whether they breed or not. Sample sizes varied between tests depending on group size and are indicated by degrees of freedom or in some cases are embedded in tables and figures.

3.2.2 Breeding Sequences as a Proxy of Molt

We recorded breeding parameters of birds both the year of deployment (‘egg laid’, ‘egg hatched’, ‘chick fledged’) and the year of recovery (‘egg laid’). If a bird laid an egg, we classified it as a bird that initiated a nest that season. Because each year we departed the colony in early April prior to the fledging of chicks (June-July), we determined fledged vs. failed nests by departure date estimated from sea-surface temperature (SST) time-series (Figure 3.2). Because albatrosses breeding at Tern Island migrate to substantially colder waters than those surrounding the breeding colony, arrival and departure dates were easily identified in SST values recorded by tags. Birds that departed the colony earlier than May 15 were considered to have had failed nests.

We used the relationship between large-scale molt patterns and breeding described in Edwards (2008, Figure 3.1b) to classify birds into different molt series (small, medium, or large) based on their breeding histories before and after the migration: *'Large'*- Birds that either failed or did not initiate nests the year of deployment were classified as those more likely to initiate the large molt series, given their early departure dates (large molts initiate as early as May 1, but not earlier); *'Small'* - Birds that completed a breeding season on deployment but did not initiate a nest the following year were classified as birds that were more likely to initiate a small molt series; Finally, birds that completed a breeding season the year of deployment *and* initiated a nest the following season were classified as birds that were more likely to initiate a medium molt series.

Breeding information on either end of the migration was necessary to inform the classification of molt extent for each bird, but for 16.0 % of trips we did not have information on whether birds initiated a breeding effort the year following the migration. In order to include these birds in analyses, we explored the viability of using a discriminant function analysis (DFA) to predict whether a bird initiated a nest the following year as a function of migration metrics (departure date, arrival date, trip duration, home range size, core area size). Discriminant functions were created separately for each sex within each species and were preceded with a stepwise forward variable selection using the 'greedy.wilks' function in R to reduce model complexity. Predicted values from the DFA were only used in further analyses if posterior probabilities for the predicted class were greater than or equal to 0.70.

3.2.3 Statistical analyses

Spatial analyses were conducted in R 3.1.1 (R Core development Team, 2014) using the 'SGAT', 'BAStag', 'adehabitatHR', 'raster', 'sp', 'rgdal', 'maps', 'maptools', 'mapproj', and 'move' packages. Statistical analyses were run in R 3.1.1 using the 'nlme', 'mgcv', 'vegan', 'pracma', 'MASS', 'klaR' and 'pscl' packages. Significance was set to $P \leq 0.05$ and marginal significance to $P \leq 0.10$. To avoid pseudo-replication, for birds with multiple trips, we randomly selected a single trip for statistical analyses, except in mixed models where individual bird was included as a random effect.

3.2.4 Estimating locations from geolocation data

We processed all geolocation data using light processing and trip estimation tools from the 'SGAT' and 'BAStag' R packages (Sumner et al. 2009). Locations were estimated twice daily from either light profiles (MK19) or estimated times of sunrise and sunset (LTD2400 and LAT2500) using a 'threshold-sensitivity' approach (Sumner et al. 2009). *Equinox fix*: During the two annual equinox periods, day-lengths are nearly uniform across the globe, consequently latitude cannot be accurately estimated from geolocation methods, and trip portions during equinox are often discarded in studies. In order to keep our tracks continuous, but correct for the equinox, we interpolated latitudes from the start and end of each equinox period, then paired these corrected latitudes with their corresponding longitudes (that are unaffected during the equinox). These preliminary geolocation coordinates (x0, y0) provided the initial locations subsequently modeled in a Bayesian framework to give final location estimations (x1, y1). A Bayesian method allowed us to incorporate geolocation estimation uncertainty (Winship et al. 2012), behavioral constraints of albatrosses (travel speeds) and geographical constraints (land mask, geographical range) to give realistic trip estimations with increased accuracy. Since for each iteration, the model uses day-lengths along with locations estimated from the previous iteration, there was a tendency for latitudes to stretch artificially north during the equinox periods after each iteration in the model. To prevent this, we constrained Bayesian estimated latitudes by including, as an additional prior, each individual's maximum latitude calculated from the initial equinox-corrected locations (x0, y0). Once parameters were initialized, 1000 iterations of MCMC simulations were run and updated three times using the metropolis algorithm to approximate the posterior probability.

The final trip path (i.e. the most likely path) was defined as the mean of the posterior distribution (Figure 3.3).

3.2.5 General characterization of post-breeding migrations

Each full path estimation was then truncated from the day the bird left the colony for the last time that breeding season (spring-summer) to when it first arrived the following breeding season (fall-winter). A buffer of 500km around Tern Island removed portions of the track that represented the immediate departure from and arrival to the breeding colony. We ran three separate general linear models to assess the response of three different migration chronology metrics – departure date, arrival date, and trip duration – to intrinsic (species, age, sex, subsequent breeding status) and extrinsic factors (year).

3.2.6 Space Use

To measure the dynamics of space-use during post-breeding migrations, we assessed total home range and core area use of all individual albatrosses across 1) the entire migration and 2) in monthly intervals to see how space-use changed over time. Individual home ranges were identified using minimum convex polygons, which measure home range by wrapping a minimum convex hull around all locations of a path. Core areas were delineated from total area used by using a gridded utilization distribution technique (Maxwell et al. 2011) – this technique measures the intensity of use within a home range by measuring the relative frequency of occurrence of an individual in a cell of a defined spatial scale and reduces over smoothing common in other utilization distribution techniques (Fieberg 2007). Given the relatively coarse spatial and temporal resolution of geolocation estimations we used a spatial grid of 100 km^2 - large enough to absorb the spatial error inherent in GLS tags but small enough to identify variability in space use of individuals. Core area was defined as the 50% utilization area. We used general linear models to test the effects of species, sex, age class, and molt series on home range size and on core area size. Home range (minimum convex polygons) was log transformed to meet assumptions of normality.

3.2.7 The dynamics of space-use change relative to molt series

To identify how molting constraints affected space use during the post-breeding migration, we examined the change of core area size across months spanning the post-breeding migration, grouped by birds of different molt series. Since we were interested in how individuals increased or decreased the size of their core area, rather than absolute size, monthly calculations of core area size were mean-centered for each individual, so that our final metric measured the relative magnitude of change in core area size per month for each individual.

We then used a generalized additive mixed model (GAMM) to identify the pattern of space use change across the post-breed migration. Individual-centered space use change was modeled as a Gaussian dependent response. Month was included as an explanatory variable in the model using a cubic regression spline and nested under breeding status. Year, species, sex and age were included as fixed factors, but were not significant and thus removed in final models. We controlled for heterogeneity in residuals across months by including a variance structure. Individual bird id was included as a random effect. Finally, GAMM monthly smoothers were nested under molt classification (i.e. large, medium, and small), so that we could discriminate differences in core use change relative to different molt series scenarios.

3.2.8 Habitat use as a function of species, sex, age, molt series and migration stage

Longhurst's biogeographical marine provinces divide the world's oceans into 33 different ecoregions defined by physical and chemical characteristics of the seas, such as wind and current patterns and salinities, which ultimately drive distinct biota within each region (Longhurst 2010) (Figure 3.4). These marine province boundaries are useful for identifying macroscale differences in habitat use among populations or groups of animals. For each bird, we calculated the percentage of its migration in each marine province for 1) the full migration, 2) for migration in molting months (May, June, July, August) and 3) for the migration in pre-breeding months (September, October). To examine broad-scale differences in habitat among groups, we modeled habitat composition (the percentage of trip spent in each province) as a multivariate response to intrinsic (sex, age-class, molt extent) and extrinsic (year) factors. Since data were compositional in structure (i.e. the sum of all the multivariate response variables sum to one) we first transformed the response according to Aitchison (1986). We then constructed a dissimilarity matrix on the multivariate response using Bray-Curtis distance before running a permutational MANOVA to test habitat composition against intrinsic and extrinsic factors. Per-MANOVAs were run separately for 1) the full trip, 2) the trip during the core molting months, and 3) the trip during the pre-breeding months. Per-MANOVAs were followed with post-hoc canonical analyses of principle components (CAP) to identify which marine provinces had more influence on group differences.

3.2.9 The dynamics of site fidelity across the migration

To quantify the degree of site fidelity of individuals to their post-breeding migration grounds, we calculated a fidelity index for birds that were tracked for two post-breeding migrations (n=9). To see if and how site fidelity changed across the migration, fidelity indices were calculated for the portions of trips of each repeat bird within each month of the post-breed migration. Fidelity indices were calculated by first identifying cells of a given spatial scale that were shared by locations from both trips. We then calculated the proportion of each trip that fell inside shared cells. The final fidelity index per bird was the mean of those two proportions. After multiple iterations fidelity analysis run at different spatial scales (grid sizes = 50, 100, 200, 300, 400, 500 km^2), we identified the spatial scale where fidelity indices were asymptotic – 300 km^2 – which was then used as the grid size for final fidelity analyses of individuals with paired trips. To see if birds showed greater site fidelity than expected by chance, we also calculated fidelity indices for random pairs of birds (n = 38), from the same species and sex and from two consecutive years. Using separate analyses for every month, we modeled fidelity indices as a response to the categorical factor of whether or not pairs were random birds or the same individual. Due to a large amount of zeros in the fidelity index response variable, we used both Poisson and zero-inflated negative binomial regressions to model the response, then used a Vuong test (Vuong 1989) to identify the model with the better fit.

3.3 RESULTS

3.3.1 Study Population Breeding Patterns

Within our study group, a larger percentage of Laysan albatrosses skipped breeding the following year than black-footed albatrosses (25/60 (41.7 %) and 10/50 (20.0 %), respectively. ($\chi^2 = 4.21$, P = 0.04). Subsequent non-breeders were as equally likely to be male or female for both species ($\chi^2 \approx 0$, P = 1, for both species). Laysan albatrosses experienced higher rates of nest failure than black-footed albatrosses (18/73 (24.7 %) and 3/61 (4.9 %) respectively, $\chi^2 = 8.67$, p = 0.003).

3.3.2 Predicting nest initiation using discriminant function analysis

Predictive power of nest initiation the following season based on migration metrics varied between species and sexes (Table 3.2). Overall, the DFA for black-footed albatross nest initiation had higher predictive power than for Laysan albatrosses, and within each species, prediction power was greater in females than males. The variables contributing most to prediction power also varied between species and sex, with the main difference being that Laysan albatross discriminant functions were less complex (i.e. were described by fewer variables) than those for black-footed albatrosses, and that the date of the end of the migration (‘End DOY’) was important in predicting nest initiation in males, but not for females.

