

AN ABSTRACT OF THE DISSERTATION OF

Robert M. Suryan for the degree of Doctor of Philosophy in Wildlife Science presented on March 23, 2006.

Title: Comparative Foraging Ecology of Five Species of Pacific Seabirds: Multi-scale Analyses of Marine Habitat Use.

Abstract approved:

Daniel D. Roby

Seabirds are an integral component of marine ecosystems, however, because humans typically observe only snapshots of their lives at sea, our understanding of seabird foraging ecology is often limited. A more complete understanding of the ecological roles of seabirds and identification of critical foraging habitats requires the ability to follow individuals at-sea. I analyzed continuous tracking data from black-legged kittiwakes (*Rissa tridactyla*) and four species of Pacific albatrosses to determine if foraging time budgets and at-sea movement patterns were associated with prey type (kittiwakes) and remotely sensed environmental variables (albatrosses). Furthermore, I identified variables affecting the spatial scale of search behavior and, for kittiwakes, the effect this has on reproductive success.

Black-legged kittiwakes in Prince William Sound, Alaska, increased the number of feeding attempts with increases in the consumption of young-of-year fish and the numbers of feeding flocks encountered, both leading to greater time spent searching for food. Greater search effort translated into longer foraging trip duration (i.e., less frequent nestling provisioning), which was a dominant variable affecting reproductive success.

Not surprisingly, area-restricted search activity for kittiwakes occurred over spatial scales two orders of magnitude less than that of short-tailed albatrosses (*Phoebastria albatrus*; 0.8 km vs. 70 km, respectively). For kittiwakes, the scale of area-restricted search was most prominently associated with prey type. I adapted first-passage time analysis to model habitat use as a continuous process along a movement path and found that area-restricted search activity of short-tailed albatrosses was greatest along the continental shelf break and slope within regions of higher gradients of depth and chlorophyll a. Wind speed also was an important variable affecting albatross movements.

By capitalizing on ocean surface wind and wave energy, albatrosses efficiently travel over vast expanses of the world's oceans. I analyzed albatross aerodynamics and satellite remote sensing data to demonstrate that the four species of albatrosses inhabiting the North and Central Pacific Ocean exhibit differences in flight morphology that are generally consistent with respect to prevailing wind and wave conditions encountered. Some individuals, however, ventured into regions of apparently suboptimal wind and wave conditions to presumably exploit preferred foraging opportunities.

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Comparative Foraging Ecology of Five Species of Pacific Seabirds: Multi-scale
Analyses of Marine Habitat Use

by

Robert M. Suryan

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APPROVED

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Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Robert M. Suryan, Author

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DEDICATION

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Comparative Foraging Ecology of Five Species of Pacific Seabirds: Multi-scale Analyses of Marine Habitat Use

Chapter 1. Introduction To The Dissertation

A species, population, or individual survives by constantly adapting to the changing environment in which it lives, with a primary concern being the acquisition of food as supplies fluctuate in time and space. How an individual adjusts its foraging behavior for a given food supply is the foundation for theoretical studies of animal foraging. The study of foraging theory stemmed from two seminal papers, MacArthur (1966) and Emlen (1966), and was an attempt to predict how natural selection molds patterns of foraging behavior (Hughes 1993). A primary assumption of foraging theory is that an animal promotes its fitness by foraging in a manner that maximizes the net rate of energy gain (optimal foraging theory) and, if given a choice, will select the prey item that maximizes the net rate of energy intake (optimal diet theory: Stephens and Krebs 1986). However, economic models of foraging that assume forage selection is at or near an optimum have several limitations: (1) they do not consider the dynamic nature of ecosystems, (2) they do not incorporate learning (i.e., they cannot explain why sympatric conspecifics exhibit different dietary habits), (3) they assume that energy is the most important dietary component, and (4) they do not consider the effects of predation risk on the behavior of the forager (Provenza and Cincotta 1993, Sih 1993). Therefore, it is necessary to understand physiology, functional anatomy, ethology, psychology, life-history, and population ecology as they influence foraging behavior (Hughes 1993).

A further consideration in the study of foraging ecology and habitat use is the scale at which the animal is interacting with the environment (Wiens 1989, Schneider 2001). The distribution of prey, the numerical response of predators to prey, and the scale at which these interactions occur have been a primary focus in a growing body of literature addressing predator-prey interactions (e.g., Mackas and Boyd 1979, Schneider and Piatt 1986, Logerwell et al. 1998). In most systems, it is clear that predator-prey interactions occur at multiple, often nested, spatial and temporal scales (e.g., Kotliar and

Wiens 1990). Recognition of such hierarchical structuring of patch dynamics has been proposed as a paradigm shift in ecology (Wu and Loucks 1995) and seems particularly pertinent to marine systems, including seabird foraging ecology (Fauchald 1999, Fauchald et al. 2000).

Seabirds are globally distributed throughout the oceans. While foraging at sea, seabirds differentiate into feeding guilds that are as diverse as the ocean regions they inhabit and include surface and sub-surface feeding planktivores and piscivores. Seabirds, therefore, are an integral part of global marine ecosystems. For many seabird species their only tie to land is during the breeding season; however, even during this period they must forage at-sea. Because humans can observe only snapshots of their lives at sea, our understanding of how seabirds search for and locate prey within the marine environment is often limited. A more thorough understanding of the ecological roles of seabirds and identification of environmental variables or threats affecting seabird populations requires the ability to follow individual birds at sea and, where possible, determine key habitats and prey species for survival and reproduction.

During the past few decades, advances in miniaturization of electronic components and pioneering efforts to attach data recorders and transmitters to seabirds (Kooyman et al. 1971, Anderson and Ricklefs 1987, Jouventin and Weimerskirch 1990) have provided new approaches to understand the mysteries of seabird travels away from their breeding colonies. Initial use of VHF transmitters (Anderson and Ricklefs 1987, Hamer et al. 1993, Uttley et al. 1994) provided point locations of individual birds, but lacked the detailed information of continuous movements patterns and were restricted to nearshore activities (< ca 30 km from shore). It was not until the studies of Irons (1998) that individual seabirds carrying VHF transmitters were continuously tracked during foraging trips from the breeding colony. In this study, Irons (1998) used a boat to follow and record the flight path and searching and foraging behaviors of individual radio-tagged black-legged kittiwakes (*Rissa tridactyla*; surface-feeding piscivorous seabirds). This pioneering work provided a means to study seabird foraging ecology directly and in detail. However, a limitation of this type of study is that it can only be conducted over relatively small spatial scales (<100 km).

Tracking of individual seabirds over larger spatial scales is currently only possible using satellite telemetry, which has become much more widespread in the past decade. Development of platform transmitter terminals and earth-orbiting satellite receivers has permitted the tracking of seabirds globally. Furthermore, by integrating satellite remote sensing data of ocean biological and physical properties, we can quantitatively assess marine habitat use of satellite-tagged birds. These developments and applications have provided an invaluable glimpse into a major portion of a pelagic seabird's life that was previously unobserved.

Herein, I address hypotheses regarding the foraging ecology and marine habitat use in five species of Pacific Ocean seabirds that forage at vastly different spatial scales. One species, the black-legged kittiwake, breeds in highly productive, sub-arctic regions and forages over small spatial scales (10s km) during the breeding season. The other four species are albatrosses that breed in sub-tropical regions. Albatrosses are the epitome of ocean wanderers, traveling across ocean basins searching for food in an environment of heterogeneous productivity (Jouventin and Weimerskirch 1990, Croxall et al. 2005). The short-tailed albatross (*Phoebastria albatrus*), Laysan albatross (*P. immutabilis*), black-footed albatross (*P. nigripes*), and waved albatross (*P. irrorata*) that I studied forage over spatial scales (1000s km) that are orders of magnitude larger than do kittiwakes.

In Chapter 2, I use data collected during a 5-yr, integrated study of black-legged kittiwakes and their prey (surface-schooling forage fishes) to investigate the relative role of key prey species in affecting kittiwake breeding success among four colonies in Prince William Sound, Alaska (each representing a distinct geographic region with differing oceanographic influences). I investigate the role of bottom-up, top-down, and timing match-mismatch effects on kittiwake reproduction. In Chapter 3, I attempt to bridge the gap between the distribution and abundance of prey and their effects on reproduction back at the colony by analyzing tracking data of kittiwake foraging trips that include continuous behavioral observations (including feeding locations) and diets. I use first-passage time analysis (Johnson et al. 1992, Fauchald and Tveraa 2003) to determine the spatial scale of foraging between different habitat types and prey species

and their effects on foraging time-budgets, a primary determinant of energy delivery rate to nestlings (Roby et al. 2000, Suryan 2002).

In Chapter 4, I integrate satellite tracking of birds and remotely sensed oceanographic data (bathymetry, chlorophyll *a* concentration, sea surface temperature, wind speed) to identify important marine habitats for the endangered short-tailed albatross. Here I create a novel approach in adapting first-passage time analysis to quantify habitat use as a multi-scale, continuous process along a movement path. In Chapter 5, I focus on remotely sensed wind speed and vector data and body and wing morphologies of the four species of Central and North Pacific albatrosses (short-tailed albatross, black-footed albatross, Laysan albatross, and waved albatross). I assess whether differences in flight aerodynamics among albatross species are consistent with regional wind patterns and their potential effects on albatross at-sea movements.

Although I focus on hypothesis-driven discussions within the primary chapters of this dissertation, it is important also to note the application-driven aspects of my research. Data collected on black-legged kittiwakes was part of a much larger, integrated study of seabirds and forage fish in the Gulf of Alaska - the Alaska Predator Ecosystem Experiment (APEX). A primary goal of APEX was to determine if food was limiting the recovery of piscivorous seabird populations following the 1989 T/V *Exxon Valdez* oil spill, in which approximately 42 million liters of crude oil were released into Prince William Sound and surrounding waters, killing an estimated 100,000 – 300,000 seabirds (Piatt et al. 1990). Potential lingering effects of the oil spill, however, also needed to be considered with respect to natural environmental fluctuation, including ecosystem regime changes within the Gulf of Alaska that appeared to cause declines in many piscivorous seabird populations prior to the *Exxon Valdez* oil spill (Piatt and Anderson 1996, Anderson and Piatt 1999). Therefore, our studies of black-legged kittiwakes included assessment of historical population trends in Prince William Sound (Suryan and Irons 2001) in addition to the intensive five years (1995 - 1999) of field work for APEX.

Our investigation of albatross distributions at sea was primary driven by conservation concerns for the endangered short-tailed albatross. Once abundant (> 1

million individuals) in the North Pacific Ocean and a common dietary component of indigenous people of coastal North America (Matthiesen 1976, Yesner 1976), the short-tailed albatross was hunted to near extinction by plume collectors during the 19th and mid-20th centuries. By 1953, 14 known colonies had been extirpated and only one extant breeding population, numbering approximately 10 pairs, had reintroduced themselves on Torishima, a volcanic island 580 km south of Tokyo, Japan (Hasegawa and DeGange 1982). An unknown number of non-breeding birds also likely remained at-sea during this period. In recent decades, the short-tailed albatross world population has increased to approximately 2,000 individuals, with 80-85% of the birds nesting on Torishima and 15-20% on the Senkaku Islands (Hiroshi Hasegawa and Paul Sievert unpubl. data, USFWS 2005). The increasing population trend is an encouraging signal for the potential recovery of this species, however, significant threats to the species still exists. For example, over 80% of the population nests on a small island (2 km diameter) with an active volcano that has erupted three times within the past 100 years (USFWS 2005). Furthermore, because albatrosses spend most of their life at sea and range over vast oceanic regions, they are susceptible to anthropogenic and natural impacts thousands of kilometers from their breeding colonies (Prince et al. 1992).

A widespread and pervasive threat to these foraging albatrosses is fisheries bycatch (Weimerskirch 1997). For instance, an estimated 1,260 Laysan albatrosses (*Phoebastria immutabilis*) and black-footed albatrosses (*Phoebastria nigripes*) were killed annually between 1993 and 1997 in demersal longline fisheries operating in the Gulf of Alaska and the Bering Sea (Stehn et al. 2001). Therefore, recent conservation efforts have been focused on birds at sea and included measures to reduce the incidental mortality of short-tailed albatross in longline fishing operations. Knowledge of the pelagic distribution and oceanic habitats exploited by short-tailed albatrosses, particularly in relation to other North Pacific albatross species, is essential to design effective conservation plans for this far-ranging pelagic seabird.

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Chapter 2. Site-Specific Effects On Productivity Of An Upper Trophic-Level Marine
Predator: Bottom-Up, Top-Down, And Mismatch Effects On Reproduction In A
Colonial Seabird

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Abstract

We investigated the relative roles of bottom-up and top-down factors in limiting productivity of an upper trophic level marine predator. Our primary working hypothesis was that the reproductive success of black-legged kittiwakes (*Rissa tridactyla*) a piscivorous, colonial-nesting seabird, was most limited by the abundance, distribution, and species composition of surface-schooling forage fishes. A secondary working hypothesis was that reproductive loss to kittiwake nest predators was greatest during years of reduced prey availability. We report on a broad-scale, integrated study of kittiwakes and their prey in Prince William Sound, Alaska. Our study spanned five breeding seasons (1995 – 1999) and focused on three colonies that differed in size (ranging from ca. 220 to ca. 7,000 breeding pairs) and proximity to each other (50 to 135 km apart). Kittiwakes in PWS encountered a variety of aquatic habitats, creating a complex foraging environment for breeding birds. We measured kittiwake reproductive success and foraging activities, while simultaneously measuring the abundance of surface schooling forage fishes throughout the foraging range of breeding kittiwakes. The abundance of primary prey species for kittiwakes (Pacific herring *Clupea pallasii*, Pacific sand lance *Ammodytes hexapterus*, and capelin *Mallotus villosus*) varied both annually and regionally, with no one region consistently having the greatest abundance of prey. Likewise, kittiwake reproductive success varied considerably among colonies and years.

We found that bottom-up, top-down, timing mismatch, and colony-specific effects were all important to kittiwake productivity. Although bottom-up effects appeared to

be strongest, they were not evident in some cases until other effects, such as geographic location (proximity of colony to prey concentrations) and top-down predation, were considered. Important bottom-up effects on kittiwake reproductive success were not only total prey abundance and distribution, but also species, age composition, and chronology of prey occurrence (match/mismatch of timing with critical brood-rearing periods); these effects varied by colony.

Top-down effects of predation on kittiwake nest contents (independent of prey abundance) confounded seabird-forage fish relationships. Ultimately, when confounding factors were minimized, non-linear asymptotic relationships were identified between kittiwakes and their prey, with an asymptotic threshold of fish school surface area density of ca. $5 \text{ m}^2/\text{km}^2$, beyond which top-down, physiological, or phylogenetic constraints likely restrict further reproductive output. The integrated approach of our investigations provided a more thorough understanding of the mechanisms underlying predator-prey relationships in the complex marine environment. However, such mechanistic theories can only be tested and refined through long-term research and monitoring of much greater duration than the 5-yr study reported herein.

Keywords: bottom-up; top-down; match/mismatch; forage fish abundance; seabird reproduction; predator-prey relationships

Introduction

The relative importance of bottom-up and top-down forces in the ecological structure of communities has been a topic of considerable attention and debate (e.g., Wilson 1987, Terborgh 1988, Floyd 1996, Menge 2000). This debate, however, has

sometimes been joined by protagonists studying idiosyncratic systems during times when their respective study environments may have been in a state of relative stability (Hunter & Price, 1992). Examples of such alternative conclusions of bottom-up or top-down control in marine systems range from rocky intertidal and subtidal communities (Estes & Palmisano 1974, Foster 1990, Robles & Desharnais 2002) to apex marine predators (Trites & Donnelly 2003, Springer et al. 2003) and basin-scale pelagic ecosystems (Cook et al. 1997, Hunt et al. 2002, Beaugrand et al. 2003). Long-term investigations demonstrate the importance of environmental heterogeneity and its effect on the relative importance of ecological forces governing community structure (Dunson & Travis 1991). Consequently, the debate is no longer focused on whether bottom-up, top-down, or other ecosystem structuring forces dominate, but rather to determine the relative influence of various forces in structuring communities and by what mechanisms they interact as environmental conditions change (Hunter & Price 1992, Matson & Hunter 1992, Menge 1992, Hunt et al. 2002).

One mechanism of bottom-up control is match/mismatch timing of primary production and year-class strength of juvenile fishes in the marine environment (Cushing 1975, Beaugrand et al. 2003, Platt et al. 2003). Cushing (1975) based the match/mismatch hypothesis on evidence that, in many systems, the chronology of fish spawning is relatively fixed compared to variation in timing of the spring bloom. A mismatch in the timing of these events could leave larval fishes with limited prey resources, resulting in population-level effects through reduced juvenile survival and recruitment. Anderson and Piatt (1999) suggested a match/mismatch mechanism could have broad-scale effects on community structure through the varying abundance of

early- or late-season spawning fishes, depending on climate regime shifts that affect the timing of spring blooms. Furthermore, if entire year classes are affected, these bottom-up processes can have profound influences on upper trophic-level marine predators that depend on a particular size or age group (Anderson & Piatt 1999).

Discussions by Lack (1967) regarding seabird communities focused on the bottom-up effect of prey abundance as the primary factor regulating community structure. Subsequent analyses by various investigators supported Lack's proposal by identifying prey abundance and competition for food as proximate causes of the geographic structure of seabird colonies (Furness & Birkhead 1984, Lewis et al. 2001, Ainley et al. 2003, Ainley et al. 2004). Reproductive success and changes (annual and decadal) in population size have been widely linked in recent literature to bottom-up processes (Hunt et al. 1986, Barrett et al. 1987, Vader et al. 1990, Crawford & Dyer 1995, Anker-Nilssen et al. 1997, Piatt 2002). However, an important factor that could confound relationships between lower trophic-level processes and seabird population dynamics is top-down control by predators.

Predators that exploit seabird breeding colonies include both mammalian and avian species that consume eggs, chicks, and adults. Previous studies have reported significant losses of seabird eggs and young to avian predators (Uttley et al. 1989, Hatch & Hatch 1990, Reghr & Montevicchi 1997, Craik 2000, Parrish et al. 2001). Such top-down predation pressure affects the distribution of breeding seabirds (Stenhouse et al. 2000) and, in some cases, can be the primary cause of population decline at a breeding colony (Parrish et al. 2001). It is necessary, however, to consider whether predation occurs independently of other causes of reproductive failure.

Whereas the occurrence of predation at seabird colonies is unequivocal, the predation of eggs or chicks also may be opportunistic, owing to decreased nest attendance in response to increased foraging effort required by adults during periods of low prey abundance (Hatch & Hatch 1990). Therefore, the relative importance of top-down controls of seabird populations is difficult to determine without also investigating the contribution of bottom-up processes related to prey availability and its effect on parental investment.

We present results of a five-year integrated study of black-legged kittiwakes (*Rissa tridactyla*) and forage fishes in Prince William Sound (PWS), Alaska. Our primary working hypothesis was that kittiwake reproductive success was most limited by the abundance, distribution, and species composition of surface-schooling forage fishes. A second working hypothesis was that reproductive loss to predators of kittiwake eggs and chicks was greatest during years of reduced prey availability. We demonstrate that the breeding success of kittiwakes in PWS was limited by bottom-up, top-down, and match-mismatch processes, with the relative influence of these forces varying under specific conditions. Moreover, seabird vs. forage-fish-abundance functional response curves were only evident when top-down forces or colony-specific effects were minimized.

Methods

Study Areas

Prince William Sound is located in the northern Gulf of Alaska (GOA). The Sound is bordered by the Chugach Mountains and open to the GOA primarily through

Montague Strait and Hinchinbrook Entrance (Fig. 2.1). The terrestrial habitat at sea-level is described as sub-arctic rainforest. Aquatic habitats in PWS include an inland sea of sufficient size to allow horizontal cyclonic circulation (Niebauer, Royer & Weingartner 1994) surrounded by an extensive network of bays and inlets that can be characterized as coastal marine, fjordic, and estuarine. Aquatic habitats in PWS range from tidal flats near river mouths to basins exceeding 600 m in depth; much of PWS is deeper than the adjacent continental shelf region of the GOA (primarily < 100 m). Gulf of Alaska water generally enters PWS through Hinchinbrook Entrance and exits to the southwest through Montague Strait (Niebauer et al. 1994); however, significant flow reversals have also been observed (Vaughan et al. 2001). Biological production within PWS often benefits from this inward flow of GOA water, which can bring significant amounts of offshore production into the Sound (Kline 1997, 1999, Eslinger et al. 2001). The outward flow can also cause a loss of biological production by the export of phytoplankton, zooplankton, and planktonic fish larvae locally produced in PWS (Norcross & Frandsen 1996, Brown 2003).

Black-legged kittiwakes nest at approximately 27 colonies located throughout PWS (Irons 1996). We conducted studies of kittiwake foraging and reproductive success at three breeding colonies (plus a fourth colony during year one) in regions representing different marine habitats in PWS. Shoup Bay, the largest colony (ca. 7,000 breeding pairs), is located in northeastern PWS where marine habitats are dominated by fjords and protected mainland bays and inlets (Fig. 2.1). Eleanor Island, the smallest of the three colonies (ca. 220 pairs), consists of two neighboring rocks in central PWS adjacent to the protected bays of the larger central islands and the influence of the GOA

near Montague Island. North Icy Bay, intermediate in size (ca. 1,800 pairs), is in southwestern PWS with adjacent marine habitats representing a combination of those characterizing northwest and central PWS (e.g. fjords, mainland bays and inlets, and open water influences of the GOA). We collected data during five breeding seasons (1995-1999). Additionally, in 1995 we collected data from the Seal Island colony (ca. 250 pairs), which was nearest and most similar to the Eleanor Island colony.