We only used predicted values for subsequent breeding initiation if the posterior probabilities of DFA predictions were greater than 0.70, which gave us an additional 4 out of 11 Laysan and 9 out of 12 black-footed albatross trips.

3.3.3 Effect of nest failure on migration chronology

Birds with failed nests left, on average, in early March and arrived to the colony the following year significantly earlier than birds that successfully fledged chicks the year of tag deployment (Laysan: 4.1 days earlier ($t = 2.18$, $P = 0.03$); black-footed: 10.5 days earlier ($t = 8.20$, $P < 0.001$)). Despite earlier arrivals, migrations of birds with failed nests were significantly longer than migrations of birds that finished a full breeding season (Laysan: 114 days longer ($t = -16.15$, $P < 0.001$); black-footed: 108 days longer ($t = -50.18$, $P < 0.001$)). All birds that did not initiate a nest the year of deployment did so the following breeding season. For birds that initiated but failed, 100 % of black-footed albatrosses and 83 % of Laysan albatrosses returned the second year to initiate a nest.

3.3.4 The influence of species, sex, and breeding on migration chronology

Species, sex, age and subsequent breeding status, but not year, all impacted departure and arrival dates and the duration of post-breed migration. Start of Migration: Species and subsequent breeding status had significant effects on departure dates of albatrosses (Table 3.3 & Table 3.4, Figure 3.1a. Laysan albatrosses left the colony on average 15.8 ± 2.7 days later than black-footed albatrosses ($t_{5,103} = 5.86$, $P < 0.001$), and within both species, birds that did not initiate nests the following breeding season left later than those that did ($t_{5,103} = -2.61$, $P = 0.010$). There were no significant sex differences in departure dates within each species although males tended to leave earlier than females ($t = -0.188$, $P = 4.71$, Figure 3.1a). End of Migration: Overall, black-footed albatrosses arrived at the colony earlier than Laysan albatrosses ($t_{5,79} = -3.92$, $P < 0.001$, Figure 3.1a, Table 3.3 & Table 3.4, Figure 3.1a). There was a significant interaction of sex and subsequent breeding status where males of both species arrived to the colony earlier if they initiated nests the subsequent breeding season than males that subsequently did not initiate a nest ($t_{5,79}$ = -2.14, P = 0.036, Table 3.3 & Table 3.4, Figure 3.1a).This was most pronounced within black-footed albatrosses, with breeding males arriving 14.96 ± 4.95 days earlier than non-breeding males ($t_{5,79}$ = -3.020, P = 0.004). There was no difference in arrival dates between females that subsequently bred or skipped breeding. Duration: Species and subsequent breeding status had the biggest effects on lengths of post-breeding migrations (Table 3.3 & Table 3.4, Figure 3.1a). Black-footed albatross migrations lasted, on average, 8.2 ± 3.6 days longer than Laysan albatrosses ($t_{5,79}$ = -2.27, P = 0.026) and migrations of subsequent breeders lasted 12.3 ± 5.8 days longer than migrations of subsequent non-breeders ($t_{5,79}$ = 2.13, P = 0.037).

3.3.5 The impact of sex, age and molt extent on total home range and core area size

The effects of species, sex, age and molt extent better explained variance in overall home range size ($F_{4,73}$ = 9.35, R^2_{adj} = 0.30) than variance in core area size ($F_{4,73}$ = 3.29, R^2_{adj} = 0.11) of albatross post-breed migrations. Overall, Laysan albatrosses had smaller total home range sizes than black-footed albatrosses ($t_{4,73}$ = -2.47, P = 0.016, Table 3.5) but larger areas of core use ($t_{4,73}$ = 1.75, P = 0.084). Molt extent had significant effects on both overall home range ($t_{4,73}$ = -2.23 , P = 0.029) and core area sizes ($t_{4,73}$ = -2.162 , P = 0.034), with sizes increasing with molt extent. Age was marginally significant in explaining variance in total home range size ($t_{4,73}$ = -1.69, P = 0.095, Figure 3.5) with older birds having a reduced home range size compared to younger birds, and although there was no significant effect of age on core area size ($t_{4,73}$ = -0.38, P = 0.711), there appeared to be a trend towards smaller core area size in older birds for Laysan albatrosses, but only in birds that bred the year following the migration (Figure 3.5).

3.3.6 Change of core area size across the migration in relation to molt extent

Core area size of individuals in both species changed across the migration in similar ways between species, with individuals reducing core area size between May-July and expanding core area size towards the end of the molting period (Aug-Oct). Monthly smoothers for large, medium, and small molts were all significant effects in the model (large: $F_{6,484} = 9.36$, $P < 0.001$, medium: $F = 9.93$, $P < 0.001$, small: $F = 5.01$, $P = 0.002$), indicating birds changed their space use across the migration no matter their molt extent. However, the dynamics of change in core area size was different for birds undergoing a large molt than those undergoing medium or small molts (Figure 3.6). Large molt birds had the greatest reduction in core area size of all birds, and this reduction occurred earlier in the migration, initiating in May. Additionally, for large molt birds, core area size also increased sooner, more rapidly, and to a greater extent than small molt birds. Core area size did not increase and peak until October in small and medium molt birds. Species, sex, and year covariates had no significant effects on change in core area size across the migration.

3.3.7 Variability in habitat use of post-breeding albatrosses

Differences in overall habitat use of black-footed and Laysan albatrosses from Tern Island followed expectations of habitat preferences and distributions from previous work on these species (Shuntov 1974, Fischer et al. 2009, Suryan and Fischer 2010, Guy et al. 2013) (Figure 3.7). Compared to Laysan albatrosses, black-footed albatrosses more heavily used two 'Coastal' Biomes: the California Upwelling Coastal Province (CCAL) and the Alaska Downwelling Coastal Province (ALSK). Two 'Westerlies' Biomes were also important for Black-footed albatrosses, as they were for Laysans: the North Pacific Polar Front Province (NPPF) and the eastern Pacific Subarctic Gyres Province (PSAE). Laysan albatrosses spent a large proportion of their post-breeding habitat use (almost 40 % on average) in the western Pacific Subarctic Gyre Province (PSAW). Both species spent time in the Bering Sea Province (BERS) in the Polar Biome, but on average, this was less than 20 % of their migrations.

Additionally, both species spent time, but marginally so, in the more southerly Kuroshio Current (KURO) and western North Pacific Subtropical Gyre (NPSW) Provinces.

Despite black-footed albatrosses using a greater diversity of habitat (they visited more marine provinces than Laysan albatrosses, Figure 3.7), this species had fewer significant within-species differences in habitat composition among sexes, age classes and molt extents than Laysan albatrosses (Table 3.6). Age: Habitat composition was significantly different between younger and older age classes within both species, but only during the molting months of the migration for black-footed albatrosses (Table 3.6, Figure 3.9), where use of the NPPF province was greater in older birds. Older Laysan albatrosses used the Bering Sea and eastern Pacific Subarctic Gyre provinces to a greater extent than younger age classes, which more heavily exploited the western Pacific Subarctic Gyre. Sex: Females of both species spent more time in pelagic waters of the North Pacific Polar Front than males during the molting months of the migration (Figure 3.9). Male black-footed albatrosses spent more of the migration in the Alaska Downwelling province than females. Both species displayed sex influenced differences along an east-west gradient within the Pacific Subarctic gyre during the pre-breeding months of September and October, with female Laysan albatrosses spending more of their time in the eastern province (PSAE), and males spending more time in the western (PSAW). Black-footed albatrosses showed the opposite pattern, with males spending more time in the eastern province, and females, the western. Molt Extent Contrary to our expectations, birds classified with large molts used the North Pacific Polar Front to a greater extent, at least for Laysan albatrosses (Figure 3.9). Black-footed albatrosses showed the opposite pattern, with birds with the smallest extents using the NPPF more than those with medium or large molt extents, although our sample sizes for birds with large molts in this species is very small and should be interpreted with caution. There was also an effect of molt on use of the western subarctic gyre (PSAW) in Laysan albatrosses, with use decreasing with the extent of molt.

3.3.7.1 *Site fidelity of albatrosses to molting grounds (Figure 3.10)*

Site fidelity to post-breeding regions from one year to the next was significantly greater within individuals compared to our control group of random pairs (Table 3.7, Figure 3.11). Furthermore, the intensity of site fidelity changed along the migration, with site fidelity increasing in months representing the core molting season (June – Sep) (Table 3.7, Figure 3.11).

3.4 DISCUSSION

Variability in the post-breeding migrations of seabirds is often explained by environmental conditions, density of competitors, and prey abundances, but we know of only one other study that has linked variability in migration patterns to different flight feather molt patterns (Catry et al. 2013b), even though flight feather molt occurs exclusively during the post-breeding interval and must have a strong influence on optimal foraging strategies. Here, by using breeding sequence as a proxy for molt extent, we show that molt extents, as well as age and sex, influence activity patterns and habitat-use in post-breeding albatrosses.

Slower reproductive turn-over rates for Laysan albatrosses relative to black-footed albatrosses at Tern Island

While albatrosses are on the slower end of the fast-slow gradient of demographic tactics, Laysan albatrosses had higher rates of both nest failures and birds skipping breeding than black-footed albatrosses, suggesting that this species has relatively slower reproductive turnover rates than black-footed albatrosses, at least for the population breeding on Tern Island. Although there is little current published data on survival rates and breeding frequencies from albatrosses on Tern Island, differences in age structure between the two species corroborate this idea: black-footed albatrosses have younger mean ages at first breeding than Laysan albatrosses (6-7 versus 8-9, respectively (*this study*, Fisher 1975, Arata et al. 2009)), and all the oldest breeding albatrosses identified from the monitored colonies in the northwestern Hawaiian Islands are Laysan albatrosses (a 48 year male (*this study*); a 63 year female breeding on Midway Atoll, USFWS unpublished data), but there remains much uncertainly on maximum life expectancies for both species, so we remain cautious with this interpretation.. Interestingly, compared to Midway Atoll, the rate of Laysan albatrosses skipping breeding was higher within our study group on Tern Island (0.418 vs 0.243, respectively, Fisher 1976), although these rates were calculated over different periods of time (1960 - 1973, Midway and 2004-2012, this study). Midway Atoll, however, lies almost 400 km further north than Tern Island in the French Frigate Shoals putting it much closer in latitude to the Transition Zone Chlorophyll Front (TZCF), a critical foraging zone for Laysan albatrosses during both the breeding and post-breeding seasons (Thorne et al. 2015, Shuntov 1974, Kappes et al. 2010, 2015). Recent work by Thorne et al. (2015) concluded that Laysan albatrosses breeding at Tern Island showed little plasticity in foraging behavior in years of poor environmental conditions (TZCF further away from colony), likely contributing to the high rate of inter-annual variability in reproductive success in this species. Black-footed albatrosses, conversely, showed greater plasticity in foraging behavior in response to poor years which corresponded to less variable reproductive success.