Forage fish abundance and proximity to colonies

We determined the abundance of surface-schooling fish species (Pacific herring *Clupea pallasii*, Pacific sand lance *Ammodytes hexapterus*, and capelin *Mallotus villosus*) during the chick-rearing period using aerial surveys conducted from fixed-wing aircraft, providing prey abundance estimates from the perspective of an aerial, near-surface feeding predator like the kittiwake (Suryan, Irons, Kaufman, Benson, Jodice, et al. 2002). Aerial surveys included all shoreline waters within 1 km of the mean lower low water tide level (very little foraging by kittiwakes or other seabirds occurred offshore; Irons 1998, Maniscalco et al. 1998) within the maximum foraging range of adult kittiwakes from our three study colonies (Irons 1992, 1998, Suryan et al. 2000a, Irons & Suryan unpubl. data; Fig. 2.1). We conducted aerial surveys during the chick-rearing period (July and August) with annual effort ranging from 13 to 28 d and 396 to 4,047 km² (Table 2.1). Transects were surveyed from a float-plane (Cessna 185) at approximately 204 km hr⁻¹. A single transect line parallel to the shore was surveyed continuously and was broken only in areas of high fish density, where the plane circled to ensure complete counts of schools. The survey altitude ranged between 274 - 366 m

based on the ability to discriminate fish school sizes. For example, an altitude of 305 m provided a swath width of 325 m, using a fixed angle of 30°, and allowed surface area estimation of the smallest schools observed ($< 10 \text{ m}^2$ surface area). We conducted all observations from the right side of the plane using a modified line transect survey method. Fish schools were counted and their surface area was estimated using a calibrated cylinder. We calculated the horizontal surface area of each school, and present the results as fish school surface area (m^2) per 1 km of transect (surface area density m^2/km). Observers used school characteristics (e.g., shape, size, location) to identify fish species. The accuracy of species identification was 96.1% for herring and 80.4% for sand lance, based on discriminate function analyses using boat-based sampling of fish schools concurrent with aerial surveys. The abundance of capelin was likely underestimated because in some areas these schools remained at depth and out of view of observers. For a more detailed description of aerial survey methodology see Brown and Moreland (2000) and Ainley et al. (2003).

In addition to the abundance of juvenile herring, we were interested in the age classes that were available to kittiwakes. Otoliths recovered from kittiwake regurgitations were used to determine juvenile herring age structure. We calculated an index of 1-yr-old herring abundance as the total juvenile herring abundance determined from aerial surveys and associated net sampling (see Brown & Moreland 2000, Stokesbury et al. 2000) multiplied by the proportion of 1-yr-old herring in kittiwake diets (age-class determination is described in *Kittiwake diets* below). This index is a reasonable age-class correction because the age-class of herring consumed by kittiwakes was nearly identical to the relative proportions determined with net and

hydroacoustic sampling during 4 yr when comparable data were available (Thedinga et al. 2000, Suryan et al. 2000b). Additionally, because forage fish surveys were only conducted during the chick-rearing period and young-of-year herring did not recruit to foraging regions until after incubation (late July through early August; Stokesbury et al. 2000), the index of 1-yr-old herring abundance and total sand lance abundance were our best estimates of prey availability during the pre-egg laying and incubation periods. However, it is possible that kittiwake diets during the early breeding season may be dominated by other species such as salmon smolts (*Oncorhynchus* spp.) or zooplankton (e.g., *Thysanoessa spinifera*), possibly making our index of early season prey availability incomplete by underestimating total prey abundance prior to chick-rearing.

We determined the proximity of forage fish schools to breeding kittiwakes by selecting all fish schools within a given colony's foraging range, then calculating distance (km) to the colony. Distances were summarized by colony foraging area, year, and species (herring, sand lance, and capelin) and presented as the mean distance to fish schools and the proportion of total surface area (m²) occurring within 10-km radial increments from each colony (10 – 100 km).

Kittiwake egg and nestling predators

The presence and activities of predators at the colonies and number of egg or chick removals were observed opportunistically during routine data collection activities and occasional predator observation periods. However, a significant predation event could have been missed, especially at small colonies (e.g. Eleanor and Seal islands) where visits by predators were sporadic. Therefore, we used the proportion of failed

productivity plots (described in detail below) to provide indirect evidence (an index) of significant egg and chick removals during unobserved depredation events. A plot was considered failed if productivity (fledglings per nest) was $\leq 10\%$ of the maximum observed from all plots within the colony. This index is based on observations that predators often targeted specific sections of a colony and the assumption that bottom-up effects constraining reproduction were more evenly distributed throughout the colony. We acknowledge that these generalizations do not hold true in all cases, but our conservative definition of a failed plot is nevertheless indicative of intense predation pressure. Our working hypothesis is that small colonies will have a greater proportion of failed plots than a large colony where predator swamping occurs (Gochfeld 1982, Wilkinson & English-Loeb 1982). We did not attempt to quantify the total amount of reproductive loss due solely to predation at each colony.

Kittiwake breeding population size and reproductive measures

We counted the number of breeding pairs at each colony during annual censuses of all colonies in PWS using methods detailed in Irons (1996). We determined reproductive success of breeding pairs by monitoring plots established throughout each colony. At the Shoup Bay and North Icy Bay colonies, the 11 to 18 plots contained approximately 150 to 400 nests. Plots at Eleanor Island ($n = 5$ plots) and Seal Island ($n = 7$) encompassed the entire colonies and represented a census of those breeding populations. We recorded the contents of nests within each plot every three days beginning before or immediately after egg laying and terminating when nestlings were approximately 34 d old and near fledging. The reproductive measures obtained from

these data included laying success, clutch size, median hatch date, hatching success, fledging success (terms defined in Table 2.2), and overall breeding success (fledglings per pair).

To measure nestling growth and survival we selected 40 to 100 accessible nests containing eggs during late incubation. Nests were located throughout the colony and included relative proportions of one and two egg clutches equal to the colony average at the time of selection. We checked individual nests daily to determine hatch dates (except Seal Island 1995 and North Icy Bay 1996) and marked alpha and beta chicks, determined by age, with colored ink to identify individuals. Once chicks were old enough, we marked them with numbered U.S. Fish and Wildlife Service leg bands. We began weighing nestlings within 3 d of hatching; thereafter, they were weighed at 4-7-d intervals. Mass was determined to the nearest 1 g using either 100 g, 300 g, or 500 g Pesola spring scales. Measurements were terminated when nestlings reached 30 ± 2 d, to reduce the risk of causing premature fledging by approaching and handling older nestlings. We obtained these detailed growth data for nearly all colonies in all years. However, in several instances nestlings did not survive long enough (Eleanor Island 1998) or were measured too infrequently and their ages were unknown (Seal Island 1995, North Icy Bay 1996) to construct complete growth curves (i.e., logistic equations). Therefore, to allow comparisons across the maximum number of colony-years, we restricted growth analysis to the linear phase of 60 - 300 g, which approximates the maximum instantaneous growth rate of a logistic growth curve (Coulson & Porter 1985). We used linear regression to determine the slope of a line, representing growth rate, for mass versus daily increments (i.e., growth rate in g/d) of

751 nestlings between the ages of 3 and 20 d. We then calculated a mean annual growth rate among nestlings for each colony, except for Eleanor Island and North Icy Bay in 1999 because nestlings did not survive long enough to be measured within the 60 – 300 g range. We included alpha, beta, and single nestlings in the annual means so that nestling growth for a given colony was represented by a single variable in multiple regression analyses.

Beta nestlings are often the first to suffer the consequences of poor foraging conditions (Braun & Hunt 1983, Irons 1992, Gill et al. 2002). Therefore, we calculated annual beta chick survival for each colony. Beta nestlings used in survival analysis were from the same broods as those used for growth rate measures. Nests were checked every 4-d and the presence or absence of individually marked beta nestlings was noted. Survival was calculated as the proportion of beta nestlings surviving to 30 ± 2 d of age.

Kittiwake diets

To assess kittiwake diets during the chick-rearing period (early July to mid-August), we collected 1,377 regurgitations from nestlings, which provided samples using non-lethal techniques from throughout the chick-rearing period, starting soon after the chicks hatched and continuing at weekly intervals, to capture potential within-season changes in diet (Suryan et al. 2002). Because the nest was our sampling unit, we combined regurgitations from alpha and beta chicks in subsequent analyses. Multiple samples were rarely collected from the same brood in one year and, if so, the collection dates were separated by at least one week and considered independent for this analysis.

Diet samples were collected from nestlings throughout the colonies and stored frozen until analyzed.

Taxonomic composition of prey consumed was determined by identifying whole fish, otoliths, scales, and bones obtained from regurgitations. We used % mass, as determined by individually weighing identifiable portions of recently ingested prey, to represent the relative contribution of each prey type to nestling growth. In addition to species of prey, prey age class has been shown to affect its nutritional quality and the foraging patterns, reproductive success, and energy expenditure of seabirds (Robards et al. 1999, Anthony et al. 2000, Roby et al. 2000, Suryan et al. 2000a, Jodice et al. 2005, Wanless et al. 2005). Therefore, we used otolith lengths to determine age classes of the primary prey species. Otoliths were measured to the nearest 0.01 mm using an ocular micrometer. Age classes of herring were inferred from modes of length-frequency distributions for otoliths (1-2 mm for young-of-year [YOY] and 2-3 mm for 1-year-old; Suryan et al. 2000a). Age classes of sand lance also were determined using modes of frequency distributions for otolith lengths (≤ 1.9 mm for YOY and > 1.9 mm for 1+ year-old), which were consistent with classifying YOY sand lance as typically less than 100 mm standard length (Robards et al. 1999).

Foraging trip duration

We determined foraging trip duration for adult kittiwakes using VHF radio transmitters and remote data loggers. We captured and radio-tagged a total of 300 adult kittiwakes, of which 161 were monitored during incubation and 220 were monitored during chick-rearing (81 were monitored during both periods). Birds were removed

from the sample when their eggs or nestlings were lost or nestlings reached 30 ± 1 d, the age at which growth measures were terminated and beyond which adult nest attendance changed considerably (Suryan & Irons unpubl. data). We captured adult black-legged kittiwakes using a noose-pole (Hogan 1985) or leg-noose (Benson & Suryan 1999). Radio transmitters (164 - 167 MHz, 9 g Advanced Telemetry Systems, Inc [ATS], Isanti, Minnesota, USA) were attached to 11 - 40 birds per colony per year. Transmitters were secured ventrally to the base of the tail feathers using methods described by Anderson & Ricklefs (1987) and Irons (1998).

We monitored the 24-hr presence or absence of radio-tagged kittiwakes at colonies with remote data logging systems (a VHF receiver, R4000, ATS) linked to a data collection computer, DCC II, ATS). In all cases, the receiving antenna was ≤ 0.5 km from the colony and signal reception range was less than 2.0 km. Activities of adult kittiwakes within this range of the colony were predominantly nest attendance, occasionally roosting away from the nest, and only rarely foraging (based on pers. obs. and radio-tracking studies; Irons 1992, Suryan et al. 2000a). We used the same procedures for system programming and error checking at all colonies and during all years (for details see Suryan et al. 2002).

Based on previous radio-tracking studies of kittiwakes in Prince William Sound, we know that adult kittiwakes rarely leave the colony for greater than 45 min without feeding (Irons 1992, Suryan et al. 2000a) and typically do not feed or travel during hours of darkness (R. Suryan & M. Kaufman pers. obs). During the chick-rearing period, foraging trips were defined as absences over 45 minutes and occurring between 0400 and 2400 hrs. During the incubation period, however, foraging trips are typically

longer and are more frequently overnight compared to the chick-rearing period, particularly during years of low food availability (Hamer, Monaghan, Uttley, Walton & Burns 1993). Therefore, we did not remove overnight trips of incubating birds (overnight trips represented 47% of incubation trips, but only 26% of chick-rearing trips). A total of 1,975 incubation trips and 12,143 chick-rearing trips were recorded. Average trip duration was determined separately for incubation and chick-rearing periods. We calculated an annual mean for each bird, then a grand mean of all birds for each colony-year.

Statistical analyses

We used multiple linear regression models to address the question, “For a given reproductive measure (response variable), which environmental measures (explanatory variables) best account for the observed variation in reproductive output?” Each response value represents one colony-year and n was ≤ 15 for all models. Therefore, not all possible explanatory variables and interactions could be included in initial models while still maintaining the number of variables less than $n - 1$ (Kleinbaum, Kupper & Muller 1988). Instead, we tested groups of explanatory variables individually (e.g., prey abundance variables and interactions) against the response to identify the variable(s) that would be retained in further model development. Moreover, collinear explanatory variables (e.g., abundance of herring or sand lance or capelin and total prey, which is the sum total of these three species) were not included together in any given model run to avoid violating the model assumption of independence. We used Akaike’s Information Criterion corrected for small sample sizes (AICc) to select

the most parsimonious final models (Burnham & Anderson 1998). We selected the models having the lowest AICc as the best model, and models < 2 AICc from the best model as competitive. If a significantly competing model was within 2 AICc of the best model and included an additional explanatory variable, we present results of both models. In addition to R^2 and Δ AICc values, we also present F -statistics and P -values for model evaluation. Results were considered highly significant if $P < 0.05$ and marginally significant if $0.05 < P < 0.10$. A total of 11 response and 17 explanatory variables and 19 possible interactions were used in our analyses (Table 2.2). We included fixed effects of year and colony size. Colony size was synonymous with a colony effect because relative colony sizes were sufficiently different. Prey abundance data were log transformed to account for their potential non-linear relationship to seabird reproductive parameters. To further control for possible colony-specific effects, we also created models using standardized data (anomalies) over the five-year period. Model residuals were evaluated using normal-probability plots.

Analysis of variance was used to compare foraging trip durations among colonies separately for incubation and chick-rearing periods. All analyses were conducted using SAS software (SAS Institute 1990).

Results

Forage fish abundance and proximity to kittiwake colonies

The abundance of all species of surface schooling forage fishes was highly variable among years and locations, with no one region consistently having the greatest abundance of prey (Fig. 2.2). Similarly, the geographic distribution of prey and its

proximity to kittiwake colonies varied regionally (Fig. 2.3) and annually (Fig. 2.4). Overall, forage fish biomass (surface area density) within a given colony's foraging range was most distant from the Shoup Bay colony and, for Shoup Bay only, herring schools occurred in closer proximity than sand lance in nearly all years (Fig. 2.3; Appendix 1.1). Thus, kittiwakes nesting in PWS encountered considerable variation in foraging conditions

Kittiwake egg and nestling predators

Depredation of eggs and chicks was observed at all three colonies. Egg predation involved primarily bald eagles (*Haliaeetus leucocephalus*) and common ravens (*Corvus corax*). Kittiwake nestlings were taken by peregrine falcons (*Falco peregrinus*), bald eagles, common ravens, and glaucous-winged gulls (*Larus glaucescens*). In addition, opportunistic species such as northwestern crows (*Corvus caurinus*), black-billed magpies (*Pica pica*), and glaucous-winged gulls took advantage of nests left unattended during disturbances by more aggressive predators.

Predation intensity was greatest at Shoup Bay, followed by North Icy Bay, and lowest at Eleanor Island. Predation events often occurred ≥ 6 times per day at the Shoup Bay colony, ≥ 3 times per day at North Icy Bay, and often < 1 per day at Eleanor Island. During 2-hr observation periods, up to 36 eggs were removed by predators at the Shoup Bay colony, 14 eggs at North Icy Bay and 0 at Eleanor Island. However, because North Icy Bay and Eleanor Island were four and 25 times smaller on average, respectively, than Shoup Bay, a few visits by a predator resulted in greater overall loss to these smaller colonies. Indeed, the proportion of productivity plots where adult

kittiwakes failed to produce chicks (an indication of selective predation) was greater at North Icy Bay (mean proportion = 0.39 ± 0.20 SE) than at Shoup Bay (0.22 ± 0.13) during all years with available data and at Eleanor Island (0.40 ± 0.21) during three of five years compared to Shoup Bay (Fig 2.5). These differences were statistically significant during 1998 ($\chi^2_2 = 13.68$, $P = 0.001$) and 1999 ($\chi^2_2 = 5.81$, $P = 0.055$). The dramatic increase in plot failure at Eleanor Island coincided with the establishment of a peregrine falcon aerie nearby in 1998 and 1999. Peregrine falcons had active aeries near Shoup and North Icy Bays in all years. We observed peregrine falcons taking two to six chicks per day at each colony. At an observed predation rate of three chicks per day, over 50% of the chicks produced at Eleanor Island would be removed during a 35-d nestling period (excluding additional loss from opportunistic predators), whereas only roughly 10% of the chicks at North Icy Bay would be removed and only 3% at Shoup Bay. Predation on the already reduced number of breeding pairs and eggs at all colonies in 1999 reduced hatching success at Shoup Bay and Eleanor Island and removed all eggs at North Icy Bay (Fig. 2.6), greatly increasing the proportion of failed plots at all colonies (Fig. 2.5).

Kittiwake reproduction, diet, and relationship to forage fish abundance

Early season breeding conditions for kittiwakes in PWS showed disparate trends among metrics, years, and colonies. In some years breeding chronology was synchronized among colonies with a median hatch occurring within 2-3 d (e.g., 1996 and 1997); however, in other years median hatch dates varied among colonies by 7-8 d (e.g., 1998, 1999; Fig 2.6a). We were unsuccessful in explaining a significant amount

of variation in annual hatch dates with our suite of explanatory variables ($R^2 < 0.01$, $F = 0.89$, $P = 0.365$; Table 2.3), although colony size was marginally significant when using standardized data ($R^2 = 0.17$, $F = 3.63$, $P = 0.081$; Table 2.4). Clutch size and laying success varied little among years and colonies with the exception of 1999 (Fig 2.6b,c). Variation in clutch size, laying success and hatching success (Fig 2.6d) were best explained by year, with a competing model for hatching success also including colony size ($R^2 \geq 0.298$, $F \geq 6.94$, $P \leq 0.021$; Table 2.3). Results of models using standardized data confirmed that variation in overall mean clutch size, laying success and hatching success was best explained by annual changes in colony size and year ($R^2 \geq 0.460$, $F \geq 5.31$, $P \leq 0.034$; Table 2.4).

Kittiwakes fed their chicks three primary prey species: juvenile herring, sand lance, and capelin, which together composed 80% of the annual diet on average. The prevalence of herring was most consistent at the Shoup Bay colony ($CV = 0.25$) and least consistent at the Eleanor Island colony ($CV = 0.94$). Capelin was more common in the diets of kittiwakes from Eleanor Island ($CV = 0.32$) and North Icy Bay ($CV = 0.15$) than those of Shoup Bay ($CV = 0.77$; Fig 2.7a).

Whereas the proportion of herring in kittiwake diets varied both regionally and annually, variation in herring age classes was greatest among years ($CV = 0.78 - 0.84$) and remarkably consistent among colonies in a given year ($CV = 0.05 - 0.44$; Fig 2.7b). The age class of sand lance in diets, on the other hand, showed little annual or regional variation ($CV = 0.01 - 0.19$); kittiwakes consumed primarily YOY sand lance (96% of all sand lance otoliths, $n = 896$, range = 67 – 100% per year; Appendix 1.1).

Beta chick survival and nestling growth showed considerable temporal and regional variation (Fig. 2.8a,b). Although variation in beta chick survival could not effectively be explained by any combination of the bottom-up environmental variables we considered ($R^2 < 0.038$, $F \leq 1.38$, $P \geq 0.265$; Tables 2.3, 2.4), an increase in nestling growth was associated with two primary variables: a decrease in foraging trip duration (Fig. 2.9) and an increase in total prey abundance, with a competing model for nestling growth also including year ($R^2 \geq 0.683$, $F \geq 13.91$, $P \leq 0.001$; Table 2.3). Analysis of standardized data provided similar results, although year was not included in a competing model (Table 2.4). The most significant positive effect on nestling growth was the reduction in foraging trip duration ($t_{12} = -4.81$, $P = 0.001$). In fact, in a simple linear regression analysis, foraging trip duration alone explained 57% of the variation in nestling growth ($F_{12} = 14.04$, $P = 0.003$, $n = 13$). Variation in fledging success (Appendix 1.1) was best explained by the proportion of 1-yr-old herring in diet (Table 2.3) and analysis of standardized data included year alone in the final model (Table 2.4). Variation in near-fledging mass (Fig 2.8c) could not be adequately explained by any combination of variables we measured ($R^2 < 0.157$, $F \leq 2.68$, $P \geq 0.140$; Tables 2.3, 2.4).

In the above nestling growth model, the weaker effect of prey abundance relative to foraging trip duration likely resulted from colony, prey species, or age-class specific responses to prey abundance. Indeed, when including only the abundance of 1-yr-old herring, an asymptotic relationship was evident, although of limited predictive value ($r^2 = 0.24$), between prey abundance and nestling growth, with the asymptote at a prey surface area density of approximately 5-7 m^2/km^2 (Fig. 2.10).

Although the effect of foraging trip duration on chick growth was clear, environmental variables affecting foraging trip duration were more complex; factors such as colony size, location, prey species or age-class, confounded the relationships. For example, trip durations were longest for kittiwakes at Shoup Bay (ANOVA $F = 5.39$, $P = 0.029$; Fig. 2.9). Therefore, colony size alone explained most of the variation in foraging trip duration during chick-rearing and incubation (1-yr-old herring abundance did occur in a competing model for incubation; Table 2.3). However, when using standardized data to control for colony-specific effects, the abundance of 1-yr-old herring and distance to herring schools had the strongest affect (inversely) on foraging trip duration during chick-rearing (explaining 92% of the variation when also including a year affect; Table 2.4).

Likewise, there was no clear relationship between prey abundance and overall breeding success (fledglings per pair; Fig. 2.11a). The lack of a relationship was, again, a result of colony-specific interactions, with prey abundance and other variables affecting breeding success (e.g., avian predators, poor early season conditions). For example, at Eleanor Island in 1998, low breeding success despite high prey abundance was primarily a result of predation on eggs by glaucous-winged gulls and on chicks by peregrine falcons. Overall breeding success was also poor at all colonies in 1999, despite moderate to high prey abundance. In 1999, most of the potential chick production was lost because of reduced laying success and clutch size at all colonies and the subsequent losses to predation, particularly at the smaller colonies, North Icy Bay and Eleanor Island. Therefore, a model including year and colony size best explained annual variation in breeding success ($R^2 \geq 0.459$, $F \geq 8.15$, $P \leq 0.006$; Tables

2.3, 2.4). Indeed, by including only the large Shoup Bay colony (reducing the relative effect of predation through predator swamping) and abundance of 1-yr-old herring (the prey item most important to successful reproduction at Shoup Bay; Suryan et al. 2000a), an asymptotic relationship was evident between breeding success and prey abundance, with the asymptote at a fish density of approximately 3-4 m²/km² (Fig. 2.11b).

Discussion

Bottom-up effects

The only reproductive parameter that showed a strong direct linkage to prey abundance was nestling growth, the parameter most independent of top-down effects of predation (nestlings must survive to be repeatedly measured). However, prey abundance appeared secondary compared to the strong effect of adult foraging trip duration. Shorter foraging trip durations resulting in greater nestling feeding frequency have been shown to be an important variable affecting kittiwake nestling growth in PWS (Roby et al. 2000, Suryan et al. 2002). Foraging trip duration was linked to prey abundance; however, this association was specific to each colony, prey species, and prey age-class, thereby confounding a simple relationship between foraging trip duration and prey abundance. This result also suggests that kittiwake foraging trip duration is a sensitive indicator of prey availability as it affects reproduction, possibly even more so than our measure of prey abundance.

For example, foraging trip duration was consistently greatest for birds nesting at Shoup Bay compared to Eleanor Island and North Icy Bay, likely because of colony size (possibly intra-specific competition at larger colonies requires birds to travel farther

to forage; Hunt et al. 1986, Kitaysky et al. 2000) and geographic location (Ainley et al. 2003). Under most conditions, kittiwakes from Shoup Bay traveled over 40 km to forage, in contrast to less than 20 km (occasionally less than 6 km) for birds at Eleanor Island (Suryan et al. 2000a); travel distances for birds at North Icy Bay were intermediate (24 – 33 km; Ainley et al. 2003). These travel distances are consistent with the proximity of fish schools to respective colonies quantified herein (Figs. 2.3, 2.4). Therefore, kittiwakes at Shoup Bay had less foraging plasticity to adjust to changes in prey distribution and abundance without affecting breeding success. Indeed, in 1997 and 1999 nestling growth and productivity at Shoup Bay were poor despite high prey abundance. However, the age class of prey in these two years was primarily YOY, which often have lower energy density than 1-yr-old fishes (Anthony et al. 2000) and are associated with longer foraging trips and reduced productivity at the Shoup Bay colony (Suryan et al. 2000a). The closer proximity of foraging grounds and reduced potential for intra-specific competition for birds from Eleanor Island and North Icy Bay allowed these birds to maintain relatively short foraging trips despite feeding on YOY prey. In fact, nestling growth remained high at Eleanor Island and North Icy Bay colonies despite dramatic fluctuations in prey abundance. This was not true for nestlings at Shoup Bay, where growth was reduced during three of the five years.

Conditions affecting adult foraging trip duration were similar during the incubation and chick-rearing periods. For a given colony, the annual trends in the duration of incubation vs. chick-rearing trips were remarkably similar throughout the course of the study, particularly at Shoup Bay and Eleanor Island (Fig. 2.9). Annual variation in prey availability appeared sufficient to affect kittiwake foraging activities even during the

much less demanding period of incubation when the energetic requirements for reproduction are limited to self maintenance while incubating an egg, in contrast to the more energetically demanding period of feeding nestlings. Additionally, this result provides evidence that incubating adults may have a reasonably accurate indication of the relative quality of conditions and the foraging effort that may be required during the subsequent chick-rearing period. Such prior knowledge of foraging conditions could play a role in determining whether an adult kittiwake commits full or partial effort to chick-rearing given the expected energetic costs (Golet et al. 2000, Kitaysky et al., 2000, Jodice et al. 2002) and potential survival costs (Golet et al. 1998, Golet et al. 2004) of raising young during periods of low food availability.

Linkages to lower trophic-level processes

Kittiwake diets at individual colonies reflected differences in habitat-specific distribution of forage fish species, with the North Icy Bay colony in southwest PWS surrounded by prey assemblages combining those characteristic of the other two colonies (Figs. 2.1, 2.3). Consequently, diets of kittiwakes from North Icy Bay, like Shoup Bay, were most often dominated by herring (occurring in nearshore, shallow water bays and inland passes; Stokesbury et al. 2000) and, similar to diets from Eleanor Island, capelin (a GOA associated species; Brown & Moreland 2000) were common in the diet. Differences in marine habitats adjacent to breeding colonies and seabird prey consumption also have been described for species breeding in the Aleutian Islands and Bering Sea, but at much larger scales (100's of km; Springer 1991, Springer, Piatt & Van Vliet 1996).

The overwinter survival of YOY herring is dependent upon sufficient somatic energy reserves from the previous summer and fall (Paul & Paul 1998). Greatest spring phytoplankton abundance during our study occurred in 1994 (particularly in central PWS) and 1995 (in north, central, and south PWS; Prince William Sound Aquaculture Corporation unpubl. data), and may have produced greater zooplankton abundance and benefited YOY herring. Indeed, kittiwakes in the following years of 1995 and, especially, 1996 collectively consumed primarily 1-yr-old herring and produced more chicks than any of the following three years (also consistent with some of the highest annual energy provisioning rates to nestlings recorded in PWS; Roby et al. 2000). Breeding chronology also was the most synchronous among colonies in 1996 compared to the other four years. Moreover, kittiwake production throughout PWS in 1996 was the greatest during the course of our five-year study (Irons unpubl. data), and it was the only year of the decade when kittiwake productivity was comparable to the high levels of the 1980s (primarily in northern PWS; Suryan & Irons 2001). Herring were considerably more abundant in that decade (Brown 2003). The above observations are consistent with Esslinger et al.'s (2001) findings in PWS that, for the years 1993 to 1997, spring bloom conditions producing the great zooplankton abundance occurred only during 1994 and 1995. Processes that produced the overall greater zooplankton stocks during the 1980s were markedly different from those contributing to lower stocks during the 1990s. Phytoplankton abundance in 1998 was the lowest recorded during our study period, indicating that over-winter condition and, hence, survival of YOY forage fishes could have been negatively impacted. In the following year, 1999, primarily YOY fish were available to kittiwakes, as evidenced by both their diets and

fish surveys (Thedinga et al. 2000) during the chick-rearing period of 1999. Therefore, the poor early season breeding conditions in 1999 may have been a result of reduced over-winter survival of forage fishes, a potential effect of low or mismatch timing of primary production the previous year (Norcross et al. 2001). In all other years of our study, laying success and clutch size were at maximum levels recorded for the Pacific population of kittiwakes (Hatch, Byrd, Irons & Hunt 1993) and comparable to those of kittiwakes provided with supplemental food *ad libitum* (Gill & Hatch 2002), indicating early-season prey abundance was above threshold levels in all years except 1999.

Match/mismatch mechanisms of bottom-up processes

The importance of 1-yr-old herring to kittiwake reproduction in PWS results not only from shorter kittiwake foraging trips (Suryan et al. 2000a) and high energetic value (Van Pelt et al. 1997, Anthony et al. 2000), but also from their early season availability to kittiwakes. Prior to and during the first two to three weeks of chick-rearing in early- to mid-July (a critical time for nestling survival; Regehr & Montevecchi 1997, Gill et al. 2002, Suryan et al. 2002), 1-yr-old herring occur in schools in nursery bays, but YOY herring are still in early stages of metamorphosis to the juvenile form (Cooney et al. 2001, Norcross et al. 2001) and are not available to surface feeding birds.

Consequences of delayed and reduced YOY herring abundance are greatest when the abundance of 1-yr-old herring is low (e.g., Shoup Bay 1997-1999; Appendix 1.1). For example, at Shoup Bay, the low abundance of 1-yr-old herring during the first two weeks of chick-rearing in 1997 and 1998 (Fig. 2.12a,b) caused increased foraging trip duration (decreasing nestling provisioning; Fig. 2.12e,f) and significantly greater beta

chick mortality (likely due to siblicide; Braun and Hunt 1983, Irons 1992) than in 1996 and 1999 (Fig. 2.12h-k; Suryan et al. 2002). However, a strong recruitment of YOY herring can benefit kittiwake nestlings during the later weeks of brood-rearing. At Shoup Bay in 1997, a large recruitment of YOY herring during the last two weeks of brood-rearing reduced adult kittiwake foraging-trip duration (Fig. 2.12e), and improved chick growth (chicks that survived the initial weeks of low prey abundance attained above average asymptotic body mass; Suryan et al. 2002). The importance of timing in prey availability and its effect on the success of breeding seabirds was also demonstrated by kittiwakes and their primary prey, capelin, at a colony in the Atlantic Ocean (Regehr & Montevecchi 1997). Thus, the match/mismatch hypothesis that Cushing (1975) originally proposed for situations when the critical period for larval fish survival and recruitment was narrower than the range in timing of the spring bloom, seems equally plausible for breeding seabirds, particularly in northern latitudes where the variation in breeding chronology is most limited.

Top-down effects

The dramatic potential for top-down control of reproduction was apparent when comparing the Eleanor Island and Seal Island colonies. In 1995, foraging locations for kittiwakes from Seal Island and Eleanor Island overlapped extensively, and their reliance on similar food sources also was indicated by their strikingly similar reproductive performance. In the years following 1995, birds from Eleanor Island extended their foraging range south beyond Seal Island, indicating the best feeding opportunities in those years were even closer for kittiwakes nesting at Seal Island

(Suryan et al. 2000a, Suryan & Irons unpubl. data). Despite prey being closer to Seal Island, reproductive output was considerably lower than for kittiwakes from Eleanor Island. Kittiwakes from Seal Island raised an annual maximum of 0.01 fledglings per nest during 1996 and 1997 (Irons unpubl. data) and evidence of extensive predation was observed there. In contrast, the Eleanor Island colony was successful, producing 0.53 and 0.40 fledglings per nest during 1996 and 1997, respectively. However, in 1998 and 1999 production at both Eleanor and Seal Islands was near zero because of predation, despite the relatively high abundance of prey. Similarly, although reduced numbers of breeders and smaller clutch sizes at all colonies in 1999 were likely not caused by top-down effects, the added predation on already reduced breeding attempts severely reduced or eliminated chick production at Shoup Bay and North Icy Bay. These top-down effects were evident despite moderate to high prey abundance during the chick-rearing period. However, the greater colony size of Shoup Bay partially masked the relative importance of the top-down effects of predation.

Intra-specific competition also can affect seabird breeding success. As originally proposed by Ashmole (1963) and later supported by Birt, Birt, Goulet, Cairns and Montvecchi (1987), seabirds may reduce prey availability adjacent to their colonies. Intra-specific competition is most evident at larger seabird colonies, causing individuals to travel to prey patches farther from the colony to reduce competition (Furness & Birkhead 1984, Hunt et al. 1986). Recent studies have provided further evidence for such mechanisms in northern gannets (*Sula bassanus*) breeding throughout the British Isles and Ireland (Lewis et al. 2001), black-legged kittiwakes in PWS (Ainley et al. 2003), and Adélie penguins in the Ross Sea (Ainley et al. 2004). Even though prey

abundance may be equal or somewhat greater at Shoup Bay compared to North Icy Bay or Eleanor Island, greater intra-specific competition at the larger colony may result in longer foraging trips and, consequently, reduced breeding success. Furthermore, the consequences of reduced prey abundance may be magnified by increased intra-specific competition at the larger colony. Indeed, our largest colony was where we saw the greatest reduction in nestling growth and the least foraging plasticity (as described above; see also Hunt et al. 1986, Kitaysky et al. 2000).

Predator-prey relationships

Our results support Cairns's (1987) hypothesis that the association between seabird reproductive measures and prey abundance take the form of non-linear asymptotic relationships. Such non-linear relationships have been supported by empirical data (Burger & Piatt 1990, Anker-Nilssen et al. 1997, Piatt 2002). Direct relationships between kittiwake reproductive measures and prey abundance in this study were most apparent when minimizing the effect of top-down forces of predation and colony-specific effects of species and age-class of prey. When considering the abundance of only 1-yr-old herring (the most beneficial prey item for kittiwakes throughout PWS) and nestling growth (a reproductive measure little affected by predation), a non-linear, asymptotic relationship existed and included data from all three colonies. Likewise, for breeding success, a nonlinear relationship with prey abundance was evident when including only the Shoup Bay colony (the largest colony) and the abundance of 1-yr-old herring (the prey type most important to successful reproduction at Shoup Bay; Suryan et al. 2000a). Furthermore both of these asymptotic relationships reached a threshold at

forage fish densities of approximately $5 \text{ m}^2/\text{km}^2$, beyond which top-down, physiological, or phylogenetic constraints likely limit reproductive output. Our data provide further support and quantitative values for these nonlinear associations of breeding seabirds and their prey. Such relationships can be difficult to identify without knowledge of how seabird reproduction is affected by bottom-up and top-down forces and the potential of colony- or prey-specific effects.

Conclusion

Matson & Hunter (1992) noted that the discussion of bottom-up versus top-down control of natural systems is “no longer about which occurs, but rather what controls the strength and relative importance of the various forces under varying conditions, and what drives the feedbacks and interactions among multiple trophic levels.” Similarly, in synthesizing their study of bottom-up and top-down controls of juvenile pink salmon (*Oncorhynchus gorbuscha*) and Pacific herring in PWS, Cooney et al. (2001) noted the importance of “seeking mechanistic rather than correlative understandings of complex natural systems.” Such mechanisms have been proposed for the Bering Sea ecosystem. Oscillations occur there between bottom-up and top-down control depending upon physical processes leading to the timing and strength of the spring phytoplankton bloom, the efficiency of zooplankton grazing, and the current adult biomass of a dominant predatory fish (Hunt & Stabeno, 2002, Hunt et al. 2002). Thus, our integrated study of the temporal and spatial variation in marine production and its effect on the reproduction of an apex predator allowed a more complete understanding of the mechanisms underlying seabird-forage fish relationships. We demonstrated that

kittiwakes in PWS are confronted with highly variable breeding conditions resulting from both bottom-up and top-down influences, as well as match/mismatch effects from the timing of breeding and prey availability. The integrated approach of our investigations allowed us to identify mechanistic relationships between seabird predators and their prey in this complex marine system.

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Table 2.1. Aerial survey effort (km²) to determine the abundance of near-surface schooling forage fishes within the foraging ranges of black-legged kittiwakes nesting at three study colonies in Prince William Sound, Alaska, during five chick-rearing seasons (July and August), 1995-1999.

Year (# of survey days)	Survey Effort (km ²)			
	Shoup Bay	Eleanor Island	North Icy Bay	Total
1995 (17)	1127	416	-	1543
1996 (20)	544	404	659	1607
1997 (13)	645	396	481	1522
1998 (29)	4047	3607	479	8133
1999 (28)	3408	1965	557	5930

Table 2.2. Explanatory variables used in multiple regression models to identify factors affecting reproductive metrics (response variables) of black-legged kittiwakes during the egg laying, incubation, and nestling periods. Response variables considered included laying success (% of nests with > 1 egg) and mean clutch size for the egg laying period, median hatch date and hatching success (% of eggs hatched that were laid) for the incubation period, and nestling growth, beta chick survival, near-fledging mass, and fledging success (% of chicks fledged that were hatched) for the nestling period. We also considered response variables of foraging trip duration and breeding success (fledglings per nest). Also noted are hypothesized links between explanatory and response variables and the relative strength of evidence to support such mechanistic links (high [included in > two models], medium [included in one model], low [not retained in final models] ranking in model selection process; see Tables 2.3 & 2.4).

Explanatory variables	n^3	Laying & Incubation	Nestling	Hypothesized Mechanistic Link	Evidence
Colony size	16	X	X	Predator swamping , Social facilitation, Colony-specific effects	high
Year	16	X	X	Inter-annual variation in environmental conditions	high
Total prey abundance	15		X	Foraging effort, Meal delivery rate to nestlings, Match-mismatch	med
Herring abundance	15		X	Foraging effort, Meal delivery rate to nestlings	low
Sand lance abundance	15	X	X	Foraging effort, Meal delivery rate to nestlings, Match-mismatch	med
Capelin abundance	15		X	Foraging effort, Meal delivery rate to nestlings	low
1-yr-old herring abundance index ¹	12	X	X	Foraging effort, Meal delivery rate to nestlings, Match-mismatch	med
1-yr-old herring and sand lance abundance index ²	12	X	X	Foraging effort, Meal delivery rate to nestlings, Match-mismatch	low
Distance to herring school	15		X	Meal delivery rate to nestlings	med
Distance to sand lance school	12		X	Meal delivery rate to nestlings	low ⁴
% mass of herring in kittiwake diets	13		X	Dietary effects on reproduction	low
% mass of sand lance in kittiwake diets	13		X	Dietary effects on reproduction	low
% mass of capelin in kittiwake diets	13		X	Dietary effects on reproduction	low

Table 2.2. Continued

% mass of 1-yr-old herring in kittiwake diets	12		X	Dietary effects on reproduction	low
Age class of herring in kittiwake diets	12		X	Foraging effort, Meal delivery rate to nestlings	med
Foraging trip duration (incubation & nestling)	11,13	X	X	Foraging effort, Meal delivery rate to nestlings	high

¹Abundance of herring (m^2/km^2) determined by aerial forage fish surveys multiplied by the % of 1-yr-old herring in kittiwake diets (see METHODS for details).

²Abundance of herring (m^2/km^2) determined by aerial forage fish surveys multiplied by the % of 1-yr-old herring in kittiwake diets plus the abundance of sand lance from aerial surveys.

³Colony-years, see Appendix 1.1.

⁴Did not retain in statistical models, but note overall closer proximity of all fish schools to Eleanor Island (Fig. 2.3) and shorter foraging trips (Fig. 2.9b) relative to other colonies.

Table 2.3. Results of multiple linear regression analyses to identify environmental (explanatory) variables affecting reproductive measures of black-legged kittiwakes (response variables). Model fit statistics (R^2 [adjusted for small n], F , P , n , $\Delta AICc$) for the final model of each response variable are provided along with the coefficient (β), t , and P values of the explanatory variables retained. If a significant competing model was within 2 $AICc$ of the final model and included an additional explanatory variable, the explanatory variable and model fit statistics are provided in italics. Models explaining a significant amount of variation are in bold. $\Delta AICc$ is the change in Akaike's information criterion between the final and next best models. Explanatory variables tested included those listed in Table 2.2 and selected interactions.

Response Variables (R^2 , F , P , n , $\Delta AICc$)	Explanatory Variables β , t , P						
	Colony Size	Year	Trip Duration Chick-Rearing	Prey Abundance			Prop. 1-yr-old Herring
				Total Prey	Sand lance	1-yr-old Herring	
Laying Success (0.438, 11.92, 0.004, 15, 2.6)		-0.095, -3.45 0.004					
Clutch Size (0.420, 11.12, 0.005, 15, 2.0)		-0.129, -3.33 0.005					
Hatch Date (0.001, 0.89, 0.365, 14, 3.4)		0.822, 0.94, 0.365					
Hatch Success (0.298, 6.94, 0.021, 15, 0.9) <i>(0.500, 5.67, 0.014, 15, 1.6)</i>	<i>0.30E-4, 2.13</i> <i>0.057</i>	-0.087, -2.63, 0.021			<i>0.093, 1.92,</i> <i>0.082</i>		
β Chick Survival (0.038, 0.56, 0.469, 13, 2.45)			-0.045, -0.75, 0.469				
Chick Growth (0.683, 13.91, 0.001, 13, 0.4) <i>(0.764, 13.96, 0.001, 13, 5.0)</i>		<i>-0.273, -2.11,</i> <i>0.064</i>	-0.757, -4.81, 0.001	0.507, 2.53, 0.030			
Fledge Mass (0.157, 2.68, 0.140, 10, 2.08)			-5.002, -1.64, 0.140				
Fledging Success (0.400, 8.34, 0.016, 12, 2.0)							0.001, 2.89, 0.016
Trip Duration - Incubation (0.643, 19.01, 0.002, 11, 0.5) <i>(0.762, 17.00, 0.001, 11, 4.4)</i>	0.001, 4.36, 0.002					<i>-1.829, -2.34,</i> <i>0.047</i>	
Trip Duration – Chick-Rearing (0.554, 15.92, 0.002, 13, 4.0)	2.59E-4, 3.99, 0.002						
Breeding Success (0.505, 8.15, 0.006, 15, 3.5)	3.59E-5, 2.27, 0.043	-0.112, -3.52, 0.004					

^aInteraction terms included: $\ln herr * dist.herr$, $\ln sala * dist.sala$, $ctrip.dur * dist.sala$, $ctrip.dur * dist.herr$, $ctrip.dur * diet.herr$, $ctrip.dur * diet.age1.herr$, $ctrip.dur * prop.age1.herr$, $ctrip.dur * diet.sala$, $ctrip.dur * diet.cape$, $ctrip.dur * colony.size$, $ctrip.dur * year$,

Table 2.3. Continued

itrip.dur*colony.size, itrip.dur*year, dist.herr*size, dist.sala*size, dist.herr*year, dist.sala*year, colony.size*year, plot.fail*year.
Where ln herr=log of herring abundance, ln sala=log of sand lance abundance, dist.herr=mean distance to herring school, mean
distance to sand lance school, ctrip.dur=chick-rearing foraging trip duration, itrip.dur=incubation foraging trip duration,
diet.herr=% mass of herring in diet, diet.age1.herr=% mass of 1 yr old herring in diet, prop.age1.herr=proportion of 1 yr old vs
YOY herring in diet, diet.sala==% mass of sand lance in diet, diet.cape==% mass of capelin in diet,

Table 2.4. Results of multiple linear regression analyses using standardized data (deviations from the mean for each colony) to identify environmental (explanatory) variables affecting reproductive measures of black-legged kittiwakes (response variables). Model fit statistics (R^2 [adjusted for small n], F , P , n , ΔAIC_c) for the final model of each response variable are provided along with the coefficient (β), t , and P values of the explanatory variables retained. If a significant competing model was within 2 AIC_c of the final model and included an additional explanatory variable, the explanatory variable and model fit statistics are provided in italics. Models explaining a significant amount of variation are in bold. ΔAIC_c is the change in Akaike's information criterion between the final and next best models. Explanatory variables tested included those listed in Table 2.2 and selected interactions (same as those listed in Table 2.3).