If the colony breeding at Tern Island is at the southern edge of what is feasible for breeding Laysan albatross that are reliant upon the TZCF, then, considering the large inter-annual variability in latitude of the TZCF, a “longer-lived” strategy in Laysan albatrosses at Tern might be selected for. Higher rates of nest failure would lead to more birds with “extra time” released as a consequence of a failed nest – time they could then allocate to a large flight feather molt; flexibility in molt pattern as a response to different food availabilities has been shown in other Procelleriform seabirds (Cory’s shearwaters: (Alonso et al. 2009, Catry et al. 2013c)). A multi-colony study relating annual and biennial breeding frequencies and adult survival rates across multiple colonies in the NWHI, where distance to TZCF varies dramatically from east to west, is greatly needed to clarify interactions between environments, molt patterns, and reproductive life history strategies in Hawaiian-breeding albatrosses.

3.4.1 Synchrony constrains trip lengths

With the exception of breeding male black-footed albatrosses, both males and females within each species had highly synchronous arrivals (Figure 3.1), although females had a larger range in arrival dates than males (Table 3.3 and Table 3.4).The significantly earlier arrival of black-footed males to the breeding colony indicates that there might be stronger selective pressure on early territory and nest establishment in this species than there are for male Laysan albatrosses, possibly due to the higher density of black-footed albatross nests at this particular colony (Flint 2009). Greater synchronicity in arrival dates than in departure dates in both species suggests that variability in the duration of post-breed migration in albatrosses is the consequence of when individuals decide to leave their chick for the last time the preceding breeding season.

Unlike arrival dates, there is a large range in departure dates of birds from the colony, but there is no current understanding of what triggers a bird's decision to leave the colony and begin the post-breed migration. In theory, this decision could be a cause or a consequence of hormonally driven molt activation: birds may sense molt activation of flight feathers thereby inducing their departure; however, it may be the departure of the bird from the colony and arrival in higher latitudes with a substantially different photoperiod that triggers molt activation. Given the strict temporal segregation of molting from breeding activities in Hawaiian albatross and in many other bird species, especially those that breed far from productive regions (Payne et al. 1972, Edwards 2008, Alonso et al. 2009 but see Catry et al. 2013b), it seems likely that molt activation plays a strong part in this decision.

Despite their smaller size, Laysan albatrosses have longer chick-rearing periods than black-footed albatrosses -165 days versus 150 days, on average (Arata et al. 2009) - likely a consequence of a heavier reliance on pelagic waters. Longer chick-rearing periods result in delayed departure dates from the colony relative to black-footed albatrosses, and correspondingly, later arrivals to the breeding colony the following season. Despite later arrivals, the durations of Laysan albatross migrations were shorter than those of black-footed albatrosses. Less time to molt and re-gain body mass during the post-breeding interval may also contribute to the higher variability in reproductive success in Laysan albatrosses. Migration duration appears to be a strong driver of overall home range sizes for post-breeding albatrosses: black-footed albatrosses, with longer migration durations, have larger home range sizes than Laysan albatrosses, and, within each species, birds with the larger molt extents (which also have the longest migration durations, have the largest home ranges (Table 3.5).

3.4.2 Large-scale molt patterns induce a larger, and earlier, reduction in activity

The larger home range sizes in birds with large molt extents was unexpected, given the assumption of reduced flight efficiency; however, when the change in space-use was examined across the migration, the effects of molt extent became apparent (Figure 3.6). Birds that left early due to nest failure or because they did not initiate a nest that season (i.e. large molt birds) were highly mobile for the first part of their migrations. But, this wide-ranging behavior persisted only until May, when bird ranges rapidly reduced range and became much more localized (Figure 3.6 and Figure 3.12). The timing of this reduction coincides unmistakably with the finding of Edwards (2008) that flight feather molt in Laysan and black-footed albatrosses never activated prior to May 1. Despite departures as early as February and March in some non-initiating albatross, birds remained wide ranging until this sharp reduction of core area use in May which persisted through July, supporting Edward’s conclusions that the timing and extent of flight feather molt is controlled by both flexible (i.e. breeding status) and inflexible factors (physiological limitations in molt activation chronology).

Despite having the largest (and earliest) reduction in space-use during molting months, large molt birds successively increased their ranges sooner and to a greater extent than birds undergoing smaller flight feather molts (Figure 3.6). By molting more flight feathers, and molting them early, these birds might have an advantage of extra time and enhanced flight capability in the pre-breeding season of September and October, where birds build-up large reserves of body fat to sustain them throughout the majority of the breeding season. Like in many animal species, in albatrosses, body condition influences both the decision to breed as well as overall reproductive success in albatrosses (Weimerskirch 1992, Chastel et al. 1995). That birds undergoing large molts have more time in the post-breeding migration to build up fat reserves for the breeding season contributes directly to the trade-off between self-maintenance and reproduction: birds that repeatedly use the large-small molt pattern sequence breed less frequently but may ultimately have a higher rate of successfully fledged chicks if they begin the breeding season in higher body condition. Additionally, biennial breeders can have relatively extended chick-rearing periods since small molts are the last molt pattern to activate (Figure 3.1b). Given more time available for self-conditioning and chick-rearing, the lower nesting frequency in biennial breeders might be compensated for by higher rates of successfully fledged, high quality chicks. A longitudinal study on the relationship between molt patterns, adult survival, breeding frequency, and reproductive success in these two species would improve our understanding of how variability in optimal life-history strategies translates to the fitness of their young in these two sympatric congeners. Individuals have flexibility in the molt patterns they activate; however, it is not known if some individuals maintain a consistent biennial breeding frequency throughout their lifetimes, while others consistently breed annually. Very recently, it was discovered that wandering albatrosses breeding at Kerguelen Island, traditionally considered strictly biennial breeders, actually have two reproductive strategies within the population: a small subset of females consistently breed annually while all other individuals breed biennially (Weimerskirch et al. 2015).

3.4.3 Hawaiian albatrosses “fine-tune” their post-breeding migrations over lifespans

Smaller home ranges in older birds suggest albatrosses use memory and experience to fine-tune foraging ranges, requiring less searching behavior. Simulations of animal movements incorporating the effects of memory have shown that memory leads to establishment of home ranges and deterministic foraging behavior (Regular et al. 2013) which leads to increased foraging efficiency ((Van Moorter et al. 2009, Nabe-Nielsen et al. 2013), especially in landscapes with patchy resources (Merkle et al. 2014, Bracis et al. 2015). That Laysan and black-footed albatrosses have high fidelity to molting grounds further highlights experience and memory as important mechanisms shaping optimal foraging strategies in long-lived seabirds (Hamer et al. 2001, Hedd et al. 2001, Patrick et al. 2014, Patrick and Weimerskirch 2014).

Banding records of wandering albatrosses suggest that juveniles likely establish home ranges and repeatable foraging behavior, solidifying these patterns into consistent individual strategies by the time they are breeding adults (Weimerskirch and Wilson 2000). This is likely also true for Laysan and black-footed albatrosses, given their similar life histories; indeed, one individual Laysan albatross visited the same coastal cove in central California from December to March for 19 consecutive years. This bird’s remarkably predictable behavior led to a local following that would await the arrival of “Mr. Al B. Tross” every year for decades (Mendocino Coast Audubon Society).

Repeatable behavior and consistent molting grounds in albatrosses has obvious conservation implications. For one, a strict adherence to an already established home range during molting months combined with poorer flight efficiency reduces adaptability to changes in local environmental conditions. An ongoing mass mortality event of common murres on the coasts of the western U.S. and Canada is a current reminder of the amplified vulnerability of molting birds to environmental variability. This mortality event of both adults and recently fledged juveniles coincided with the molt season of common murres in a year of unusually warm sea-surface temperatures. At the time of writing, the mortality event is still ongoing and the causes are not yet fully understood, but a main hypothesis is that warm sea-surface temperatures caused shifts in prey distributions, potentially both horizontally and vertically, and molting murres, given their reduced mobility and foraging efficiency, were not able to adapt to shifts in lower trophic levels.

3.4.4 Birds with large molt extents have molting grounds in a variety of habitats

We expected that birds classified with the largest molt extents would limit molting grounds to the least pelagic, most predictably productive regions in the North Pacific, such as the Aleutian Islands and the California Current since food availability is considered seasonally more predictable in these areas (Longhurst 2010). Molting birds, however, used a variety of ecoregions, including, for Laysan albatrosses, a heavy use of the North Pacific Polar Front – an entirely pelagic habitat during the core months of molt (Figure 3.12b). Despite being pelagic, the North Pacific Polar Front is a highly energetic frontal zone, where warm-core and cold-core eddies born at the western confluence of the Kurishio and Oyashio currents propagate eastward and concentrate flotsam, including food, at their outer boundaries (warm) and cores (cold) (Longhurst 2010). Coherent structures formed by convergences and divergences in areas of high eddy kinetic energy aggregate prey and appear to be areas of predictable resources for marine predators such as seabirds (i.e., Burger 2003, Tew Kai et al. 2009, Tew Kai and Marsac 2010). A climatology of chlorophyll-a concentrations ([chl-a]) from the years spanning this study show a consistent increase of [chl-a] during spring in the western and eastern regions of the NPPF (Figure 3.12a) when it is consistently visiting by large molt birds during the molting months (May-July) (Figure 3.12b).

3.4.5 Samalga Pass in the Aleutian Islands as a point of habitat delineation

In accordance with other studies (Shuntov 1974, Fischer et al. 2009, Suryan and Fischer 2010, Gutowsky et al. 2014), Laysan and black footed albatrosses maintained distinct habitat segregation in the post-breeding seasons, with black-footed albatrosses more heavily exploiting the coastal biomes of the Alaska Downwelling and California Upwelling provinces, and with Laysan albatrosses predominantly using the more pelagic waters of the North Pacific Polar Front and the western Pacific Subarctic Gyre (Figure 3.7). Both species showed heavy use of the Aleutian Island archipelago (in the PSAW and PSAE provinces) but a clear point of delineation between the two species distributions occurred in the vicinity of Samalga Pass in the eastern Aleutians (170˚ W). Interestingly, the pass is a known point of transition between two environmental and ecosystem regimes (Hunt and Stabeno 2005, Jahncke et al. 2005): east of the pass, waters are warmer and fresher and the ecosystem has a heavier influence of the continental shelf, while west of the pass, waters are colder and more saline, and the ecosystem is comprised of species associated with more oceanic waters. Accordingly, the more oceanic and pelagic of the two species, Laysan albatrosses, occur much more frequently west of Samalga Pass, while black-footed albatrosses, known to be continental shelf specialists, increase in numbers east of the pass (Figure 3.13). Sea-surface temperature has been identified as a good predictor of Laysan and black-footed albatross distributions, with Laysan albatrosses occurring in waters a few degrees Celsius colder than black-footed albatrosses (Kappes et al. 2010). Given the delineation of albatross distributions at Samalga Pass, which separates a warmer water mass from a colder water mass, it appears SST likely remains an important predictor of albatross distributions into the post-breeding migrations as well.

3.4.6 Habitat partitioning between ages and sexes in post-breeding migrations

Much focus on understanding niche partitioning between and within seabird species takes place during the breeding season when birds are constrained to their nests and are therefore limited in range due to the constraints of central place foraging. Less attention is given to understanding niche partitioning during the post-breeding season when individuals disperse from the colony and are released from central place constraints and are therefore “free” to forage where they please. However, accumulation of evidence showing clear habitat segregation among breeding colonies within species (Wanless and Harris 1993, Grémillet et al. 2004, Wakefield et al. 2011, 2013) suggests that this stage of the annual cycle is not devoid of competition, especially given the localized behavioral patterns once albatrosses migrate to their molting grounds. Post-breeding migrations are critical for self-maintenance in the form of flight feather replacement and regaining lipid stores for subsequent breeding efforts; and, thus the quality of an individual's post-breeding season can have significant carryover effects impacting the success of subsequent breeding efforts (Oppel and Powell 2009, Sorensen et al. 2009, Catry et al. 2013a, O'Connor et al. 2014). Dense aggregations of birds in limited areas during molting months might impose a level of competition just as strong, or stronger, than during the breeding season. The sex and age driven differences in habitat use in Laysan and black-footed albatrosses that we identified in post-breeding migrations could be explained as a response to intra-specific competition, although another possibility is that habitat differences reflect group-specific requirements, such as differences in nutrition or wind-regimes.

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Table 3.1 Sample sizes of GLS deployments over eight years

	2004	2005	2006	2008	2009	2010	2011	2012	Total
LAAL	5	12	12	11	11	6	12	7	**76**
BFAL	0	12	13	10	10	5	10	7	**67**
Total	**5**	**24**	**25**	**21**	**21**	**11**	**22**	**14**	**143**

Table 3.2 Discriminant Function Analysis to Predict Subsequent Breeding Initiation

The performance of the DFA varied between species and between sexes within a species. Trip metrics were more successful, in general, in predicting nest initiation for black-footed albatrosses than for Laysan albatrosses. In both species, female nest initiation was better predicted by migration metrics than in males. Sample sizes are italicized in parentheses

	Discriminant Function[1]	Predictive Success		
		Combined	Subsequent Non-Breeders	Subsequent Breeders
BFAL				
Male	Duration + MCP[2] + End DOY[3]	85 % *(20)*	80 % *(5)*	87 % *(15)*
Female	Duration + MCP	91 % *(22)*	50 % *(4)*	100 % *(18)*
LAAL				
Male	Duration + End DOY	71 % *(17)*	78 % *(9)*	50 % *(10)*
Female	MCP	83 % *(18)*	72 % *(7)*	91 % *(11)*

[1] Variables used in DFA were using stepwise forward selection
[2] MCP = maximum convex hull area, representing home range size
[3] DOY = "Day of Year"

Table 3.3 . Post-Breeding Migration Chronology of Laysan albatrosses

Mean departure and arrival dates, identified from SST records, and trip durations are provided with standard deviations. Metrics of migration chronology were summarized only from birds that initiated and completed a breeding effort the year of deployment and whose tags recorded complete trips. We did not have nest initiation data from all birds for the subsequent year (Year 2), and this is reflected in varying sample sizes.

			Departure Year 1		**Arrival Year 2**	**Duration**
		n	μ ± SD (days)	***n***	μ ± SD (days)	μ ± SD (days)
All Birds		*53*	July 07 ± 15	*47*	Nov 20 ± 9	142 ± 17
	Year 2: Breeding	*21*	July 05 ± 12	*19*	Nov 20 ± 9	144 ± 16
	Year 2: Not Breeding	*22*	July 12 ± 14	*18*	Nov 20 ± 11	135 ± 15
Males		*27*	July 07 ± 15	*24*	Nov 22 ± 7	144 ± 16
	Year 2: Breeding	*9*	July 05 ± 12	*8*	Nov 21 ± 3	144 ± 13
	Year 2: Not Breeding	*12*	July 14 ± 12	*10*	Nov 23 ± 9	137 ± 15
Females		*25*	July 06 ± 14	*22*	Nov 19 ± 10	141 ± 18
	Year 2: Breeding	*12*	July 05 ± 12	*11*	Nov 19 ± 12	144 ± 19
	Year 2: Not Breeding	*9*	July 09 ± 17	*7*	Nov 19 ± 12	135 ± 17

Table 3.4 Migration Chronology of Black-footed albatrosses

Mean departure and arrival dates, identified from SST records, and trip durations are provided with standard deviations. Metrics of migration chronology were summarized only from birds that initiated and completed a breeding effort the year of deployment and whose tags recorded complete trips. We did not have nest initiation data from all birds for the subsequent year (Year 2), and this is reflected in varying sample sizes.

			Departure Year 1		**Arrival Year 2**	**Duration**
		n	μ ± SD (days)	**n**	μ ± SD (days)	μ ± SD (days)
All Birds		*58*	June 19 ± 13	*54*	Nov 13 ± 8	152 ± 13
	Year 2: Breeding	*36*	June 17 ± 14	*33*	Nov 12 ± 7	154 ± 14
	Year 2: Not Breeding	*11*	June 24 ± 12	*10*	Nov 16 ± 8	149 ± 15
Males		*28*	June 18 ± 14	*27*	Nov 12 ± 8	153 ± 13
	Year 2: Breeding	*16*	June 16 ± 17	*15*	Nov 9 ± 5	152 ± 15
	Year 2: Not Breeding	*5*	June 23 ± 9	*5*	Nov 20 ± 6	156 ± 9
Females		*29*	June 21 ± 11	*26*	Nov 15 ± 7	152 ± 14
	Year 2: Breeding	*20*	June 19 ± 11	*18*	Nov 14 ± 8	155 ± 13
	Year 2: Not Breeding	*5*	June 25 ± 17	*4*	Nov 13 ± 9	141 ± 19

Table 3.5 Differences in home range and core area sizes relative to molt extent, sex and age for each species

Range sizes summarized only for trips that were complete.

	Molt Extent			Sex		Age Class	
	Large	Medium	Small	Male	Female	Older	Younger
LAAL	12	22	17	38	27	17	40
BFAL	3	40	11	30	26	7	36
Home Range Size (10^4 km^2) (Mean ± SE)							
LAAL	714.9 ± 65.7	579.2 ± 54.4	401.8 ± 55.9	577.0 ± 46.0	578.5 ± 57.5	482.0 ± 60.8	616.6 ± 46.0
BFAL	1034.1 ± 157.1	677.6 ± 31.1	495.0 ± 47.7	656.9 ± 36.8	668.0 ± 45.5	607.5 ± 104.6	671.1 ± 32.0
Core Area Size (10^4 km^2) (Mean ± SE)							
LAAL	30.8 ± 3.3	28.6 ± 2.1	22.6 ± 2.0	28.0 ± 1.6	30.0 ± 2.2	24.7 ± 2.4	30.9 ± 1.7
BFAL	29.5 ± 1.7	22.9 ± 1.7	22.6 ± 2.9	23.8 ± 1.7	23.3 ± 2.3	25.9 ± 5.0	23.7 ± 1.8

Table 3.6 Results from per-MANOVA analyses testing habitat composition as a function of sex, age class, and molt extent

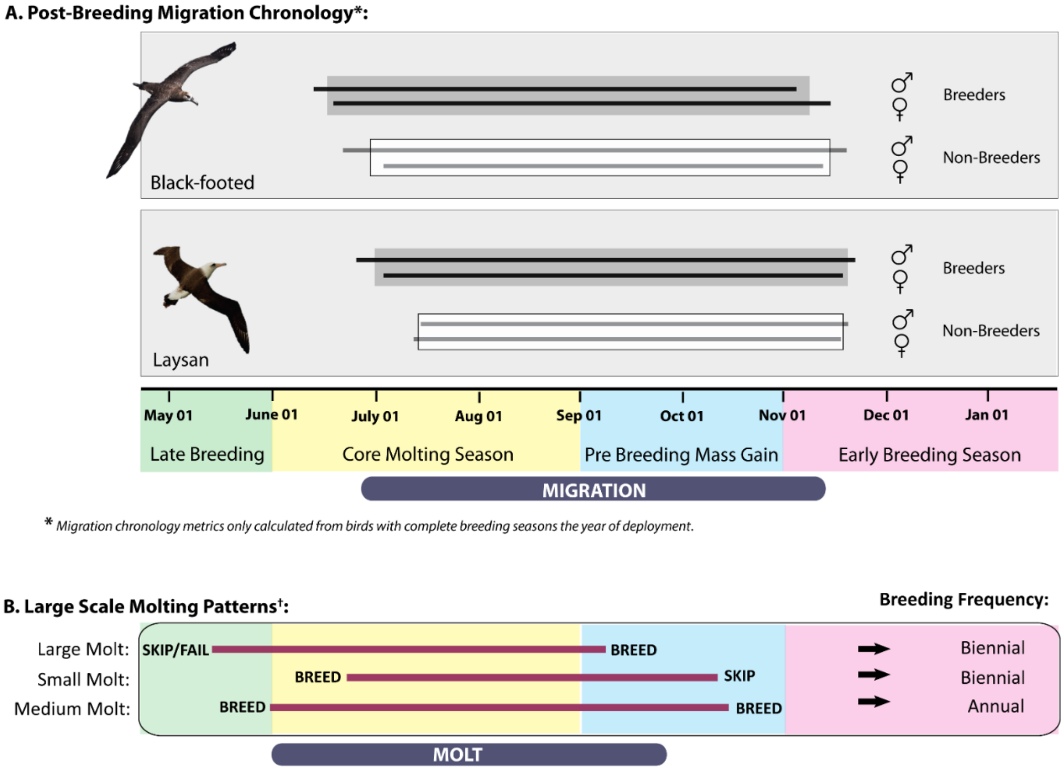
Separate models were run within each species for full tracks, tracks portions of molting months (May-August), and track portions during pre-breeding months (September - October). Significant effects are in bold and asterisks indicate significance (**) and marginal significance (*).