Response Variables (R^2 , F , P , n , ΔAIC_c)	Explanatory Variables β , t , P								
	Colony Size	Year	Trip Duration Chick-Rearing	Prey Abundance			Distance to Herring Sch.	Prop. 1-yr-old Herring	Size*Year
				Total Prey	Sand Lance	1-yr-old Herring			
Laying Success (0.852 , 27.92 , <0.001 , 15 , 6.1)	-492.2, -3.39, 0.006	-0.319, -4.17, 0.002							0.247, 3.40, 0.006
Clutch Size (0.617 , 12.26 , 0.001 , 15 , 0.7) (<i>0.680</i> , <i>10.91</i> , <i>0.001</i> , <i>15</i> , <i>2.9</i>)	0.430, 2.75, 0.018	-0.441, -4.34, 0.001							<i>0.196, 1.84,</i> <i>0.094</i>
Hatch Date (0.168, 3.63, 0.081, 14, 2.8)	-0.495, -1.90, 0.081								
Hatch Success (0.46 , 5.31 , 0.034 , 11 , 2.5)	0.535, 2.58, 0.033	-0.470, -3.07, 0.015							
β Chick Survival (0.030, 1.38, 0.265, 13, 3.3)			-0.334, -1.17, 0.265						
Chick Growth (0.543 , 7.53 , 0.012 , 12 , 2.0)			-0.669, -3.30, 0.009	0.225, 2.50, 0.034					
Fledge Mass (0.007, 1.06, 0.333, 10, 4.6)								0.321, 1.03, 0.333	
Fledging Success (0.471 , 10.79 , 0.008 , 12 , 2.5)		-0.445, -3.28, 0.008							
Trip Duration - Incubation (0.174, 2.90, 0.127, 10, 3.14)					0.608, 1.70, 0.127				
Trip Duration – Chick-Rearing (0.917 , 34.32 , <0.001 , 10 , 8.3)		-0.243, -3.16, 0.020				-0.729, -5.02, 0.002	-0.766, -8.32, <0.001		
Breeding Success (0.459 , 12.88 , 0.003 , 15 , 0.68) (<i>0.680</i> , <i>10.91</i> , <i>0.001</i> , <i>15</i> , <i>2.9</i>)	<i>0.299, 1.67,</i> <i>0.120</i>	-0.444, -3.59, 0.003							

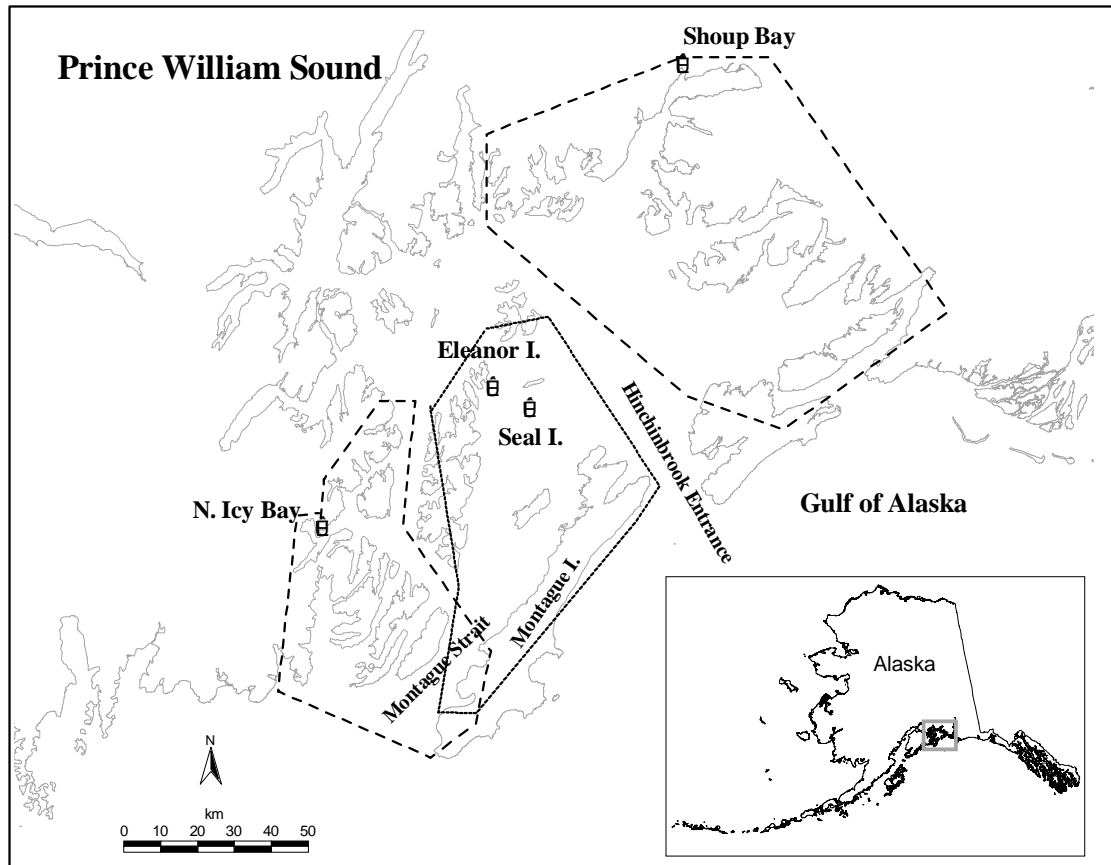


Figure 2.1. Locations of four black-legged kittiwake colonies (stars) where we conducted studies from 1995 to 1999 in Prince William Sound, Alaska. Dashed polygons encompass the maximum foraging range of adult kittiwakes from each colony (determined by radio-tracking studies). The flight paths for aerial surveys of forage fish schools included all shorelines within the polygons.

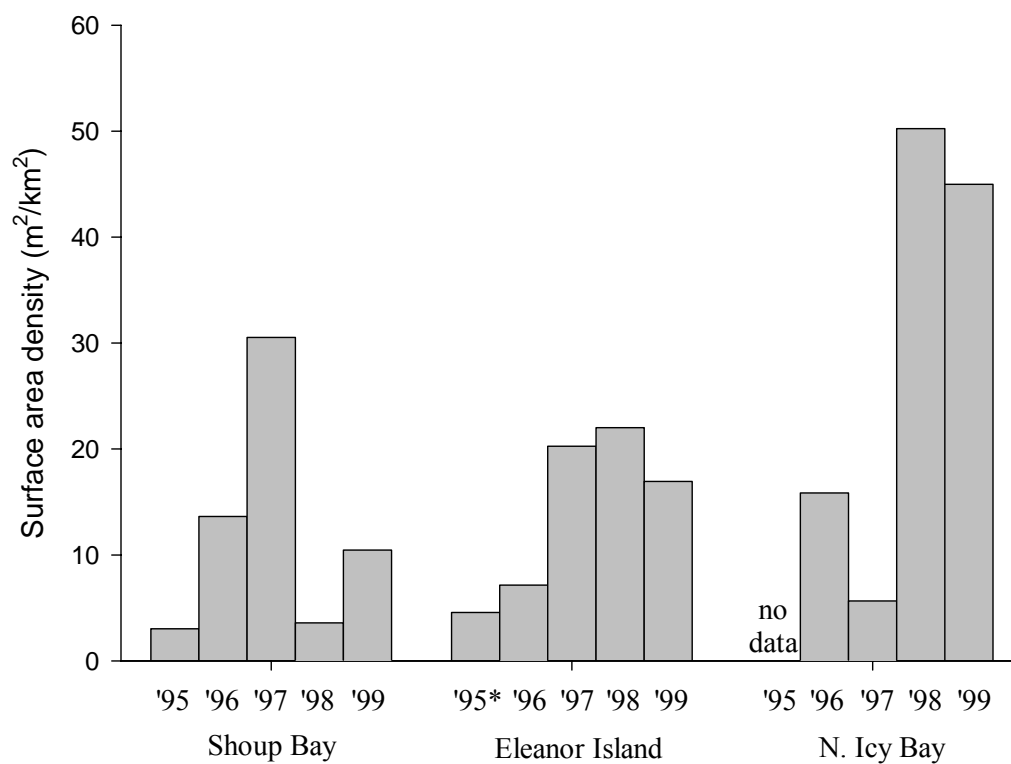


Figure 2.2. Annual abundance estimates for surface schooling forage fishes (Pacific herring, *Clupea pallasii*, Pacific sand lance, *Ammodytes hexapterus*, and capelin *Mallotus villosus*) within the foraging ranges of adult kittiwakes from the three study areas in Prince William Sound, Alaska, 1995 - 1999. Note (*) that Seal Island (1995 only) is within the same forage fish sampling area as Eleanor Island.

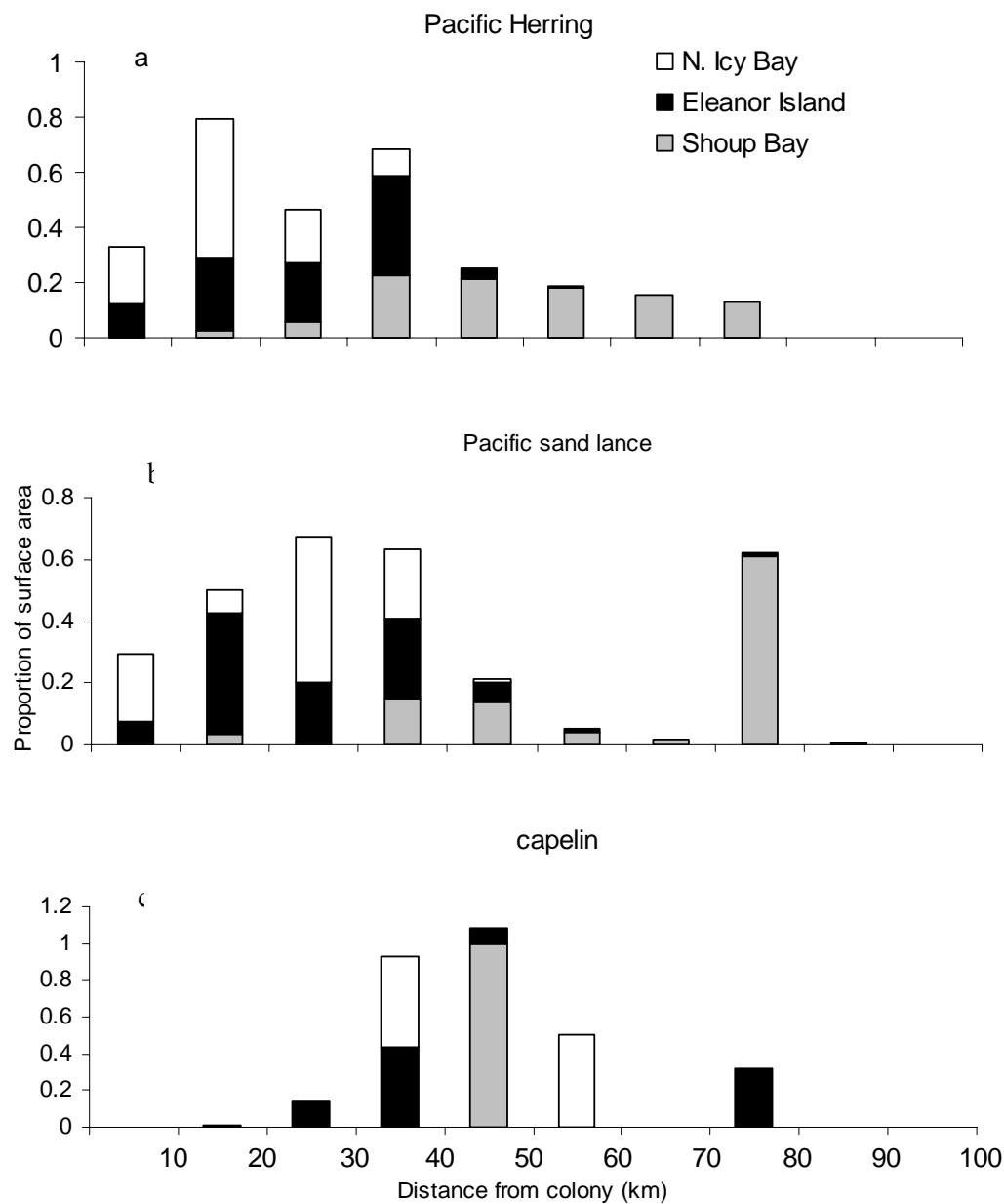


Figure 2.3. Proximity of forage fish by species to three black-legged kittiwake breeding colonies in Prince William Sound (PWS), Alaska. Data for each forage fish species are presented as a proportion of the total surface area (m^2) within each colony's respective kittiwake foraging range and occurring within 10 km increments from the colony.

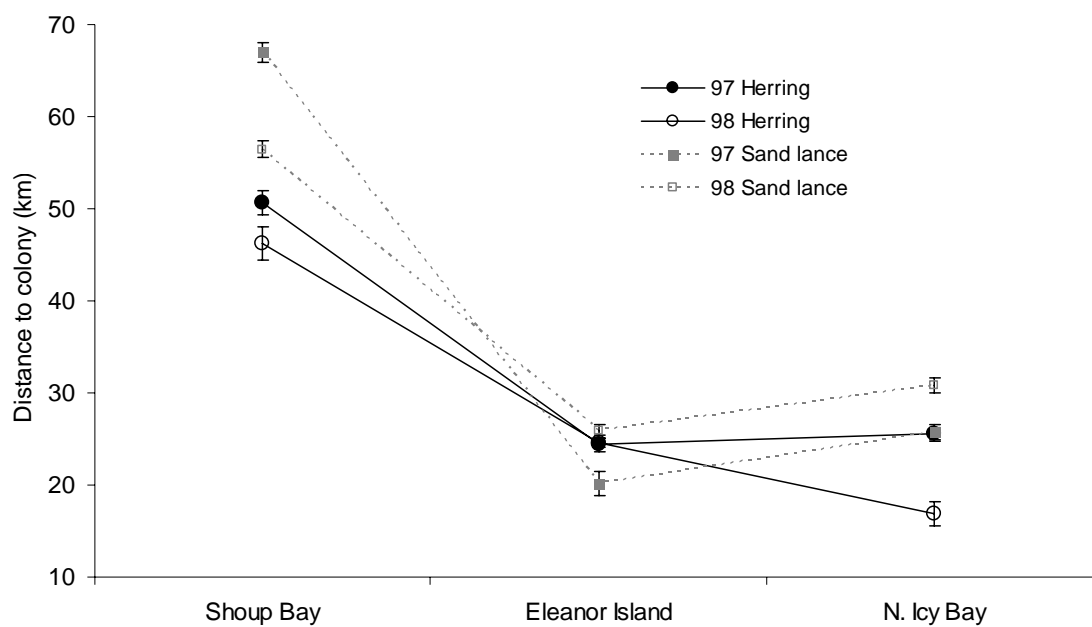


Figure 2.4. Interannual variation in mean (\pm SE) distance (km) to three black-legged kittiwake colonies for schools of Pacific herring and Pacific sand lance ($n = 51-544$ schools per species per colony-year). Data from 1997 and 1998 are presented as examples of observed variation

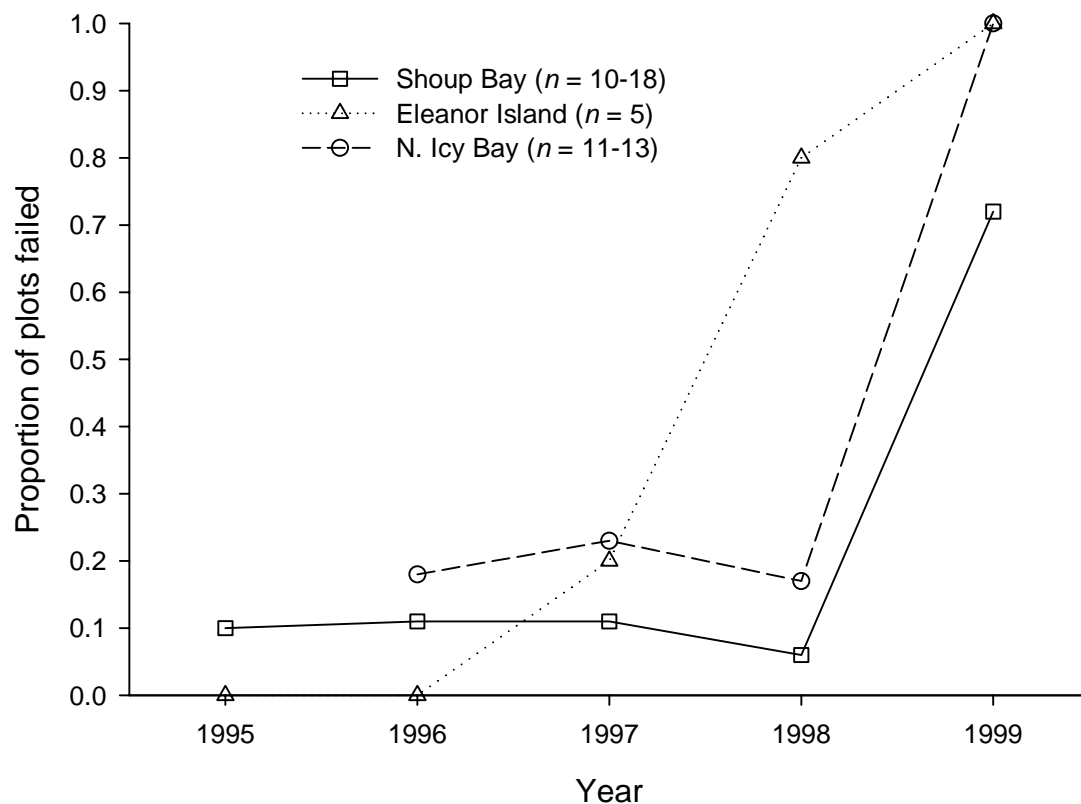


Figure 2.5. Proportion of plots within a colony-year where black-legged kittiwakes failed to produce chicks. Failure was defined as $\leq 10\%$ of the maximum productivity (chicks fledged / nest structure) within a colony-year. Maximum productivity per plot was 1.2 chicks/nest at Shoup Bay (1995 and 1996), 1.4 at Eleanor Island (1996 and 1997), and 1.2 at North Icy Bay (1997 and 1998).

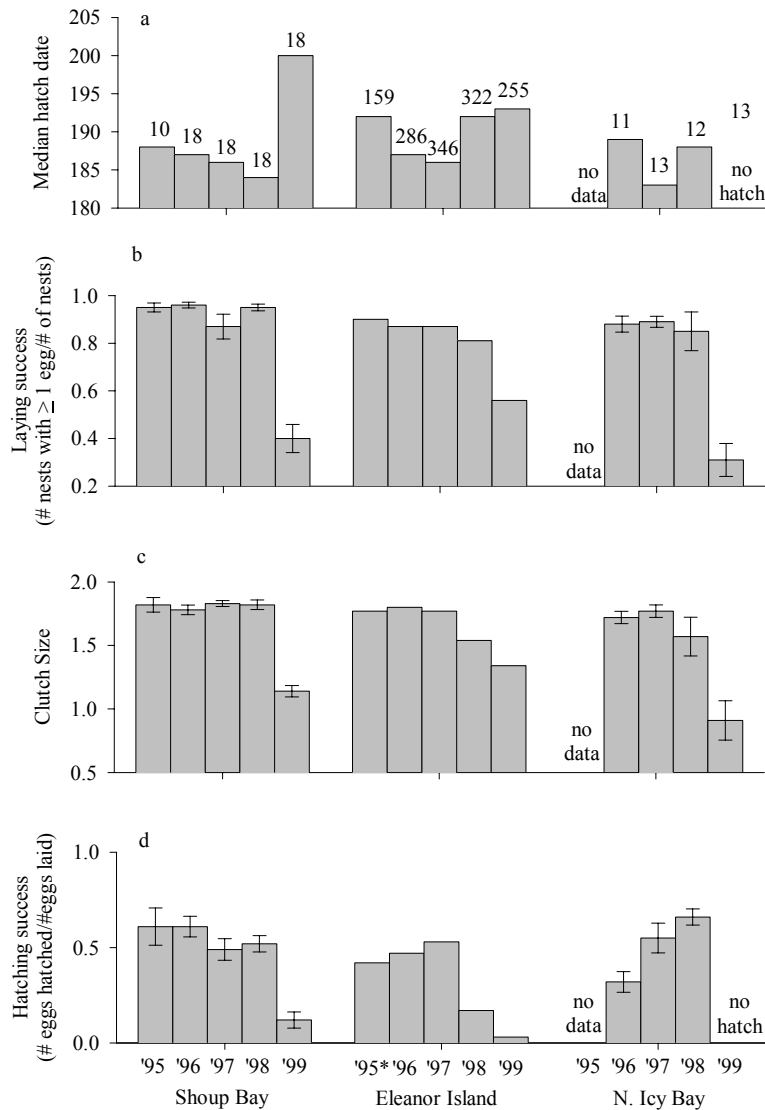


Figure 2.6. Metrics of egg laying and incubation performance for breeding black-legged kittiwakes at three study colonies in Prince William Sound, Alaska, 1995 - 1999. Note (*) that values for Seal Island (1995 only) were similar to Eleanor Island and are presented in Appendix 1.1. Sample sizes are noted above bars in upper graph (a) and represent plots at Shoup Bay and North Icy Bay and total nests (census) at Eleanor Island. Error bars are ± 1 SE (Eleanor Island was a census, therefore no error bars). Also noted are occasions when data collection was not attempted (no data) and no nestlings hatched thereby preventing data collection (no hatch).