Full Trip								
	Sex		**Age Class**		**Molt**		**Sex*Age Class**	
	P	Pseudo F	P	Pseudo F	P	Pseudo F	P	Pseudo F
LAAL	5.761	**0.004 ** **	7.388	**< 0.001 ** **	3.271	**0.011** **	0.764	0.515
BFAL	1.590	0.210	1.751	0.156	1.076	0.376	1.438	0.232
Molting Months								
LAAL	2.535	**0.075 ***	3.704	**0.018 ** **	1.838	0.127	NA	NA
BFAL	0.890	0.462	2.174	**0.087 ***	0.797	0.643	0.717	0.543
Pre-Breeding Months								
LAAL	3.904	**0.019 ** **	2.731	**0.037 ** **	4.159	**0.002 ** **	0.155	0.930
BFAL	1.352	0.244	1.543	0.188	1.156	0.322	2.821	**0.040 ** **

Table 3.7 Site Fidelity across the migration

Results of Poisson or zero-inflated binomial (ZIBM) models that measured if fidelity indices of paired trips from the same individual were significantly different from fidelity indices calculated from trips paired from random birds. Poisson and ZIBM models were run for each month and compared using a Vuong test. Results from the better models selected by the Vuong statistic are presented below. Comparisons between repeat and random birds were not performed for the months of March, April and May due to small sample sizes.

	Fidelity Index (Mean ± SE)						
Month	**Repeat Birds**	**Random Pairs**	**Model**	**estimated coefficient**	**SE**	**z value**	**P**
March	0.16 ± 0.16(2)	0.11 ± 0.06 (4)	*NA*	*NA*	*NA*	*NA*	*NA*
April	0.26 ± 0.26 (2)	0.16 ± 0.08 (4)	*NA*	*NA*	*NA*	*NA*	*NA*
May	0.25 ± 0.02 (2)	0.39 ± 0.08 (7)	*NA*	*NA*	*NA*	*NA*	*NA*
June	0.45 ± 0.10 (7)	0.17 ± 0.08 (14)	Poisson	1.09861	0.12546	8.757	**< 0.001**
July	0.43 ± 0.11 (9)	0.15 ± 0.04 (34)	ZIBM	-2.079	1.110	-1.873	**0.061**
August	0.43 ± 0.11 (9)	0.23 ± 0.05 (38)	ZIBM	-2.194	0.854	-2.568	**0.010**
September	0.35 ± 0.12 (8)	0.20 ± 0.04 (36)	ZIBM	-2.521	1.109	-2.274	**0.023**
October	0.23 ± 0.07 (7)	0.16 ± 0.03 (36)	ZIBM	-1.150	0.891	-1.29	0.197



Migration chronology metrics only calculated from birds with complete breeding seasons the year of deployment.

†*Generalization of Fig. 3 in Edwards AE, 2008*

Figure 3.1 Post-Breeding Migration Chronology Relative to Flight Feather Molting Chronology

1A. Migration Chronology: Dark grey rectangles represent duration of post-breeding migration for birds that initiate a nest ('Breeders') the season following the migration. White rectangles represent migration durations of birds that do not initiate a nest the season following the migration ('Non-Breeders'). Solid lines within each box represent durations separately for males (♂) and females (♀). The start and end of the generalized durations represent mean dates of departure and arrival. The monthly timeline is separated into 4 sectors of time relevant to both molt and migration: 1) Late Breeding 2) Core Molting Season, 3) Pre-Breeding Mass Gain, and 4) Early Breeding Season.
1B. Molting Chronology: Adapted from Edwards et al 2008. The three molt series (large, medium, and small) are each represented by a distinct generalized chronology (pink lines) relative to the post-breeding migration. Reproductive patterns influenced by each molt series are shown by breeding decisions ('breed', 'skip/fail', 'skip') spanning the migration. Also shown are the consequences of each molt pattern on breeding frequency (annual, biennia).

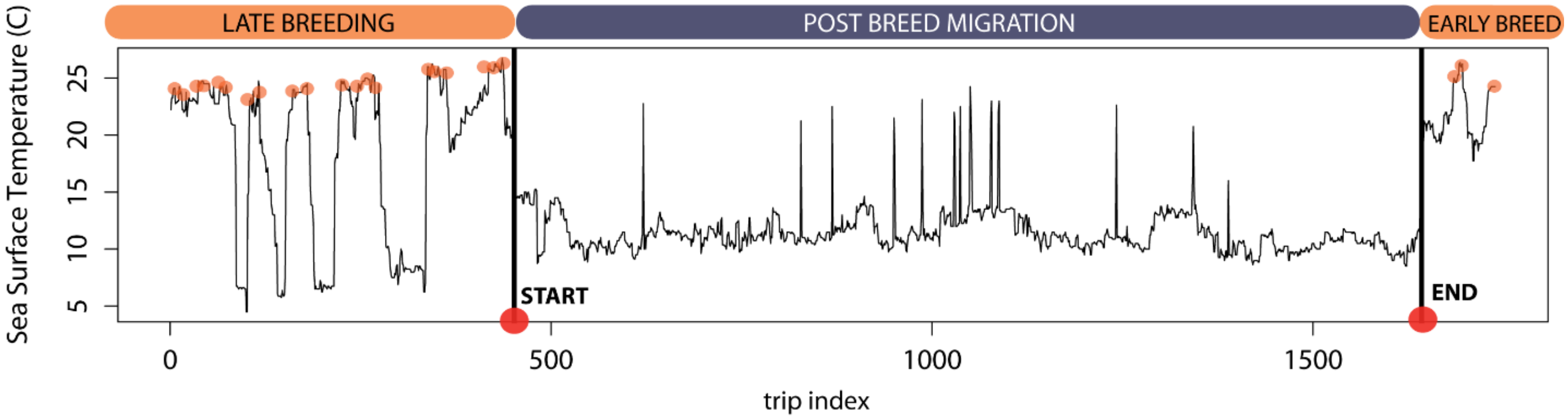


Figure 3.2 Using sea-surface temperature (SST) time-series records to truncate post-breeding migrations

An example of a SST record recorded from a LTD2400 used to identify departure (start) and arrival (end) dates (red circles) for a post-breeding migration trip. Notice the dramatic drop in SST from ~25 ˚C to 15-10 ˚C around index 490 and sudden increase back to ~ 25 ˚C around index 1600. Fluctuations in SST during the late breeding season most likely represent foraging trips during the chick-rear period, while short spikes in SST during the post-breed migration are likely from times the bird tucked its leg into feathers, inducing an artificial temperature increase. SST around Tern Island range between 20-27 ˚C . Orange circles represent when bird is back at the colony.

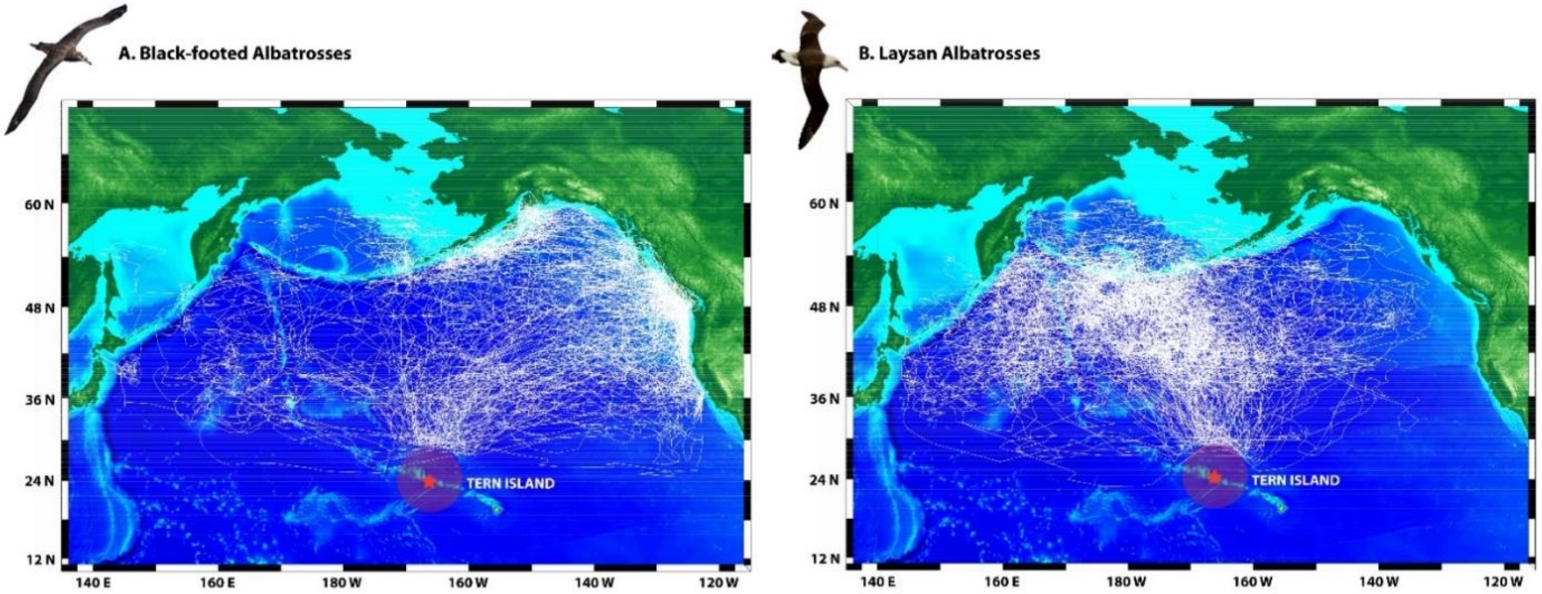


Figure 3.3 Final Trip Estimations from geolocation data processed through 'BAStag' and 'SGAT' packages in R for a) black-footed albatrosses and b) Laysan albatrosses

Tern Island is indicated with a red star and surrounded by a 500 km buffer.

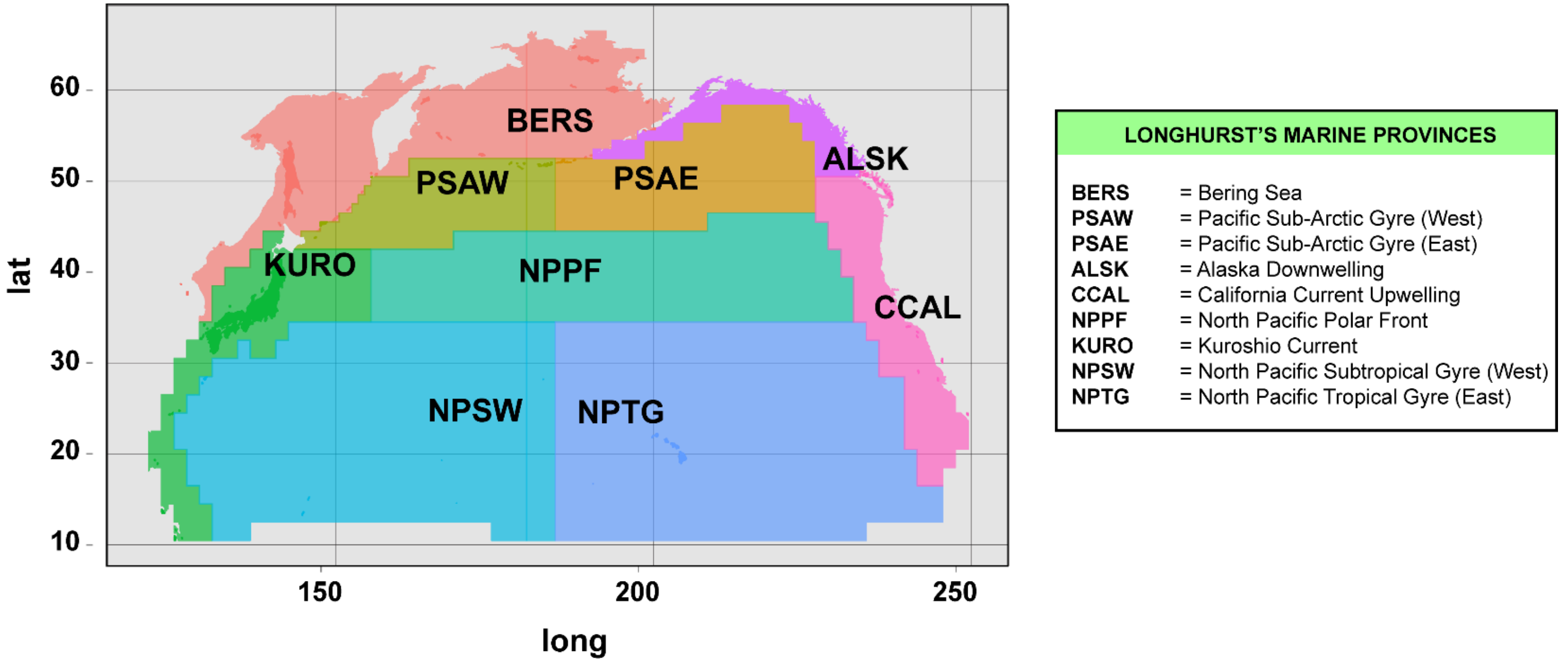
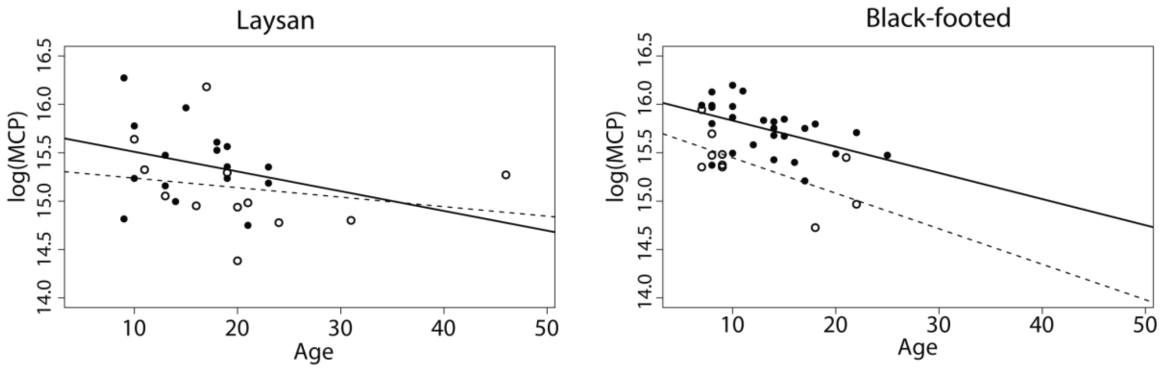


Figure 3.4 Longhurst's Marine Provinces

Nine provinces across the North Pacific basin were used to delineate broad habitat differences within and between species.

a) Total Home Range Size



b) Core Area Size

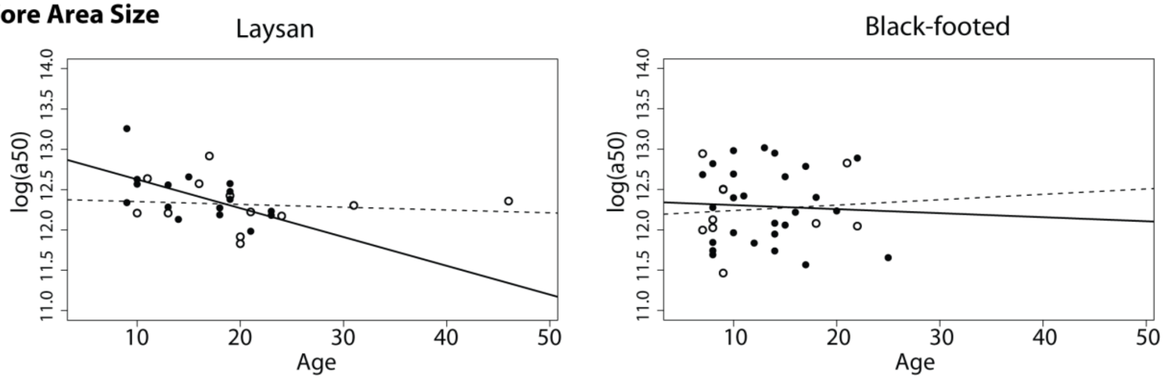


Figure 3.5 Home range size (km2) decreases with age in both a) black-footed albatrosses and b) Laysan albatrosses

This trend persisted regardless of breeding status the year following the migration. Filled circles and solid lines represent birds that initiated nests the following season while open circles and dotted lines represent those birds that did not initiate. Birds only with known ages were used in regression. Core area size only decreased in Laysan albatrosses that initiated nests, but this was not significant in the linear model.

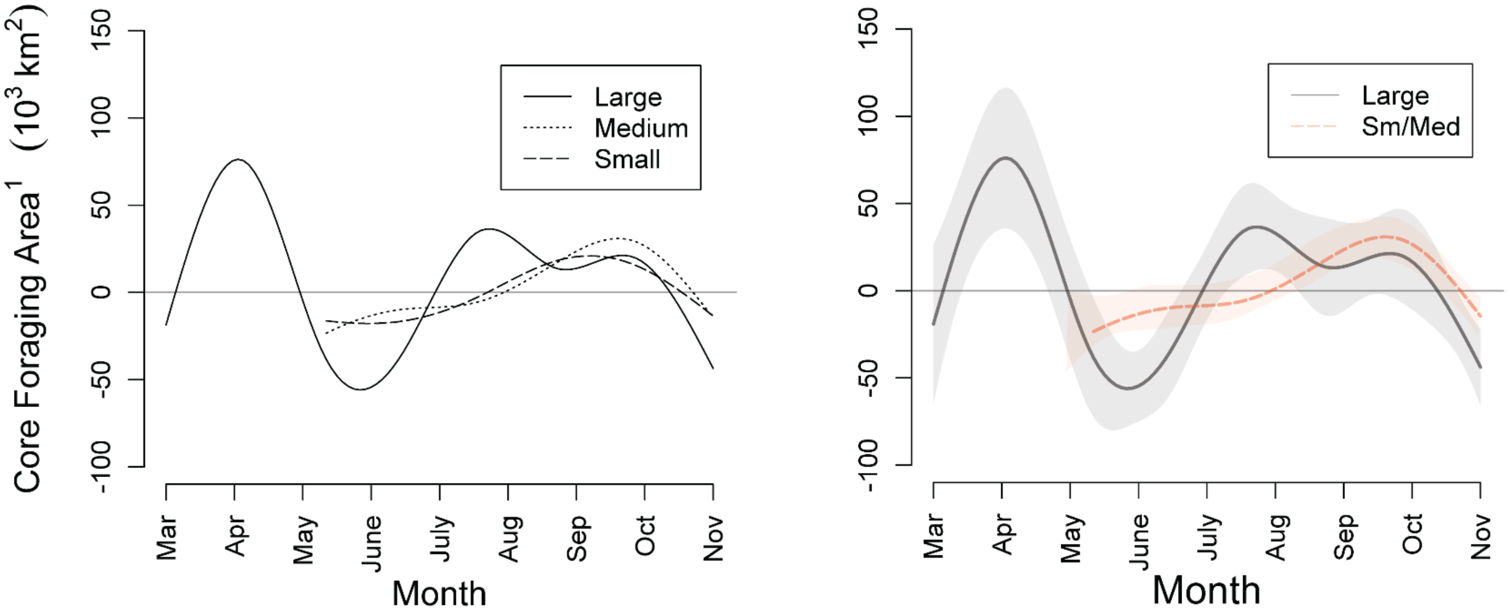


Figure 3.6 The effect of molt extent on activity (core area size) across the post-breeding migration in albatross

Activity was defined as the change in core area size, measured on a monthly scale. [1]Monthly core area sizes were mean-centered for each individual to give relative values of change in core foraging areas. A) Monthly smoothers nested under all three molt scenarios B) Medium and small molts combined into a single smoother and plotted with 95% confidence intervals. Birds with the largest molt extent have trips beginning much earlier than the other molt extents, because these birds either did not initiate a breeding effort or they initiated a nest but it failed, the year of deployment.