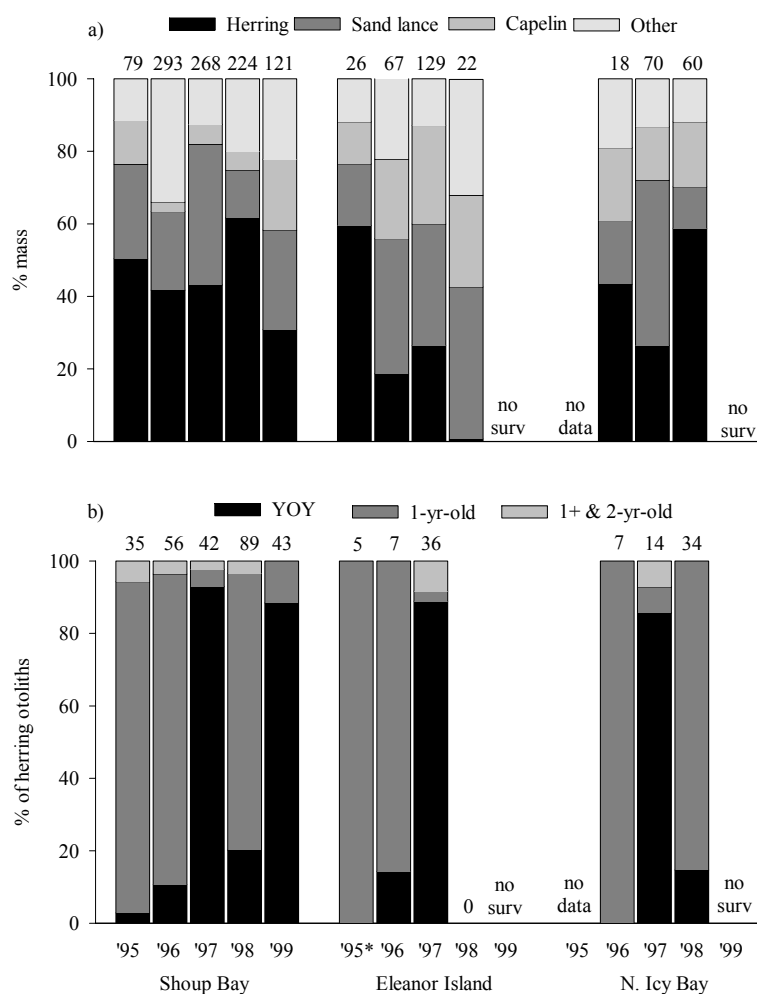


Figure 2.7. Percent mass of prey (a) and age class of herring (b) consumed by black-legged kittiwakes during the chick-rearing period at three study colonies in Prince William Sound, Alaska, 1995 - 1999. Note (*) that values for Seal Island (1995 only) were similar to Eleanor Island and are presented in Appendix 1.1. Sample sizes are noted above bars and represent number of regurgitates (a) and total number of otoliths recovered (b). Also noted are occasions when data collection was not attempted (no data) and when nestlings did not survive to allow collection of diet samples (no surv). For a list of species included in the “other” category, see Suryan et al. 2000a and 2002.

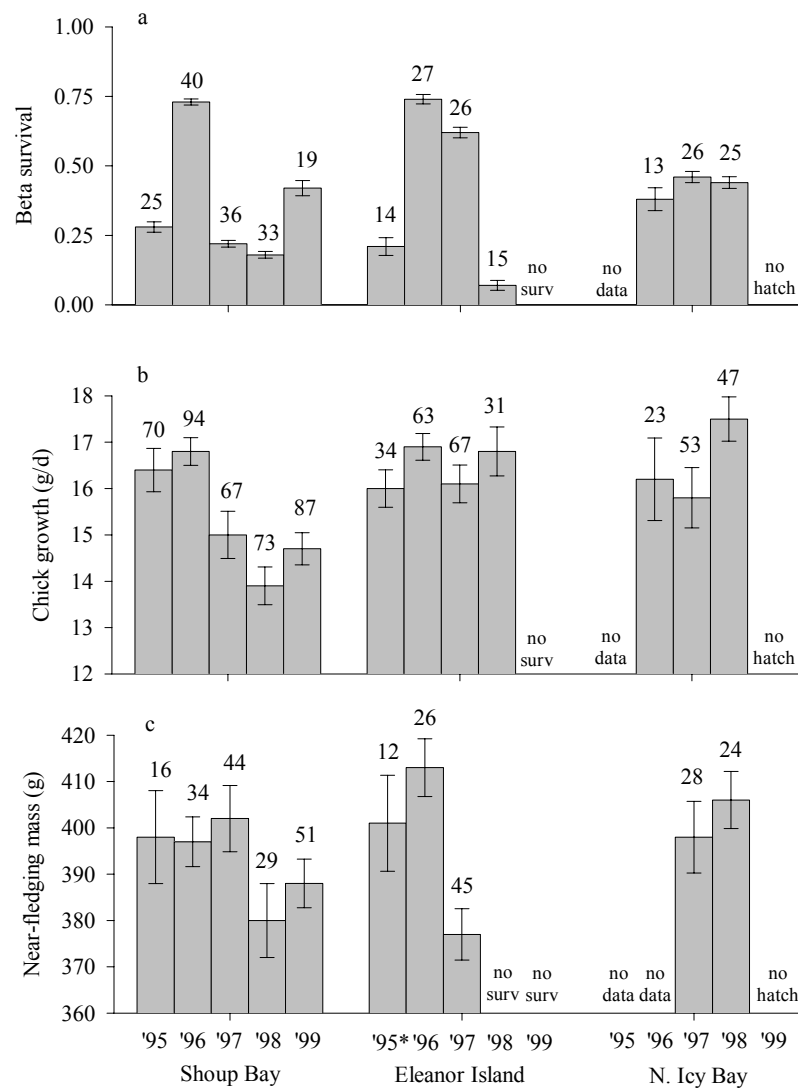


Figure 2.8. Mean (\pm SE) metrics of chick-rearing performance for breeding black-legged kittiwakes at three study colonies in Prince William Sound, Alaska, 1995 - 1999. Note (*) that values for Seal Island (1995 only) were similar to Eleanor Island and are presented in Appendix 1.1. Sample sizes (# of nestlings) are noted above bars. Also noted are occasions when data collection was not attempted (no data), nestlings did not survive long enough to complete measurements (no surv), and no nestlings hatched thereby preventing data collection (no hatch).

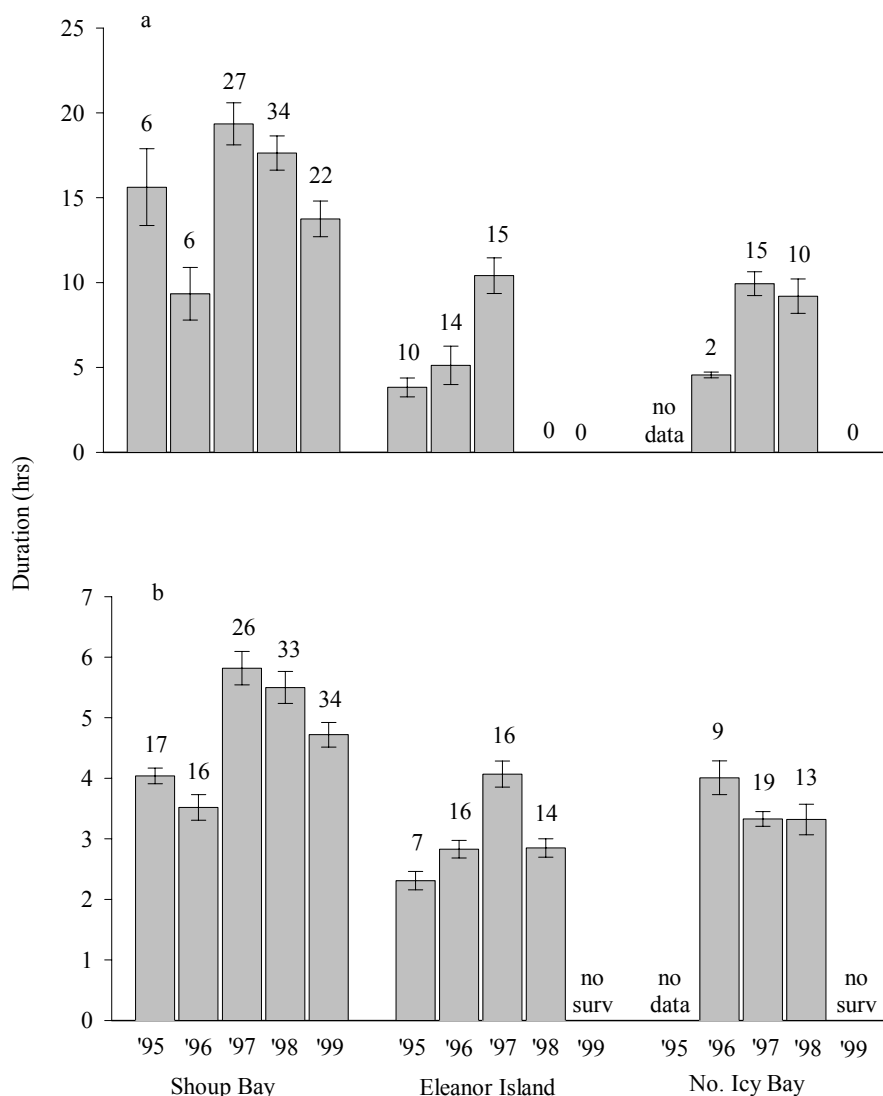


Figure 2.9. Mean (\pm SE) annual foraging trip durations for black-legged kittiwakes during the incubation (a) and chick-rearing (b) periods at three study colonies in Prince William Sound, Alaska, 1995-1999. Foraging trips during incubation include overnight and daytime trips, whereas chick-rearing are day-time only (occurring between 0400 to 2400 hrs; see *foraging trip durations* in Study area and methods for reasoning; note different scales of y-axes). Also noted are occasions when data collection was not attempted (no data) and nestlings did not survive long enough to collect data comparable to other years (no surv).

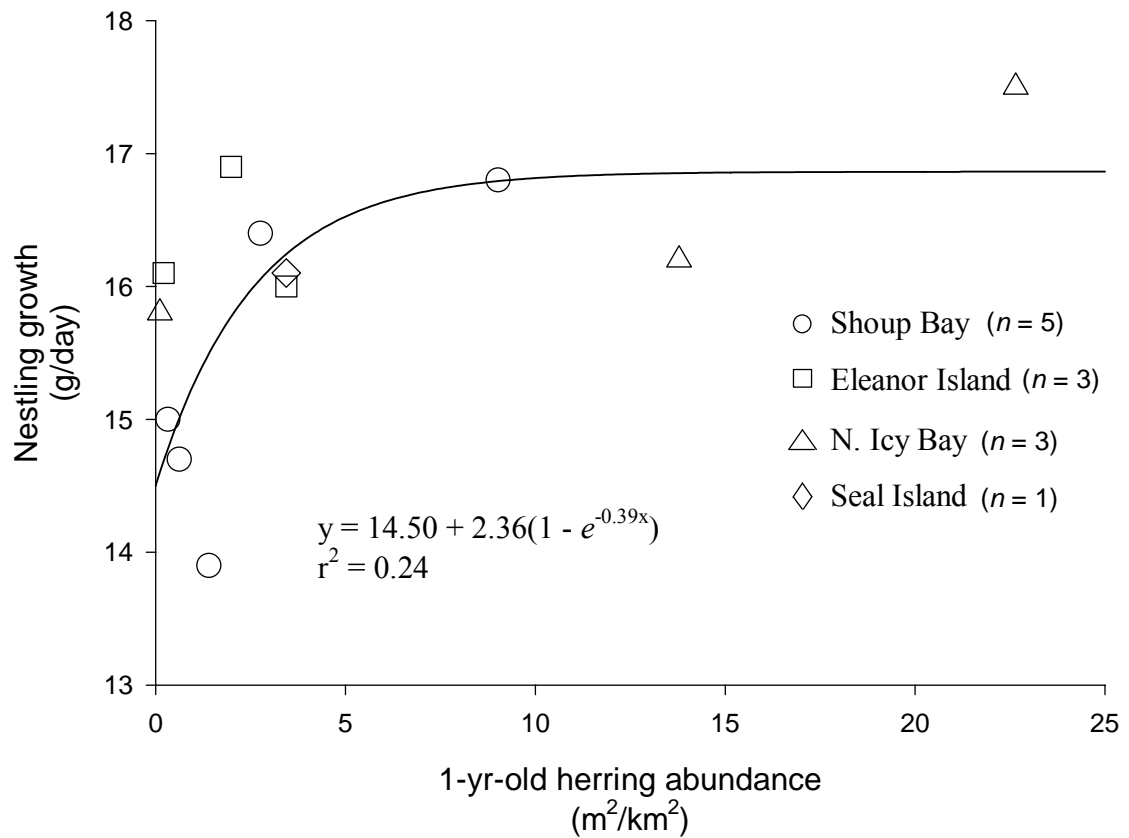


Figure 2.10. A non-linear, asymptotic relationship between black-legged kittiwake nestling growth and the abundance of 1-yr-old herring in Prince William Sound, Alaska. Data points are identified by colony. The best fit equation included a y-intercept (β_0) of 14.5, which is slightly above the minimum value we recorded.

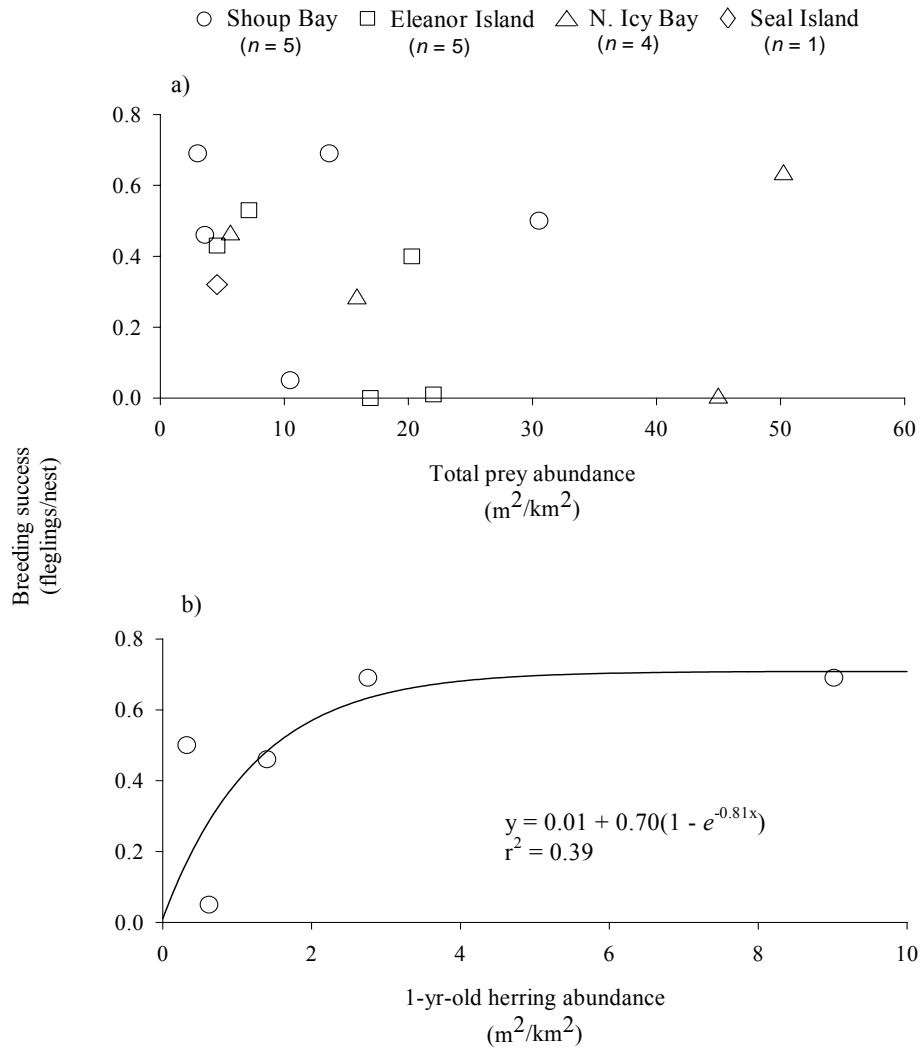


Figure 2.11. Relationships between black-legged kittiwake breeding success at four colonies and prey abundance (within foraging ranges of birds at each colony) in Prince William Sound, Alaska. Data points are identified by colony. There was no relationship between kittiwake breeding success and total prey abundance (a) because of colony-specific and top-down effects of egg and chick predators. In contrast, a nonlinear, asymptotic relationship existed between breeding success and the abundance of 1-yr-old herring at Shoup Bay (the largest colony with the most effective predator swamping) and the most dependent on 1-yr-old herring (b).

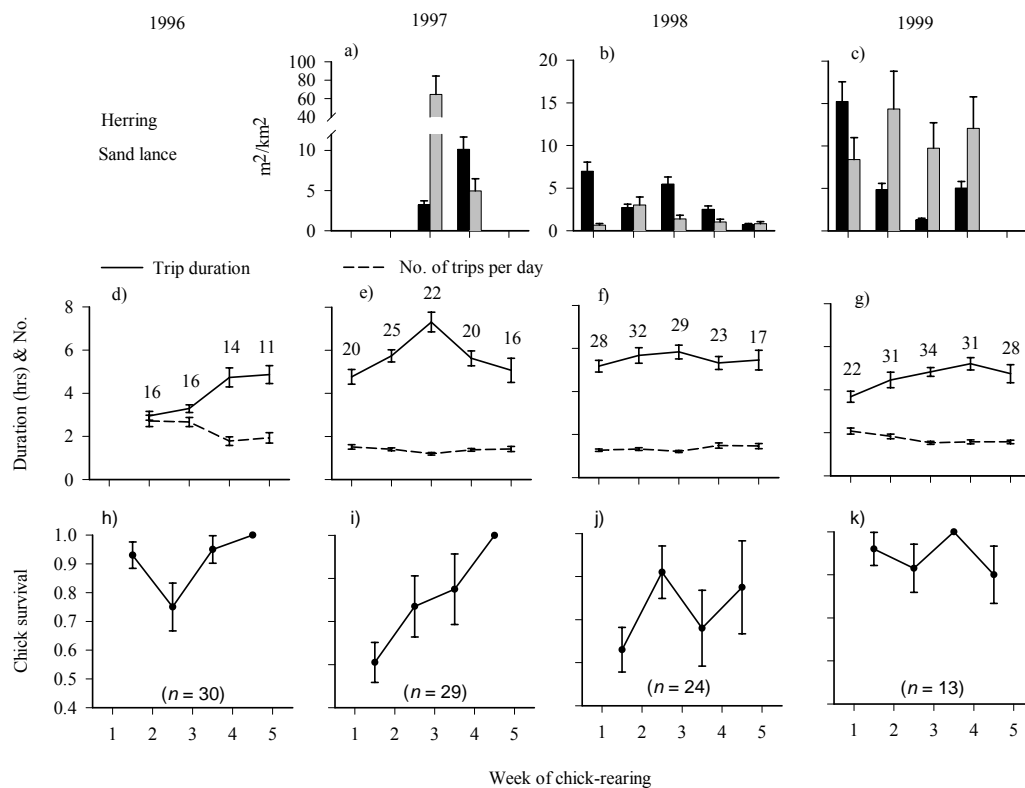


Figure 2.12. Weekly changes in forage fish abundance (a-c), foraging trip duration and number of trips per day (n = no. of adults; d-g), and β chick survival (n = no. of chicks; h-k) of black-legged kittiwakes at the Shoup Bay colony, Alaska, 1996-1999. Data from Suryan et al. (2002).

Appendix 1.1. Data for response and explanatory variables used in multiple regression analyses to identify environmental factors affecting black-legged kittiwake reproductive success at Shoup Bay, Eleanor Island, North Icy Bay, and Seal Island during 1995 to 1999 in Prince William Sound, Alaska.

	Shoup Bay					Eleanor Island					North Icy bay					Seal Island
	1995	1996	1997	1998	1999	1995	1996	1997	1998	1999	1995	1996	1997	1998	1999	1995
Colony Size	5628	6537	7150	7849	6128	127	268	263	284	175	1706	1877	2084	2104	1459	252
Prey abundance (m ² /km ²)																
Total	3.02	13.61	30.53	3.58	10.46	4.57	7.14	20.26	22.01	16.93	-	15.85	5.66	50.23	44.98	4.57
Pacific herring	3.02	10.52	6.78	1.83	5.34	3.44	2.32	7.62	2.69	4.72	-	13.79	1.57	26.56	3.61	3.44
Pacific sand lance	0.00	3.09	23.74	1.41	5.12	0.00	4.82	11.87	19.15	10.50	-	2.06	4.09	23.68	4.22	0.00
Capelin	0.00	0.00	0.00	0.00	0.06	1.13	0.00	0.02	0.17	1.66	-	0.00	0.00	0.00	35.96	1.13
1-yr-old herring (see footnote Table 2.2)	2.76	9.02	0.32	1.40	0.62	3.44	1.99	0.21	-	-	-	13.79	0.11	22.65	-	3.44
1-yr-old herring and sand lance (see footnote Table 2.2)	2.76	12.11	24.07	2.81	5.74	3.44	6.81	12.08	-	-	-	15.85	4.20	46.33	-	3.44
Prey distribution (distance to colony, km)																
Pacific herring	55.01	54.70	50.69	46.27	52.42	30.82	28.28	24.44	24.67	24.45	-	13.57	25.72	16.99	20.32	22.05
Pacific sand lance	-	61.53	67.02	56.47	49.68	-	21.06	20.25	26.06	27.23	-	13.95	25.86	31.05	24.69	-
Capelin (not used in regression due to numerous missing data)	-	-	-	-	47.38	60.35	-	36.55	29.95	46.52	-	-	-	-	32.62	49.87
Clutch Size	1.82	1.78	1.83	1.82	1.14	1.77	1.80	1.77	1.54	1.34	-	1.72	1.77	1.57	1.70	1.55
Median hatch date (Julian date)	188	187	186	184	200	192	187	186	192	193	-	189	183	188	-	192
Laying success	0.95	0.96	0.87	0.95	0.40	0.90	0.87	0.87	0.81	0.56	-	0.88	0.89	0.85	0.31	0.80
Hatching Success	0.61	0.61	0.49	0.52	0.12	0.42	0.47	0.53	0.17	0.03	-	0.32	0.55	0.66	0.00	0.41
Fledging Success	0.64	0.60	0.61	0.51	0.56	0.65	0.66	0.45	0.06	0.00	-	0.61	0.52	0.61	0.00	0.65

Appendix 1.1. Continued

Productivity	0.69	0.69	0.50	0.46	0.05	0.43	0.53	0.40	0.01	0.00		0.28	0.46	0.63	0.00	0.32
Proportion of productivity plots that failed	0.10	0.11	0.11	0.06	0.72	0.00	0.00	0.20	0.80	1.00		0.18	0.23	0.17	1.00	0.14
Incubation foraging trip duration (hr)	15.62	9.34	19.35	17.63	13.75	3.83	5.12	10.41	-	-	-	4.56	9.94	9.20	-	-
Chick-rearing foraging trip duration (hr)	4.04	3.52	5.82	5.50	4.72	2.31	2.83	4.07	2.85	-	-	4.01	3.33	3.32	-	3.72
Beta chick survival	0.28	0.73	0.22	0.18	0.42	0.21	0.74	0.62	0.07	-	-	0.38	0.46	0.44	-	0.41
Chick growth (g/day)	16.4	16.8	15.0	13.9	14.7	16.0	16.9	16.1	16.8	-	-	16.2	15.8	17.5	-	16.1
Near fledging mass (g)	398	397	402	380	388	401	413	377	-	-	-	-	398	406	-	-
Nestling Diets (% mass)																
Pacific herring	50.4	41.7	43.2	61.7	30.8	59.6	18.7	26.5	0.7	-	-	43.3	26.5	58.8	-	48.6
Pacific sand lance	26.0	21.7	38.7	13.1	27.5	16.9	37.2	33.5	41.9	-	-	17.6	45.5	11.4	-	1.0
Capelin	12.1	2.6	5.5	5.2	19.5	11.6	21.9	27.1	25.2	-	-	20.1	14.8	17.9	-	20.4
% 1-yr-old herring	91.4	85.7	4.8	76.4	11.6	100.0	85.7	2.8	-	-	-	100.0	7.1	85.3	-	100.0
% young-of-year sand lance	90.1	98.4	97.0	98.4	100.0	100.0	87.5	96.8	80.0	-	-	66.7	96.0	90.0	-	-

Chapter 3. Prey-Mediated, Multi-Scale Foraging And The Effect On Time-Budgets Of A Piscivorous Marine Bird

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Abstract

Predator-prey interactions occur at multiple, often nested, spatial scales. In marine systems, quantification of predator-prey associations are typically based on ship-based observations of predator and prey aggregations, and not by tracking individual foragers. We used continuous radio-tracking of individual black-legged kittiwakes (*Rissa tridactyla*) and first-passage time analysis to quantify the spatial scale of area-restricted search (ARS) associated with different foraging habitats and prey species, and the affect on foraging time budgets. We found that breeding kittiwakes exhibited a hierarchical search strategy, in which the spatial scale of ARS varied by foraging habitat and prey type. Kittiwakes nesting at the Eleanor Island colony in central Prince William Sound, Alaska, searched for prey within one of two primary destinations, the central islands of Prince William Sound or the barrier islands adjacent to the Gulf of Alaska. Within each of these foraging areas, however, the extent of fine-scale search differed. Kittiwakes foraged over a much smaller spatial scale when feeding on schools of primarily juvenile Pacific herring (*Clupea pallasii*) and Pacific sand lance (*Ammodytes hexapterus*) along the shorelines of the central islands of Prince William Sound vs. when feeding primarily on schools of capelin (*Mallotus villosus*) among the barrier islands. We demonstrate that even within what are considered “high quality” schooling forage fishes, differences among fish species, fish age classes, and presence of seabird feeding flocks can result in a nearly three-fold increase in search time while foraging and a four- to eight-fold increase in the spatial scale of foraging for this surface-feeding seabird. Depending on proximity of prey to the breeding colony, if sufficient time budget buffers do not exist, the increased time spent foraging will ultimately result in reduced breeding success.

Key words: black-legged kittiwakes, feeding flocks, first-passage time, diet, multi-scale foraging, radio-tracking, time budgets

Introduction

The distribution of prey, the aggregative response of predators to prey, and the scale at which these interactions occur have been a primary focus in a growing body of literature addressing predator-prey interactions (e.g., Mackas and Boyd 1979, Schneider and Piatt 1986, Logerwell et al. 1998, Fauchald and Erikstad 2002). In most systems, it is clear that predator-prey interactions occur at multiple, often nested, spatial and temporal scales (e.g., Kotliar and Wiens 1990). Recognition of such hierarchical structuring of patch dynamics has been proposed as a paradigm shift in ecology (Wu and Loucks 1995).

In navigating through an environment of hierarchical prey field structure, a forager must employ a complementary form of hierarchical search strategy to successfully locate nonrandomly distributed prey (Russell et al. 1992, Grünbaum 1998). Fauchald (1999) describes a hierarchical search strategy where a forager travels long distances with a low turning frequency within large-scale, low-density patches in an effort to find medium-density patches. Once a medium-density patch is found, the forager then searches for small-scale, high-density patches by increasing turning rate and reducing travel distances. Hence, the forager exhibits a hierarchical reduction in the spatial scale of area-restricted search (ARS) activity. This type of hierarchical search strategy has been observed in highly mobile marine predators such as seabirds. For example, wandering albatrosses (*Diomedea exulans*) foraging from their breeding colony exhibited two scales of prey searching: (1) large scale curvilinear routes with infrequent landings and (2) small scale ARS activity with frequent changes in flight direction and landings (Weimerskirch et al. 1997). Moreover, each scale of search tended to occur within specific habitats, large-scale within oceanic and small-scale within neritic waters.

For a seabird foraging from a central place (i.e., a breeding colony), locating prey patches when engaged in ARS is also typically nonrandom. Seabirds are hypothesized to use a mixed search strategy, where memory is used to return to the foraging area, then local enhancement is used to find specific food patches (Irons 1998,

Davoren and Montevecchi 2003). In many cases, the dominant local enhancement cue is the presence of other birds actively foraging within flocks. Feeding flocks for seabirds serve as a highly visible cue of the presence of prey and the potential for successful feeding and are important to seabird foraging in a wide variety of marine habitats (e.g., Hoffman et al. 1981, Hunt et al. 1988, Ballance et al. 1997). However, competition among foragers also occurs within feeding flocks, causing some individuals to be selective about joining flocks (Hoffman et al. 1981, Maniscalco et al. 2001) or bypassing them and feeding solitarily (Hebshi 1998, Irons 1998, Davoren and Burger 1999).

Black-legged kittiwakes (*Rissa tridactyla*), a piscivorous, colonial nesting seabird, exhibit prey switching in response to changes in availability of prey species within Prince William Sound, Alaska (Suryan et al 2000). These dietary changes are most dramatic for colonies in central Prince William Sound (Suryan et al. 2006), a dynamic region that is influenced by oceanographic processes outside Prince William Sound to a greater degree than other regions in the Sound (Brown 2002). Herein, we investigate the spatial scale of foraging, diets, and time budgets of kittiwakes at the Eleanor Island colony in central Prince William Sound. We conducted the study during five breeding seasons when kittiwake foraging destinations and diets exhibited the maximum variation recorded for Prince William Sound kittiwake colonies (Suryan et al. 2006). We used continuous radio-tracking of individual kittiwakes and first-passage time analysis (Fauchald and Tveraa 2003) to quantify the spatial scale of ARS associated with different foraging habitats and prey species, and the affect on foraging time budgets. Suryan et al (2000) found that search and prey capture times were only weakly related to trip duration in this population of black-legged kittiwakes. Therefore, we hypothesized that time allocated to search and prey capture would be affected by prey species and age class more so than differing spatial scales of foraging.

Methods

Study area

We studied black-legged kittiwakes at the Eleanor Island colony (ca. 220 breeding pairs) located in central Prince William Sound, Alaska (Fig. 3.1). This colony is located near the protected bays of the central islands, but also within foraging range of the barrier islands that separate Prince William Sound from the Gulf of Alaska. Diets of kittiwakes at this colony, therefore, reflect the influence of both these major habitats (Suryan et al. 2000).

Radio tracking

We captured adult black-legged kittiwakes at their nests and attached radio transmitters (164-167 MHz, 9-11 g [$< 3\%$ of body weight] Advanced Telemetry Systems, Inc.) ventrally to the base of the tail feathers with two nylon cable ties and Loctite 494 instant adhesive (Loctite Corporation; Irons 1998). In addition, we dyed (Nyanzol D and Rhodamine B-base) the head, breast, tail, and underwings of radio-tagged kittiwakes one of three color combinations. The dye permitted identification of kittiwakes at a distance during at-sea tracking. Radio-tracking was conducted throughout the chick-rearing period (nestling ages ranged from 1 to 30 days) and included only individuals provisioning nestlings. We determined foraging trip duration, distance, location, and behavior by tracking radio-tagged kittiwakes with a receiver and a 4-element yagi antenna from a 7.3 m Boston Whaler capable of traveling 65 km hr^{-1} . Observers waited nearby until a radio-tagged bird left the colony, then attempted to keep the kittiwake in view until it returned to the colony, constituting a complete track. Herein, we use only complete tracks where $\geq 75\%$ of the foraging trip was observed (Table 3.1).

The distance between the boat and the radio-tagged kittiwake during a track varied between ca. 700 m and less than 100 m, depending on circumstances. In all cases, we remained at a maximum distance to prevent noticeable alterations of the kittiwake's activities while maintaining visual contact to record behaviors. Behaviors

recorded included traveling (straight flight), searching for prey (back and forth flight), foraging (surface plunge or surface seize; Ashmole 1971), resting, and lost (bird out of view). Because duration of pursuit and handling of prey for kittiwakes is negligible compared to search time (Irons 1992), we combined feeding with searching in final analyses of time budget data. We determined locations during tracking using a Lowrance LMS-350A global positioning system receiver (Lowrance Electronics Inc.). Positions were recorded at 1-min intervals or whenever there was a change in behavior, including feeding attempts.

While visually tracking birds (radio telemetry was used only to relocate a bird lost from view) we recorded all feeding flocks observed and divided them into two categories, aggregated feeding flocks and dispersed feeding flocks. An aggregated feeding flock was defined as ≥ 2 birds flying in a “back-and-forth” pattern with ≥ 2 feeding attempts within a distance of 10 m. An aggregated feeding flock could be larger than 10 m in diameter as long as the farthest feeding bird was not > 10 m from any other feeding bird. The definition of a dispersed feeding flock was similar, except that there was greater spacing among individuals while still maintaining group cohesion (generally < 500 m between most distant individuals). These categories are consistent with feeding flock types I and II, respectively, as defined by Hoffman (1981).

First-passage time analysis

To calculate first-passage time (FPT; the time required to cross a circle of a given radius), we first linearly interpolated each kittiwake track at 0.05 km intervals while retaining original locations. We calculated FPT at every location along the track of each kittiwake for radii ranging from 0.1 km to 10 km by 0.1 km increments. We then plotted mean variance in FPT (log transformed) among individuals vs. radii to ascertain the peak, or dominant spatial scale of ARS (Fauchald and Tveraa 2003). The variance peak identifies which spatial scale is best to differentiate high (ARS) vs. low (transitory) passage times.

Foraging distributions

We created kernel density distributions of feeding locations to graphically depict changes in foraging areas among years. Kernel densities were generated in an Albers equal-area (Alaska) conic projection using the Animal Movement Extension (Hooge and Eichenlaub 2000) in ESRI ArcView 3.3 with a 2.5-km smoothing factor and 0.25-km cell size.

Prey composition

To determine prey consumed by adults during foraging trips, we collected 244 regurgitations from nestlings. Regurgitations were collected throughout the colony (including chicks of untagged birds) for the duration of the chick-rearing period (ca. 1 July to 15 August). One sample was collected per nest in most cases. Repeat samples from a nest were collected at ≥ 1 week intervals and were therefore considered independent. Samples from alpha and beta chicks were combined to represent a single foraging trip by an adult. Prey were identified using otoliths, morphological characteristics, scales, and bones. We were most interested in relating kittiwake foraging to the spatial distribution of prey and, therefore, present kittiwake diets as frequency of occurrence in regurgitations (i.e., species obtained per foraging trip). Otoliths were measured to the nearest 0.01 mm using an ocular micrometer. Age classes of herring were inferred from otolith length and the modes of length-frequency distributions (1-2 mm for young-of-year [YOY], 2-3 mm for one-year-old, and 3+ mm for age 1+ or 2), which were confirmed by personnel from the University of Alaska Fairbanks and the Alaska Department of Fish and Game (Stokesbury et al. 1999, Kevin D. E. Stokesbury, pers. comm.). Age classes of sand lance also were determined using modes of frequency distributions for otolith lengths (≤ 1.9 mm for YOY and > 1.9 mm for 1+ year-old), which were consistent with classifying YOY sand lance as typically less than 100 mm standard length (Robards et al., 1999).

Statistical analyses

We compared the percent occurrence of prey species in nestling diets among years and between colonies using contingency tables with chi-square analyses. Tukey-type multiple comparison tests for proportions were used when significant differences were detected in chi-square analyses. Data exhibiting non-normal distributions and unequal variances were compared using nonparametric statistics (Mann-Whitney *U* and Kruskal-Wallis *H*). Relationships between independent and dependent variables were tested with linear regression. Results were considered significant at $\alpha = 0.05$.

Results

Foraging destinations

Kittiwakes from Eleanor Island had two primary foraging destinations, the central islands near the colony and the barrier islands nearest the Gulf of Alaska (Fig. 3.1). The central islands were the most common foraging destination (65%, $n = 60$), followed by trips to the barrier islands (27%), and trips including both destinations (8%). Total distance traveled was over twice as long and foraging locations were twice the distance from shore for trips that included the barrier island region (Table 3.2).

Spatial scale of area-restricted search and association with prey consumed

When foraging among the central islands, the peak in FPT and, therefore spatial scale of ARS, was well-defined and averaged 0.4 km (Fig. 3.2a). In contrast, when foraging among the barrier islands, the scale of ARS was less well-defined and much larger, averaging 3.4 km, but with a broad peak from 2 km – 5 km (Fig. 3.2b). Birds that foraged in both regions during a single foraging trip showed a bimodal distribution in the scale of ARS with peaks at 0.7 km and 2.7 km (Fig. 3.2c).

Primarily YOY sand lance ($\geq 80\%$ of otoliths recovered) were consumed in all years, regardless of foraging destination. Prey consumed during foraging trips to the central islands were primarily juvenile (YOY and 1-yr-old) forage fishes (herring and sand lance, and only occasionally capelin) occurring in small surface schools. In

contrast, during trips to the barrier islands, kittiwakes often fed on adult capelin, which occurred in large, dispersed schools, consistent with the greater relative spatial scale of ARS. For example, after leaving the colony, kittiwake #9709 first foraged within small areas in the nearshore region among the central islands, then traveled to the barrier islands and foraged over a much larger area between Green and Montague islands (Fig. 3.3). A regurgitation from this individual following this foraging trip contained, by mass, 53% herring, 15% sand lance, and 18% capelin.

Interannual variation in foraging destinations, prey consumed, and time budgets

The frequency of foraging trips to the two destinations varied among years; trips to the more distant barrier islands were rare in 1995 and 1998 (< 5%) and most frequent in 1997 (70%; Table 3.1, Fig. 3.4). Furthermore, there was considerable annual variation in the percent occurrence of prey species in diets and the age class of herring consumed, both of which appeared to affect the spatial scale of foraging and foraging time budgets. Trips to the barrier islands were associated with higher occurrence of capelin in the diets. For trips to the central islands, the duration of search tended to increase with increasing sand lance (Fig. 3.5a,b), although, this relationship was not statistically significant ($R^2 = 0.80$, $F_{1,3} = 8.03$, $P = 0.105$). However, the number of feeding attempts did show a significant relationship to both the percent of YOY herring in the diet ($R^2 = 0.90$, $F_{1,4} = 26.16$, $P = 0.014$), and the mean number of feeding flocks encountered ($R^2 = 0.93$, $F_{1,4} = 38.93$, $P = 0.008$; Fig. 3.6). The mean number of feeding attempts per trip was also positively related to search duration ($R^2 = 0.86$, $F_{1,4} = 17.84$, $P = 0.024$).

Discussion

Multi-scale hierarchical search strategy

Black-legged kittiwakes breeding at Eleanor Island exhibited a hierarchical search strategy. At the first level, kittiwakes would opt to forage either along the shorelines of the nearby central islands or travel greater distances to forage over

relatively open water near the barrier islands. Once within these particular regions, the second level of search activity occurred at finer scales where prey were encountered. Our findings through the tracking of free-ranging kittiwakes provide support for the expected behavior of a forager within a hierarchical prey patch system, as described by Fauchald (1999) and Fauchald et al. (2000), but their description was based on static observations of birds and prey (i.e., not following individual foragers). Moreover, the spatial scale of the two hierarchical levels of kittiwake foraging were within the range of the two lower levels of the three-level murre-capelin association quantified by Fauchald et al. (2000); medium scale patches of ~50 km and fine-scale patches of ~3 km.

Interestingly, Fauchald (2000) found spatial overlap between murre and capelin at the medium and large (> 300 km) scales, but not at the fine-scale. In our study, we could confirm that the fine-scale ARS activity was associated with foraging on prey patches (e.g., Fig. 3.3). Possible explanations for this apparent discrepancy between studies are that foragers may not always select prey patches of greatest density or prey may seek refuge from predators, which can lead to a lack of, or a negative, association between predators and prey (e.g., Rose and Leggett 1990, Horne and Schneider 1994). Additionally, when predator-prey data are point observations in space and time, the predator may not be actively foraging at the time of the observation, but rather waiting for appropriate conditions when prey become available. In contrast, when tracking individuals throughout their foraging trip, as in the present study, you are certain to capture the actual feeding events, which can be a small fraction of the entire trip duration.

We further demonstrated that within the lowest level of hierarchical search strategy, the spatial scale of ARS can vary four- to eight-fold depending on habitat and the prey type consumed. The bays within Prince William Sound are known as important nursery areas for juvenile forage fishes, particularly herring and sand lance (Stokesbury et al. 2000, Brown 2003), but also capelin (Brown 2002), which occur in relatively small schools in nearshore habitat (Brown 2003). ARS for kittiwakes foraging in this habitat was likewise over a similarly small spatial scale. Schools of

adult capelin among the barrier islands, including spawning aggregations, are abundant offshore (> 1 km) and peak in July (Brown 2002), the main period of kittiwake brood-rearing. In contrast to schools of juvenile fishes, schools of adult capelin are much larger and dispersed, as was kittiwake ARS associated with these aggregations. Among the barrier islands, however, kittiwakes did not forage exclusively on adult capelin, but sometimes fed on juvenile forage fishes. The peak in variance of first-passage time was, therefore, not as well defined as for the central islands where kittiwakes fed almost exclusively on juvenile fishes.

Foraging conditions for adult kittiwakes nesting at Eleanor Island were most anomalous in 1997, when overall foraging trip durations were the longest recorded during the study and when the majority of foraging trips to both destinations occurred. Visiting multiple feeding areas during a foraging trip is thought to reflect exploratory behavior (Wanless et al. 1990, Benvenuti et al. 1998). Given that central-place foraging kittiwakes can rely to some extent on memory (Irons 1998) for locating prey, kittiwake foraging behavior indicated that prey available was less predictable in 1997 compared to other years. Similarly, during the same time period in the Northeast Pacific, but further south in British Columbia, Davoren (2000) noted that although prey abundance was similar to other years, prey were dispersed over larger spatial scales, resulting in increased foraging duration for rhinoceros auklets (*Cerorhinca monocerata*). Fauchald and Erikstad (2002) noted that during years of low capelin density, there was low concordance between the distribution of murre and capelin.