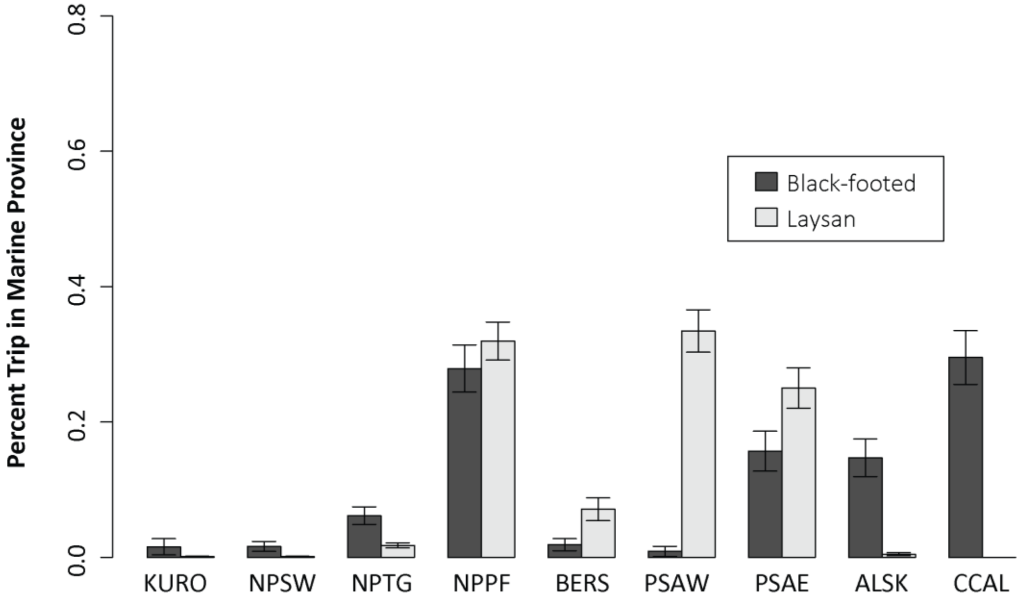


Figure 3.7 Habitat composition during molting months of post-breeding albatross migrations

KURO=Kuroshio Current Province, NPSW = North Pacific Subtropical Gyre (West), NPTG = North Pacific Tropical Gyre, North Pacific Polar Front (NPPF), BERS = Bering Sea, PSAW=Pacific Subarctic Gyre (West), PSAE=Pacific Subarctic Gyre (East), ALSK = Alaska Coastal Downwelling, CCAL = California Current.

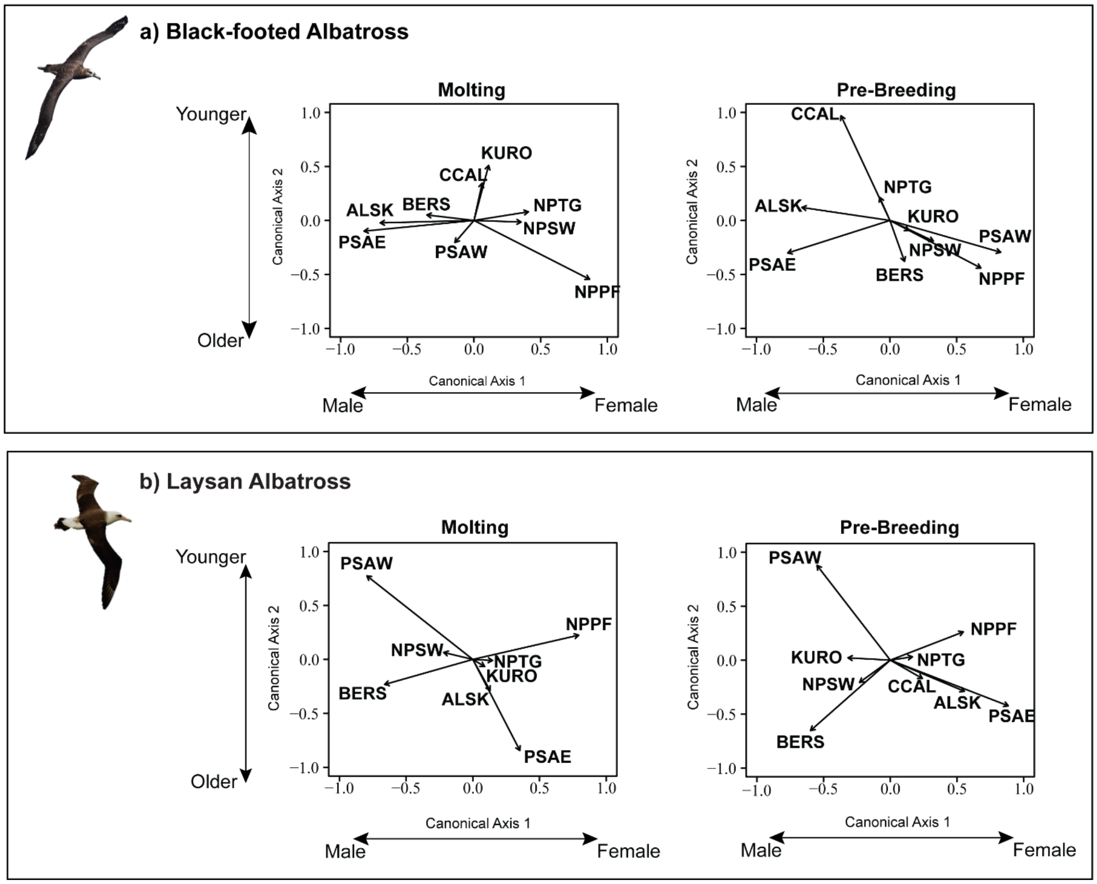
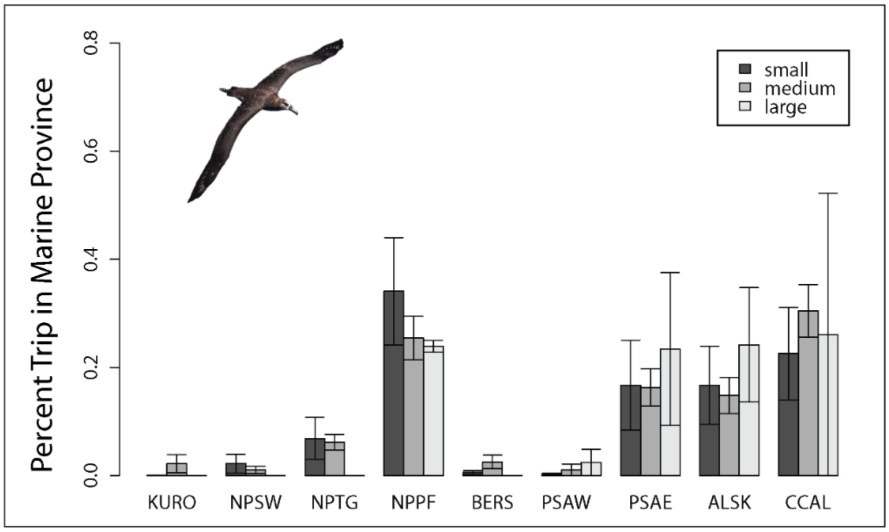


Figure 3.8 Results of four separate canonical analyses of principle components showing the effect of sex and age class on habitat composition in post-breeding migrations for a) black-footed and b) Laysan albatrosses, for two phases of the post-breed migrations: core molting months (Aug. - Sep.) and pre-breeding months (Sep. – Oct.)

Length of arrows indicate strength of correlation between marine province and canonical axes, while direction of arrows indicate which axis (sex or age) the marine province is associated with. KURO=Kuroshio Current Province, NPSW = North Pacific Subtropical Gyre (West), NPTG = North Pacific Tropical Gyre, North Pacific Polar Front (NPPF), BERS = Bering Sea, PSAW=Pacific Subarctic Gyre (West), PSAE=Pacific Subarctic Gyre (East), ALSK = Alaska Coastal Downwelling, CCAL = California Current Upwelling.

a. Black-footed albatrosses



b. Laysan albatrosses

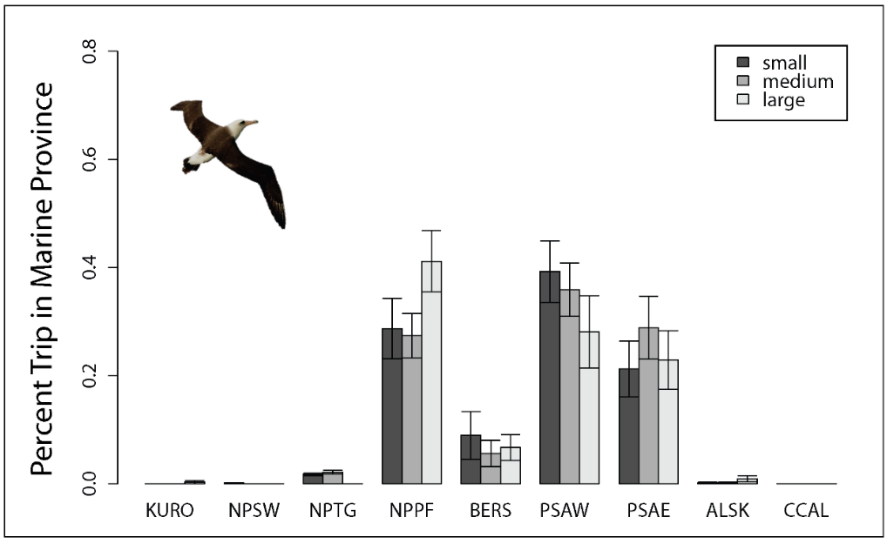


Figure 3.9 . Effect of molt extent on habitat composition in post-breeding migrations of a) black-footed and b) Laysan albatrosses

KURO=Kuroshio Current Province, NPSW = North Pacific Subtropical Gyre (West), NPTG = North Pacific Tropical Gyre, North Pacific Polar Front (NPPF), BERS = Bering Sea, PSAW=Pacific Subarctic Gyre (West), PSAE=Pacific Subarctic Gyre (East), ALSK = Alaska Coastal Downwelling, CCAL = California Current Upwelling.

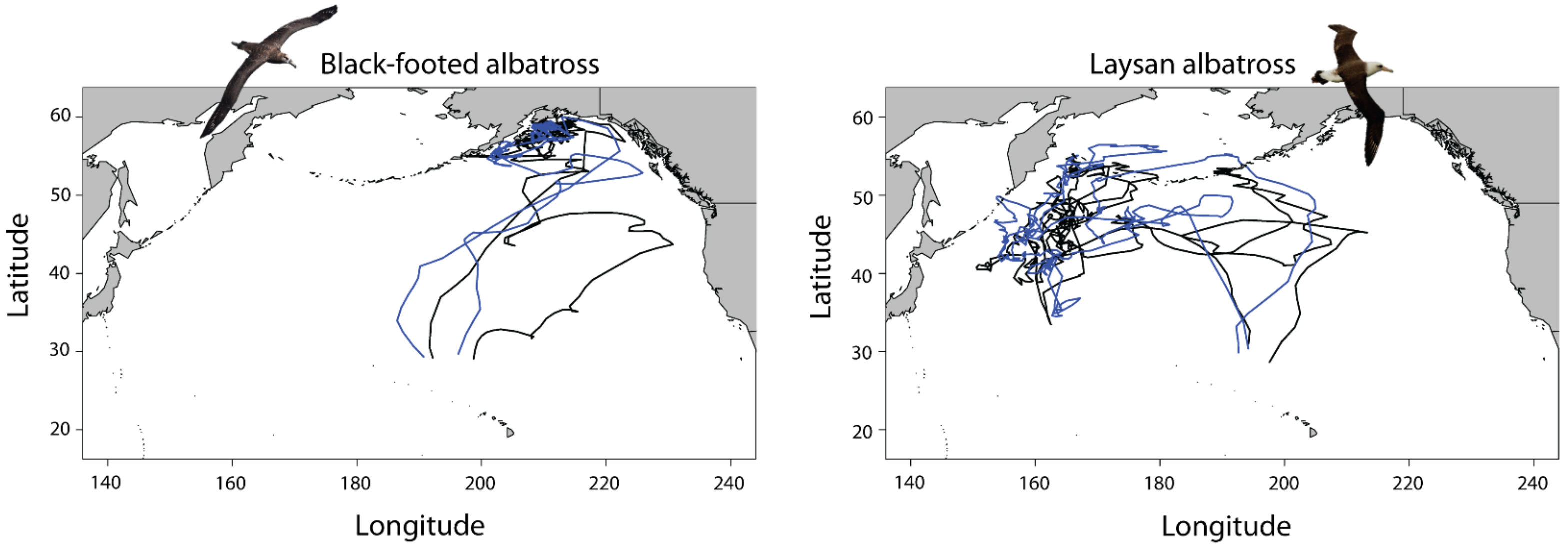


Figure 3.10 Tracks of two individuals with migrations tracked in two consecutive years indicate a high level of site fidelity in these species

Black lines represent migrations in 2010 while blue lines represent migrations from 2011.

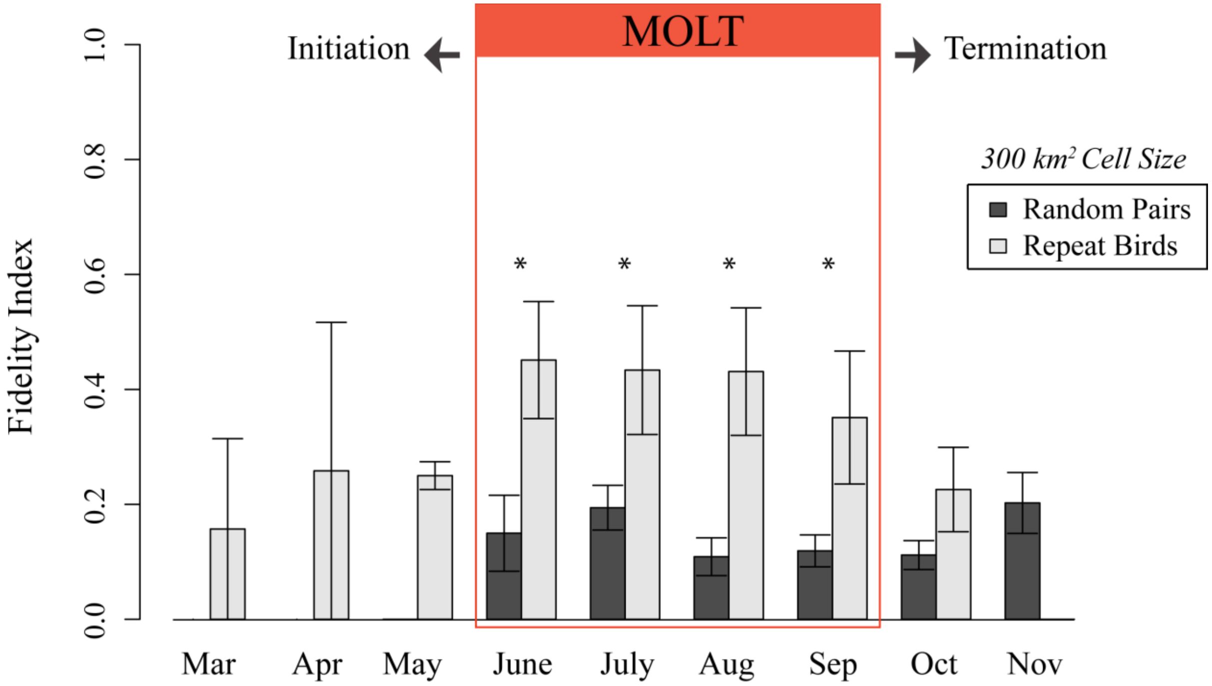


Figure 3.11 Site fidelity across years in post-breeding migrations is greatest in molting months

Asterisks indicates a significant difference ($P < 0.05$) between fidelity indices from random paired tracks and from same individual paired tracks

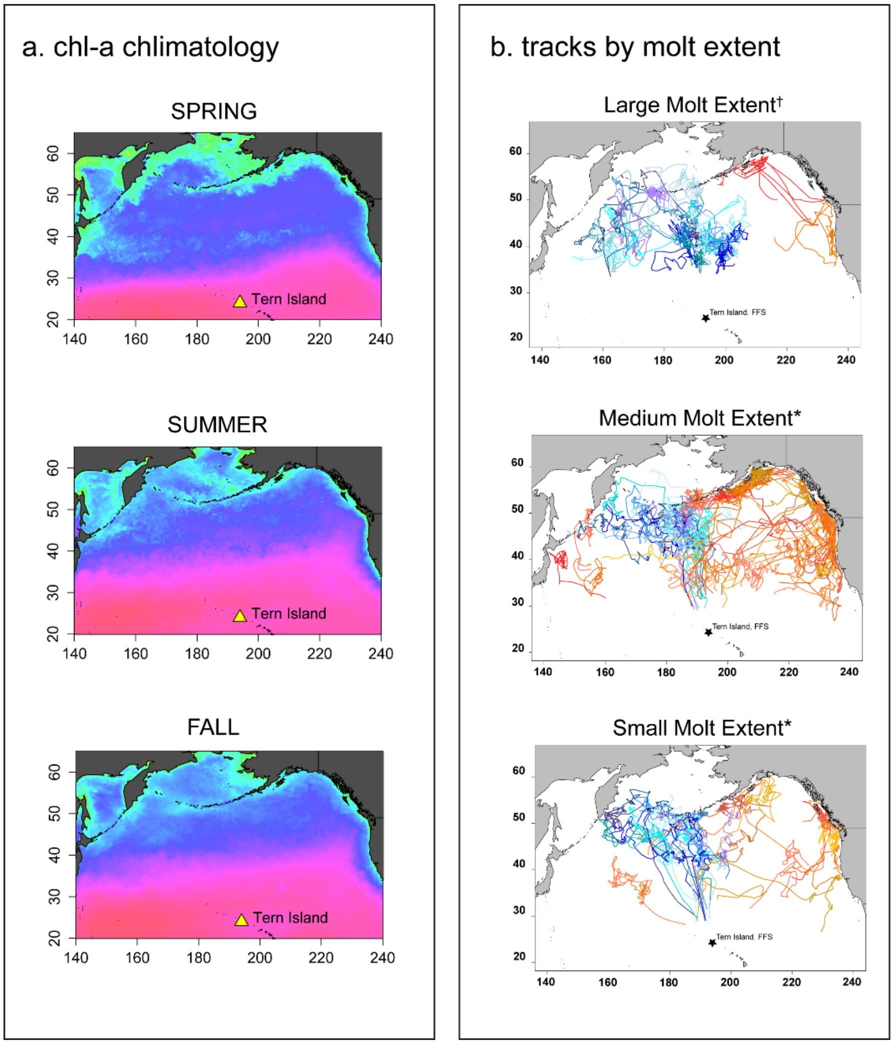


Figure 3.12 Laysan albatrosses with large extent molts appear to take advantage of a spring bloom of primary productivity in the Transition Zone Chlorophyll Front

a) Chlorophyll-a climatologies for the seasons of Spring (Mar-May), Summer (June-Aug) and Fall (Sep-Nov) from the years of this study (2004-2012). Rasters of chlorophyll-a concentrations were downloaded from BloomWatch 360 (*http://coastwatch.pfeg.noaa.gov/coastwatch/CWBrowserWW360.jsp*). Chlorophyll-a concentrations are represented by colors ranging from pink (lowest [chl-a] to green (highest [chl-a]). b) Laysan albatross tracks are truncated to core molting months. For large molt birds (†) trips were truncated to May, June and July (Spring/Summer), while for medium and small molt birds (*) tracks represent the trips during July August and September (Summer/Fall). Tracks from Laysan albatrosses are represented by shades of blue, while black-footed albatross tracks are represented by shades of red and orange.

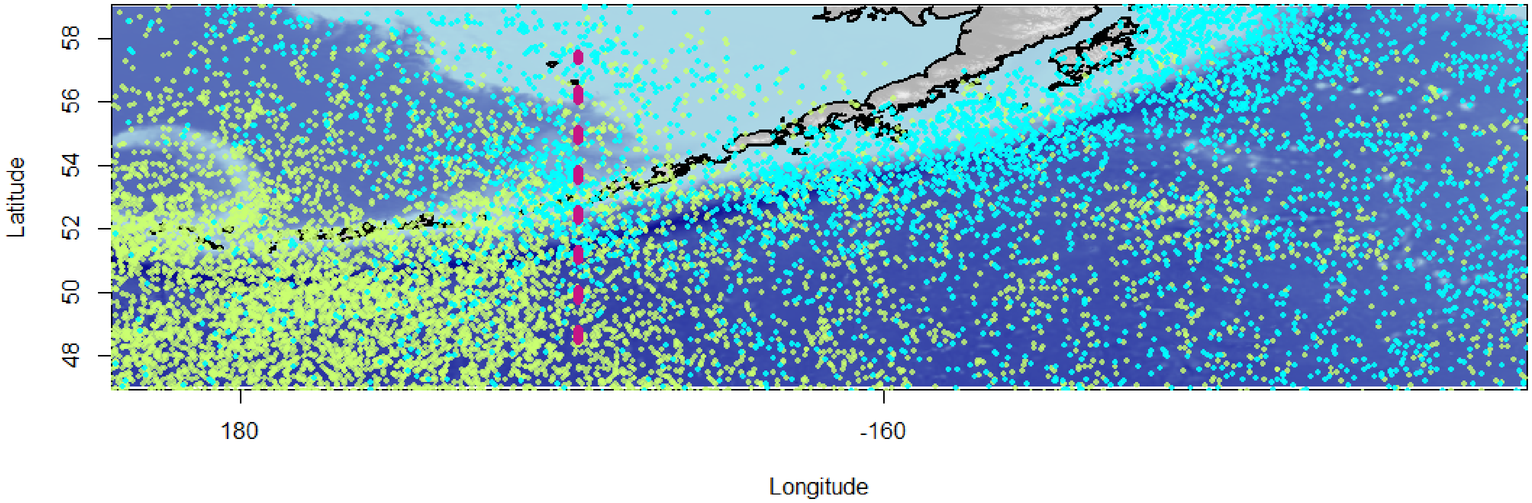


Figure 3.13 Samalga Pass (indicated by red dashed line) as a point of habitat delineation between Laysan albatross (yellow circles) and black-footed albatross (cyan circles).