Foraging time budgets

Suryan et al. (2000) noted that for kittiwakes in Prince William Sound, dietary changes were accompanied by changes in foraging time budgets; duration of travel and trip distance increased with greater trip duration. Search and prey capture times, however, were only weakly related to trip duration and it was hypothesized that these activities may more strongly reflect strategies that vary with different species or age classes of prey consumed. Our current analyses support this hypothesis and demonstrate that the number of feeding attempts per trip, and, hence, duration of prey

acquisition, varies with the number of feeding flocks encountered and age class of prey. Feeding flocks are highly visible cues to the presence of prey for foraging birds (Hoffman et al. 1981, Hunt et al. 1988, Davoren and Montevecchi 2003), yet feeding flocks are sometimes avoided (Irons 1998, Davoren and Burger 1999), likely because of interference competition from other foragers (Shealer and Burger 1993, Ballance et al. 1997, Maniscalco et al. 2001). However, the use of feeding flocks can also vary depending on prey type. Davoren and Burger (1999) found that rhinoceros auklets foraged in flocks when capturing small fish for self-feeding, but fed solitarily when capturing larger fish to feed their chicks. Similarly, kittiwakes in Prince William Sound fed more often in flocks when diets were dominated by young-of-year fish (Irons et al. 2000). In our analysis, we could not distinguish whether the greater number of feeding attempts was necessary for acquiring sufficient quantities of smaller YOY fish or a result of competition when using feeding flocks. In either case, our results help elucidate the causes of variation in duration of searching behavior and prey acquisition associated with different prey types.

Litzow and Piatt (2003) demonstrated that foraging time budgets of pigeon guillemots, a pursuit-diving piscivorous seabird, varied depending on whether their diet was dominated by abundant and lipid-rich schooling fishes vs. non-schooling fishes. When consuming the former (primarily sand lance), time spent foraging was less and discretionary time near the colony was more, typically resulting in greater breeding success. In the present study, we further demonstrate that even within the prey category of schooling forage fishes, differences among species and age classes can result in a nearly three-fold increase in search duration (Table 3.2) and a four- to eight-fold increase in the spatial scale of foraging for a surface-feeding seabird (Fig. 3.2). Depending on proximity of prey to the breeding colony, if sufficient buffers within time budgets do not exist, the increased time spent foraging will ultimately result in reduced brood-rearing success (Suryan et al. 2000, Litzow and Piatt 2003).

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Table 3.1. Tracking effort for black-legged kittiwakes rearing young at Eleanor Island, Prince William Sound, Alaska, 1995-1999. Data include: number of birds tracked and total number of tracks (some birds were tracked multiple times); date range of tracking effort; total number of feeding attempts; and number of tracks to the central islands (CI), barrier islands (BI), or to both locations (BO).

Year	# Birds	# Tracks	Track Period	# Feeding Attempts	# Tracks To		
					CI	BI	BO
1995	6	6	13 July – 9 Aug	35	6	0	0
1996	13	14	3 July – 8 Aug	117	8	5	1
1997	12	13	7 July – 4 Aug	246	4	6	3
1998	12	21	9 July – 5 Aug	318	19	1	1
1999	4	6	11 July – 20 July	110	2	4	0
Total	47	60	3 July – 9 Aug	826	39	16	5

Table 3.2. Time budgets and cumulative distance traveled (SE) for black-legged kittiwake foraging trips to the central islands, barrier islands, or both regions in Prince William Sound, Alaska, 1995-1999.

Destination ¹	Trip Dur. (hr)	Time Budgets (hr)				Dist. To Shore (km)	Trip Dist. (km)
		Travel	Search	Rest	Unk		
Central (<i>n</i> = 31)	2.37 (0.22)	0.81 (0.09)	0.88 (0.12)	0.56 (0.09)	0.14 (0.03)	0.58 ² (0.13)	38.0 (4.4)
Barrier (<i>n</i> = 15)	4.98 (0.45)	1.98 (0.20)	1.70 (0.33)	1.21 (0.28)	0.09 (0.05)	2.60 (0.57)	103.8 ³ (8.8)
Both (<i>n</i> = 5)	6.54 (1.39)	2.10 (0.19)	2.23 (0.60)	1.88 (0.76)	0.33 (0.24)	1.03 (0.46)	91.6 (11.5)

¹For multiple tracks of a single individual, tracks to different locations were treated as independent and not averaged. Therefore sample sizes differ in some cases compared to Table 3.1.

²*n* = 28

³*n* = 14

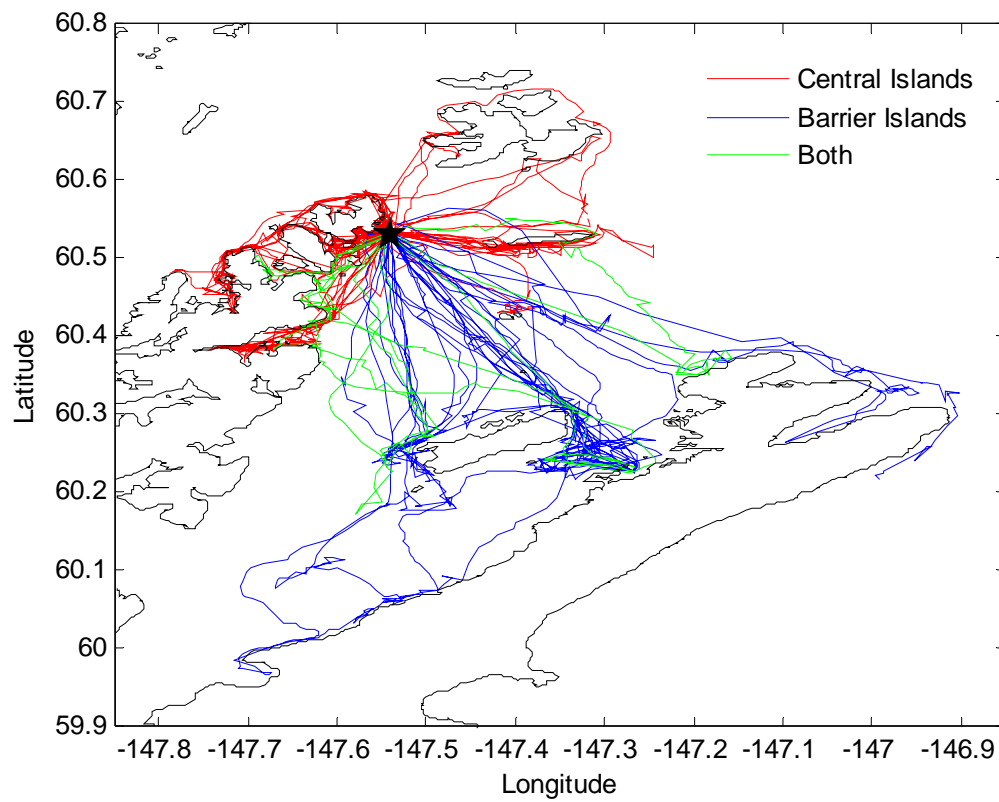


Figure 3.1. Tracks of black-legged kittiwake foraging trips from the Eleanor Island colony (★) to the central islands, barrier islands, or both destinations in Prince William Sound, Alaska, 1995-1999.

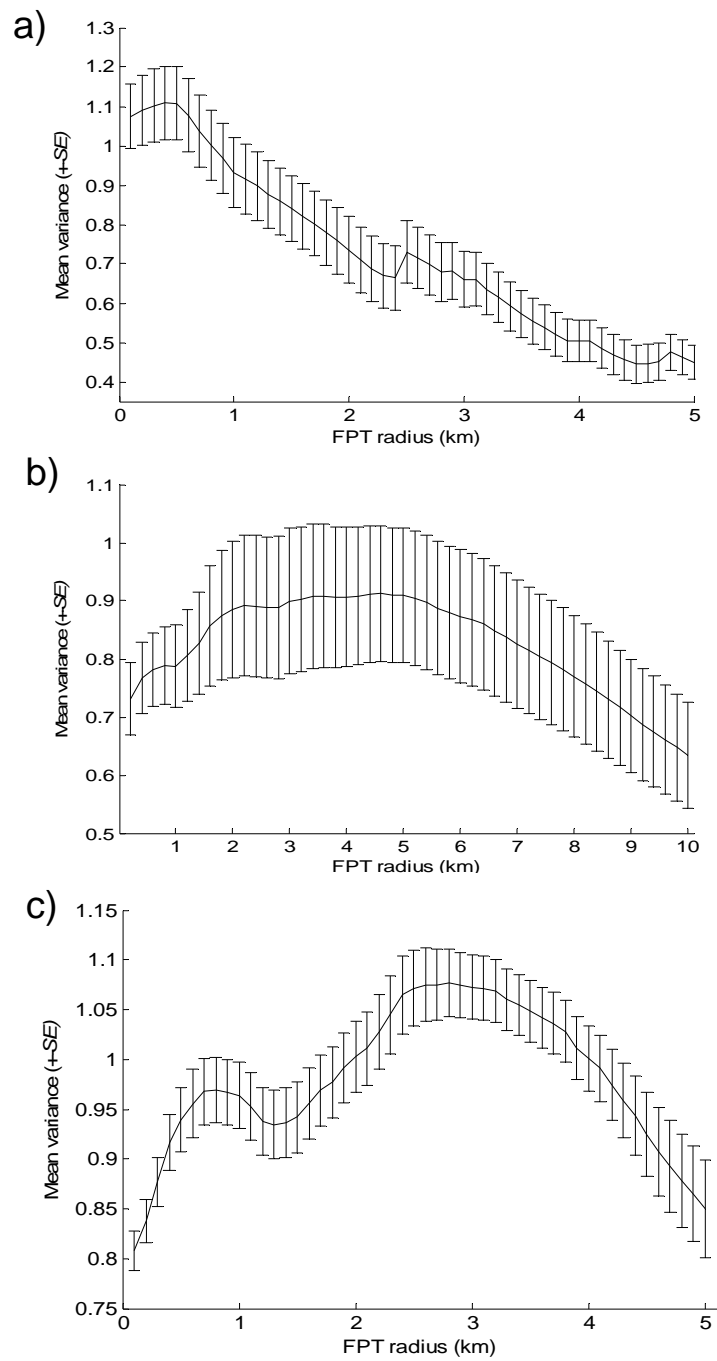


Figure 3.2. First-passage time analysis of black-legged kittiwake foraging trips where feeding occurred within the central islands (a), the barrier islands (b), or both (c).

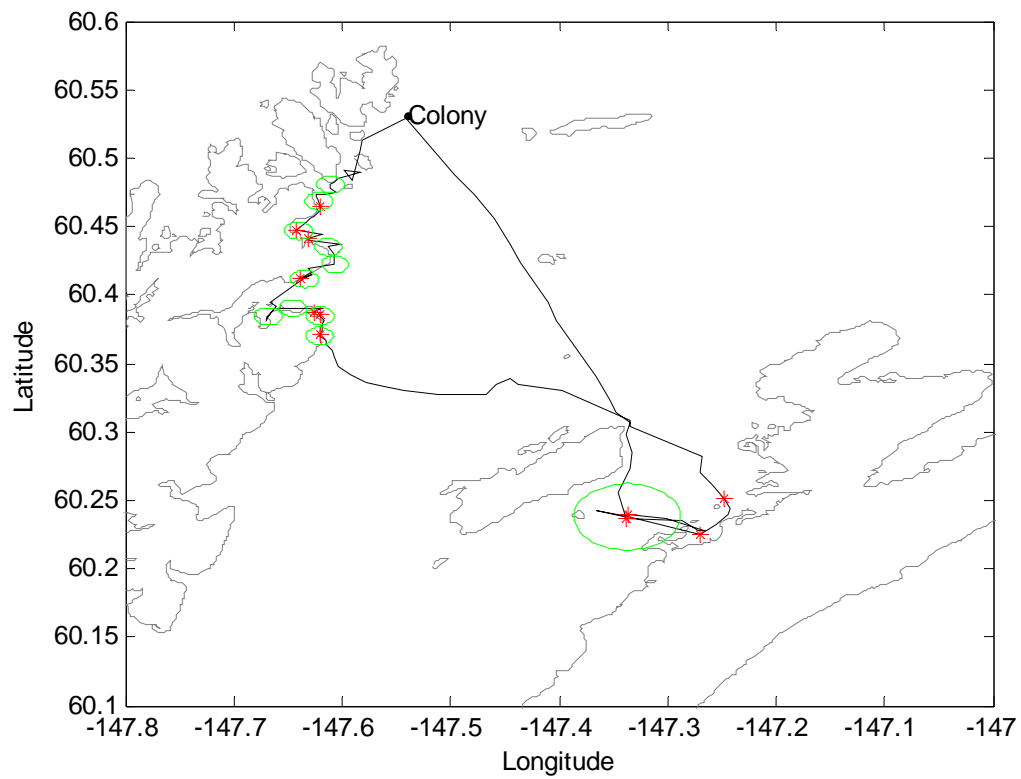


Figure 3.3. Track of a black-legged kittiwake showing feeding locations (*) and maximum first-passage time radii at the 0.7 km radius among the central islands and feeding locations and maximum FPT at 2.7 km radius among the barrier islands. Prey consumed during this foraging trip included Pacific herring, Pacific sand lance, and capelin.

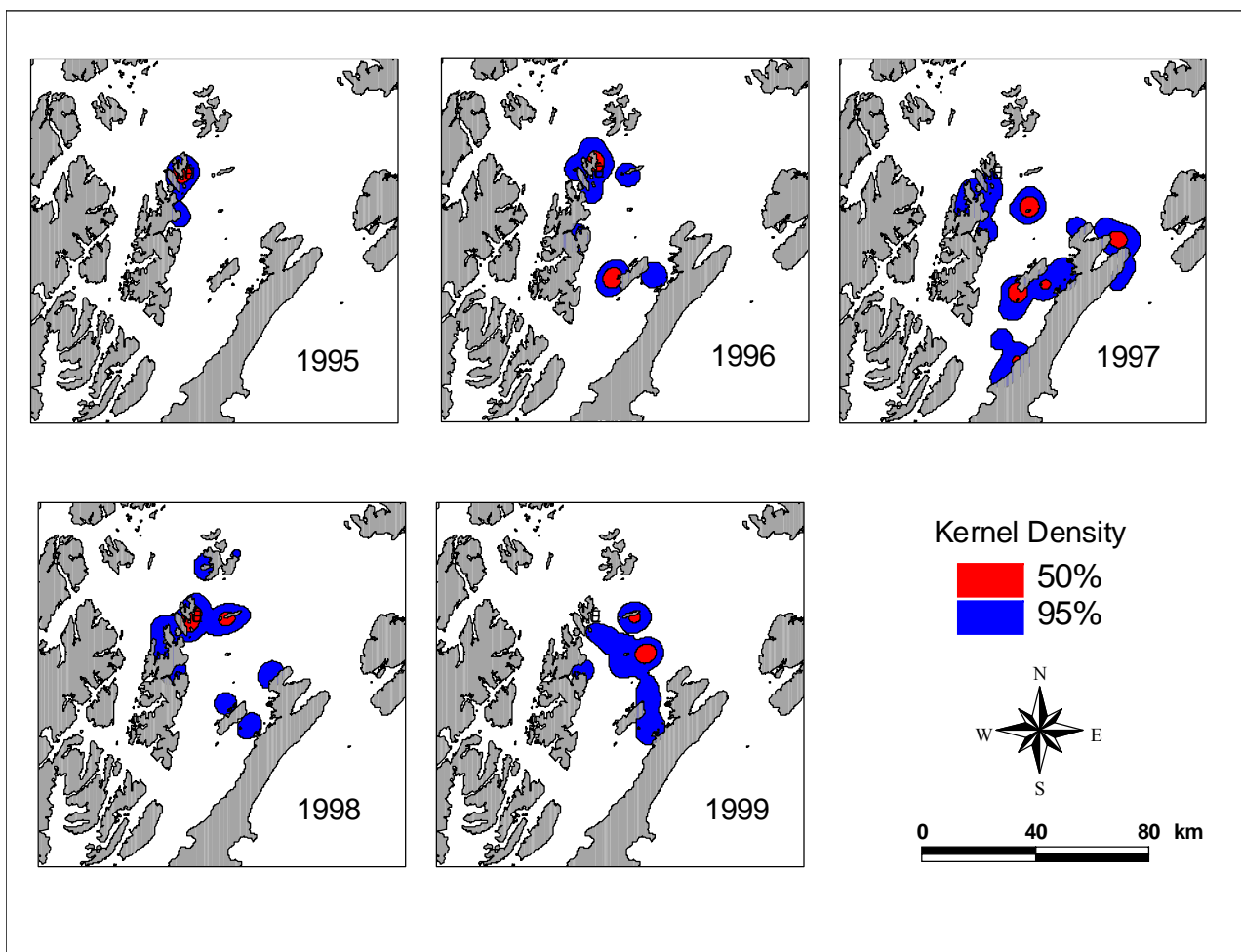


Figure 3.4. Kernel density plots of locations of feeding attempts for black-legged kittiwakes nesting at the Eleanor Island colony (★) in Prince William Sound, Alaska, 1995-1999.

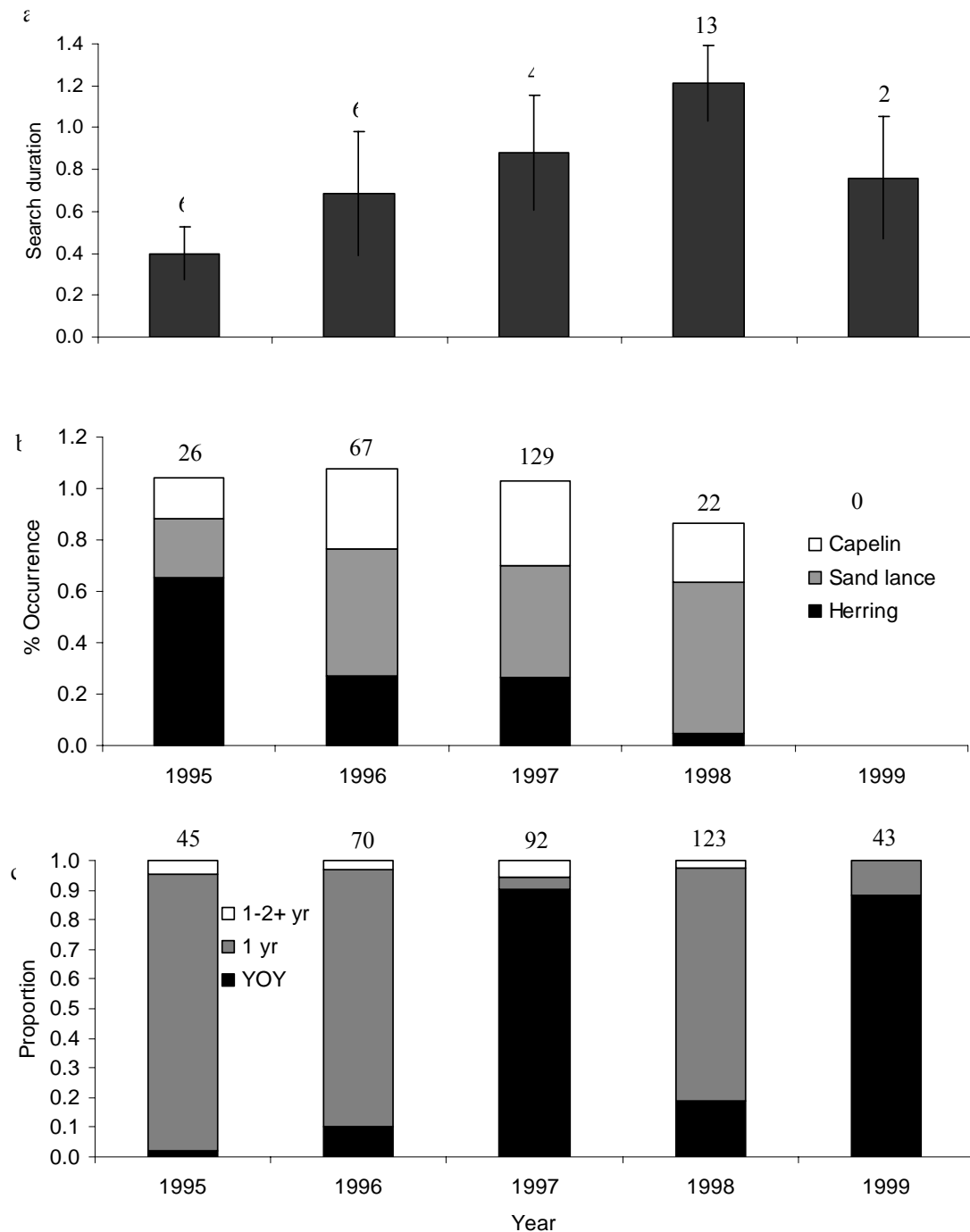


Figure 3.5. (a) Duration of search by year for black-legged kittiwake foraging trips to the central islands of Prince William Sound, Alaska, 1995-1999, (b) Percent occurrence of prey in diets of kittiwakes from Eleanor Island, and (c) age class of herring consumed by kittiwakes in Prince William Sound.

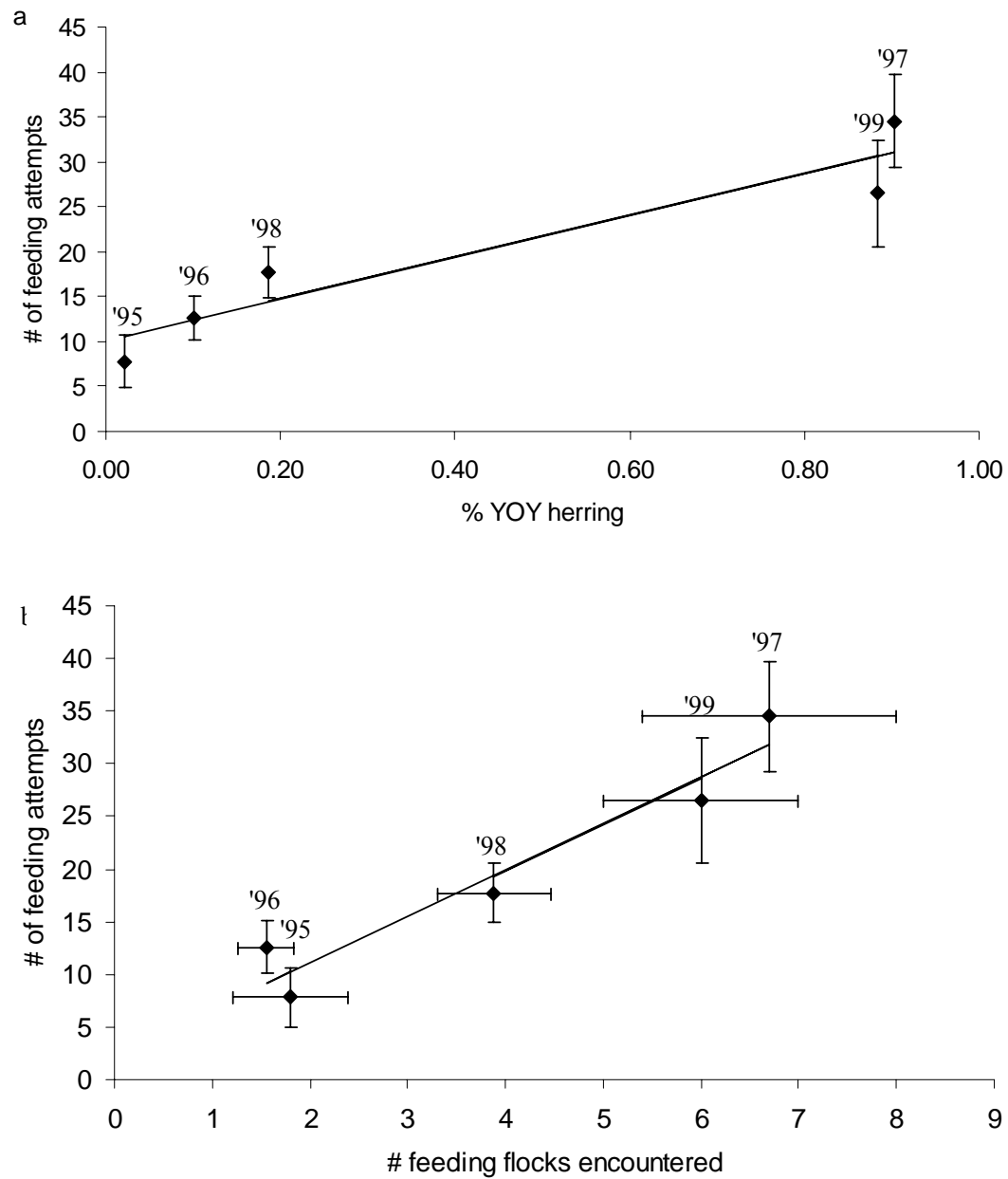


Figure 3.6. Mean (\pm SE) number of feeding attempts per foraging trip in relation to % of young-of-year herring in the diet (a) and the number of foraging flocks encountered (b) for kittiwakes at the Eleanor Island colony, Prince William Sound, Alaska, 1995-1999. Year is labeled above points.

Chapter 4. Foraging Destinations And Marine Habitat Use Of Short-Tailed Albatrosses: A Multi-Scale Approach Using First-Passage Time Analysis

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Key words: Bering Sea, Aleutian Islands, first-passage time, hot spots, multi-scale habitat use, Kuroshio-Oyashio Currents, satellite tracking, short-tailed albatross

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Abstract

We used satellite telemetry, remotely sensed data (bathymetry, chlorophyll *a* [chl *a*], sea surface temperature [SST], wind speed) and first-passage time (FPT) analysis to determine the distribution, movement patterns, and habitat associations of short-tailed albatrosses (*Phoebastria albatrus*) during the non-breeding season in 2002 and 2003. Satellite transmitters were deployed on birds immediately prior to their departure from a breeding colony at Torishima, Japan ($n = 11$), or at-sea in the Aleutian Islands ($n = 3$). Tracking durations ranged from 51 to 138 days for a total of 6,709 locations after filtering (131 – 808 per bird). FPT (time required to transit a circle of given radius) revealed the location and spatial scale of area-restricted search (ARS) patterns along flight paths. On average, ARS occurred within 70 km radii. Consequently, the fit of the habitat use models increased at spatial scales beyond a 40 km FPT radius ($R^2 = 0.31$) and stabilized for scales of 70 km and larger ($R^2 = 0.40 - 0.51$). At all scales, wind speed, depth or depth gradient, and chl *a* or chl *a* gradient had a significant effect on FPT (i.e., residence time). FPT increased within regions of higher gradients of depth and chl *a*. In contrast, FPT decreased within regions of greater depth and wind speed, with a significant interaction of wind speed and depth at some scales. Sea surface temperature or its interactions were only significant at large spatial scales (≥ 160 km FPT radius). Albatrosses engaged in ARS activities primarily over the shelf break and slope, including Kuroshio and Oyashio regions off the western subarctic gyre. Occasionally, birds transited the northern boundary of the Kuroshio Extension while in-route to the Aleutian Islands and Bering Sea, but overall spent little time in the western gyre. In the Aleutian Islands, ARS occurred within straits, particularly along the central and western part of the archipelago. In the Bering Sea, ARS occurred along the northern continental shelf break, the Kamchatka Current region, and east of the Commander Islands. Non-breeding short-tailed albatross concentrate foraging in oceanic areas characterized by gradients in topography and water column productivity. This study provides an understanding of the foraging ecology for a highly migratory, imperiled seabird, and confirms the importance of shelf

break and slope regions as hot spots for a variety of top marine predators in the North Pacific.

Introduction

The distribution of upper trophic-level consumers often reflects the patchy productivity of dynamic marine ecosystems, with the highest densities typically occurring within productive shelf-slope regions, coastal upwelling zones, regions of water mass convergence or divergence, and transition zones between current systems (Shuntov 1972, Gould and Piatt 1993, Springer et al. 1996a, 1999). The aggregation and behavior of upper trophic level consumers has, therefore, been proposed as proxies for identifying biological “hot spots”; regions of increased productivity and energy transfer through marine food webs. Apex consumers may be particularly useful bio-indicators because their occurrence reflects an integration of bio-physical processes resulting in the production of prey resources. Furthermore, because consumers require dense prey aggregations for efficient foraging (Piatt and Methven 1992, Fauchald and Erikstad 2002), their distributions can identify areas of elevated production and prey concentration (e.g., Ancel et al. 1992, Hunt et al. 1996).

On an ocean basin scale, this approach can be applied using satellite telemetry to track movements and remote sensing to identify habitat associations of far-ranging species such as albatrosses (Wilson et al. 2002). Albatrosses, like other pelagic predators, frequently seek out locations of physical and biological oceanographic features that enhance the availability of prey. Satellite tracking studies demonstrate that albatrosses will travel thousands of kilometers seeking hydrographic (e.g., polar frontal zone; Rodhouse et al. 1996) and bathymetric (e.g., Patagonian Shelf; Prince et al. 1997) features that characterize foraging hot spots. However, not all species or populations equally utilize similar oceanographic features and these differences are typically associated with the exploitation of distinct prey assemblages (Cherel et al. 2002, Hyrenbach et al. 2002, Waugh et al. 2002). It is, therefore, critical to consider species- or population-specific differences in interpreting the biological importance of a potential hot spot, as identified by apex consumers.

Other important considerations are how an animal is sampling the environment (e.g., actively searching for prey or simply traveling through the area) and the spatial and temporal scales of response (Hunt and Schneider 1987, Wiens 1989, Fauchald 1999, Fauchald et al. 2000). An analytical approach to address both of these concerns for animal tracking data is First-Passage Time (FPT) analysis (Johnson et al. 1992, Fauchald and Tveraa 2003). FPT is the time required for an individual to cross a circle of a given radius. When calculated for every location along an animal's path and for radii of varying size, this technique quantifies the spatial scales of area restricted search (ARS) patterns (highly tortuous movements associated with prey searching and foraging). FPT analysis should therefore be a precursor to modeling habitat use (e.g., Pinaud and Weimerskirch 2005). Herein, we apply a novel FPT approach to create habitat use models for a far-ranging marine predator, the short-tailed albatross (*Phoebastria albatrus*).

The short-tailed albatross inhabits the North Pacific Ocean above 20°N (Hasegawa and DeGange 1982, McDermond and Morgan 1993). Little is known about the at-sea distribution and migrations of this once abundant (> 1 million individuals), but now rare (~ 2,000 individuals) species that breeds on remote islands in Japan (Hasegawa and DeGange 1982, Sievert and Hasegawa, unpubl. data). Opportunistic sightings from shipboard observers (Hasegawa and DeGange 1982 and references therein, Piatt et al., this volume) indicate that short-tailed albatrosses primarily range along the continental shelf and slope regions of the North Pacific. Therefore, the main objectives of our study included: (1) to determine post-breeding season migration routes; (2) to identify an optimum spatial scale(s) to analyze short-tailed albatross habitat relationships; and (3) to quantify marine habitat affinities of short-tailed albatrosses. We present a novel technique to investigate resource selection as a multi-scale continuous process along a flight path, and construct the first habitat use models for this rare species.

Methods

Satellite telemetry

All short-tailed albatrosses were tracked during the post-breeding season, 8 May – 23 September 2002 and 7 May – 30 November 2003. We deployed satellite transmitters (Platform Transmitter Terminal, PTT) on albatrosses at two locations over a two-year period. During 6 – 10 May 2002 and 2003, 16 albatrosses were captured at the Tsubame-zaki breeding colony on Torishima (30° 28.3' N, 140° 18.6' E; Fig. 4.1), Izu Islands, Japan. In 2003, we captured four individuals at-sea in Segum Pass (52° 25.8' N, 172° 46.4' W; Fig. 4.1) Aleutian Islands, Alaska, between 12 and 17 August. The reproductive status of tagged birds was unknown; however, no birds returned to the colony during tracking. Fourteen transmitters provided long-term (>15 days) data considered herein. We determined ages of captured albatrosses from banding records (chick banding at Torishima began in 1977; H. Hasegawa, unpublished data) and gender from blood samples (Fridolfsson and Ellegren 1999).

We attached satellite transmitters to the dorsal feathers of albatrosses with either adhesive tape (#4651, Tesa Tape, Inc.) or Velcro[®] tape and epoxy. Several models of PTTs were used (Table 4.1) and all weighed 35 - 100 g, < 2.5 % of the animal's body mass. All PTTs were programmed to operate on a duty cycle (Table 4.1) and to transmit at a 75- or 90-s repetition rate.

Satellite-derived position fixes of PTTs were provided through the Argos system (Service Argos, Inc.). Argos assigns each position a location quality code ranging from level 3, the most accurate (< 150 m radius), to level B, in which accuracy is unknown. Therefore, we applied a filtering algorithm (prepared by David Douglas, USGS, Alaska Science Center, Juneau, Alaska, USA) to the data. First, we retained all level 3 positions. Other locations were evaluated for filtering based on a maximum speed cut-off of 80 km h⁻¹ (a prominent break in the frequency distribution of movement rates between consecutive level 3 locations) and a minimum redundant distance of 1 km (≥ 2 consecutive locations ≤ 1 km apart were retained). These filtering procedures are similar to those previously employed by other investigators (Hyrenbach et al. 2002,

Austin et al. 2003) and retained 86% (6,709) of all locations obtained. When this filtering algorithm was applied to data from stationary PTTs ($n = 11$), the average accuracy was < 1.2 km ($SE = 0.66$) for LQCs 3 - A and < 7.1 km ($SE = 15.3$) for B fixes. Thus, we believe the resolution of our filtered locations was sufficient to analyze movement paths and habitat associations at spatial scales considered herein.

First-passage time analysis

In calculating FPT, we first linearly interpolated each albatross track at 5 km intervals while retaining original locations. We included the ≤ 24 hr PTT off-cycle when interpolating because FPT was often much greater than 8 hrs (days to weeks in some cases, especially at larger spatial scales). We calculated FPT at every location along the track of each albatross for radii ranging from 5 km to 500 km by 5 km increments. Next, we plotted variance in FPT (log transformed) for each individual and a mean across individuals vs. radii to ascertain the peak, or dominant spatial scale of ARS (Fauchald and Tveraa 2003). The variance peak identifies which spatial scale is best to differentiate high (ARS) vs low (transitory) passage times.

FPT analysis permitted a multi-scale analysis of habitat use, whereby FPT for any given location could be associated with habitat variables at various spatial scales (within radii of varying size). However, because FPT analysis produces results for overlapping radii along a track, we developed a two-stage approach to subsample the FPT data for habitat analysis, and thereby reducing spatial autocorrelation. First, we used only the original (not interpolated) locations to address habitat associations. Second, we selected the location of maximum FPT for a given radius and excluded all other locations with overlapping radii (within 2X the radial distance from that location), and then searched for the maximum FPT (most intense ARS) among the remaining locations. This iterative approach was repeated until the entire track had been subsampled such that none of the radii overlapped (Fig. 4.2). The outcome of these subsampling iterations was a range of possible FPTs for any given individual, including the less tortuous portions of the flight path (lower FPT). As FPT radius increases, the sample size (n) and range of FPT values decreased with this subsampling procedure.

We then analyzed the habitat characteristics within the various radii from the subsampled points, using the FPT metric as a continuous response variable.

Marine habitats

We selected 7 variables to characterize marine habitats; seafloor depth, chlorophyll *a* concentration (chl *a*), sea surface temperature (SST), gradients in these 3 variables, and wind speed. Depth was obtained from the General Bathymetric Chart of the Oceans (British Oceanographic Data Centre, www.bodc.ac.uk). We used a grid of 5 min latitude and longitude resolution (~ 8 km). We defined bathymetric domains as: continental shelf (≤ 200 m depth), shelf break (> 200 m and ≤ 1000 m), slope (> 1000 m and ≤ 3000 m), and oceanic (> 3000 m). Chl *a* concentration (mg m^{-3}) was obtained from Moderate Resolution Imaging Spectroradiometer Terra imagery (level 3 post processing) provided by the Physical Oceanographic Data Archiving and Acquisition Center (NASA Jet Propulsion Laboratory, <http://podaac.jpl.nasa.gov>). We used a ~ 4 -km spatial resolution for chl *a*, and monthly composites to compensate for frequent cloud cover. We obtained SST from the same source as chl *a* imagery and of the same spatial resolution. However, we were able to use a finer temporal resolution of 8-day composites. As a proxy for frontal boundaries, we calculated gradients in SST, chl *a*, and depth over distance (3 X 3 pixel) using the Sobel Gradient Operator (Russ 1995).

We obtained QuikSCAT ocean wind data for 10 m above the ocean surface from the SeaWinds sensor aboard the QuikBird satellite. These data were obtained from Remote Sensing Systems (www.remss.com; sponsored by the NASA Ocean Vector Winds Science Team) and provided in a global coverage of 0.25 degree latitude / longitude (~ 23 km) spatial resolution grids of wind speed (m s^{-1}), direction, and a binary rain flag. We used a temporal resolution of three day averages, and removed erroneous data affected by rainfall.

Albatross habitat associations

In our multi-scale analysis of albatross habitat associations, we used a lower threshold of ~ 20 km spatial scale (10 km FPT radius); because this was the coarsest

resolution of the habitat data. The upper limit was constrained by sampling limitations: as FPT radius increased, sample size is diminished. For each subsampled FPT location along a track, we extracted median values (to reduce the influence of outliers) of each habitat variable, including gradients, within areas of different radii. When FPT in a given area was greater than ~ 1.5 times the temporal resolution of a particular environmental coverage, we time-averaged multiple consecutive files within the given FPT radius. For example, if FPT was 16 days at a search radius of 160 km, we extracted the median from a single chl *a* file (monthly composite) within the radius, but extracted the median from two SST files (8-day composite) and 5 wind speed files (3-day composite).

Statistical analyses

We used mixed effects linear models (SAS 1990) with FPT as the response variable to assess habitat affinities. Individual albatross was included as a random effect in all models, whereas habitat variables (chl *a*, SST, depth and their gradients, wind speed, and interactions) were fixed effects and retained only if they improved model fit. We did not include sex or age variables in the models because of limited sample sizes. We used Akaike's Information Criteria (AIC) to identify the most parsimonious model (Burnham and Anderson 1998). For competing models with a $\Delta AIC < 2$, we selected the model with the least number of parameters. All possible combinations of main effects and interactions were considered. All variables were visually tested for normality using normal probability plots; FPT and depth were the only variables requiring transformation [$y = \ln(x + 1)$]. All model residuals were examined for secular (i.e., linear) or periodic (i.e., cyclic) signals and evaluated with autocorrelation metrics (Priestley 1982). Remote sensing data processing and FPT analyses were conducted with custom programs using Matlab software (The MathWorks, Inc.).

Results

Albatross migration and movements

The ages of 11 of 14 albatrosses (three were unbanded) tracked during this study ranged from < 1 yr to 18 yrs, with an unequal sex ratio of 9 males to 4 females, and one individual of undetermined gender. The three youngest albatrosses (≤ 2 yr) were males captured in the Aleutian Islands (Table 4.1). Deployment durations ranged from 51 to 138 days. After filtering, we obtained ~ 5 locations per individual per day ($\bar{X} = 5.3$, $SE = 0.45$, range = 2.6 – 8.3, $n = 14$ PTTs).

Albatrosses tracked from Torishima ($n = 11$) initially traveled north within the Kuroshio Current system (Fig. 4.1). From here, however, two different migration patterns were observed: 6 individuals remained within the coastal realm, while the five others traveled offshore and northeast to the western Aleutian shelf. There was a notable difference in the at-sea distribution and movement patterns of individuals captured at Seguam Pass and Torishima (Fig. 4.1). Seguam Pass birds ranged much more widely, venturing into coastal waters of the western Bering Sea and California Current. Indeed, the < 1 yr old birds captured in Seguam Pass traveled nearly twice the distance per day ($\bar{X} = 245 \pm 8$ km d⁻¹) than older albatrosses ($\bar{X} = 133 \pm 8$ km d⁻¹; Table 4.1).

The peak in variance of FPT among all individuals occurred at a search radius of 70 km (Fig. 4.3). However, as evidenced by the dispersion about the mean, there was considerable variability among individuals in scale of interaction with the environment. A comparison of albatrosses B0899 and A1181 illustrates these differences. Upon leaving Torishima, albatross B0899 took a direct route to the western Aleutian Islands, where his flight path became highly tortuous within a consistent spatial scale (Fig. 4.4a), thus producing a narrow peak in FPT variance at 70 km (Fig. 4.4b). In contrast, albatross A1181 exhibited ARS patterns within two different regions and at greater spatial scales (Fig. 4.4a), producing a broader peak in FPT variance and at a much larger radius (230 km) than albatross B0899 (Fig. 4.4b). The radius of maximum FPT variance was not related to the total number of PTT locations ($R^2 < 0.12$, $P < 1.59$, $n =$

14, $P = 0.23$) or to the mean number of locations per day ($R^2 < 0.07$, $n = 14$, $P = 0.35$). Therefore, differences in the spatial scale of ARS among individuals were not merely artifacts of variability in PTT performance and deployment lengths.

Variability in the scale of ARS was also evident within a given movement path, as exemplified by albatross A0837. For this individual, small-scale and large-scale ARS occurred in different regions, although large-scale ARS sometimes encompassed regions of small-scale ARS (Fig. 4.5). To assess the effect of variation in ARS scales on habitat associations, we constructed models of habitat use for 8 FPT radii (10-220 km, at 30-km increments). Mean (range, n) FPT varied from 0.30 days (0.01-3.1, 931) for 10 km radius to 7.3 days (0.44-56.6, 113) for 220 km radius.

Albatross habitat associations

Our most parsimonious models included wind speed, depth (median or gradient), and chl a (median or gradient) as highly significant variables at all spatial scales (Table 4.2). There was a positive relationship between FPT and depth gradient and chl a gradient. The relationship between FPT and chl a was positive at the smallest spatial scale (10 km), but negative at larger scales (≥ 160 km; Table 4.2). FPT was inversely related to water depth and wind speed. SST was only a significant model component at two of the larger spatial scales (Table 4.2). Interactive effects of habitat variables on FPT included depth*depth gradient at 10 km, wind speed*depth at 70 km and 160 km, and chl a *SST and chl a gradient*SST at the 160 km search radii.

Model fit was lowest at the 10 km and 40 km FPT radii ($R^2 = 0.30$ and 0.31 , respectively), improved for 70 km ($R^2 = 0.40$), and stabilized at $R^2 < 0.51$ for larger FPT radii (Table 4.2). Because of changes in FPT variance, number of model parameters, and n , R^2 values are not directly comparable. However, this trend was consistent when holding the number of parameters constant and despite decreases in sample size at larger scales. The improvement in model fit for the 70 km FPT radii coincides with the peak variance in FPT (Fig. 4.3), indicating that habitats measured at this spatial scale explained more variance in FPT. Graphically, the improved fit of a 70 km FPT radius model over a 10 km model is exemplified by the ARS behavior for

albatross B2493 (Fig. 4.2). Therefore, the remaining results focus on the 70 km FPT spatial scale.

Among the bathymetric domains, FPT was greatest within continental shelf break and slope regions, compared to shelf and oceanic waters (Fig. 4.6a) and generally increased within regions of greater bathymetric gradients (Fig. 4.7a). FPT was higher in waters of greater chl *a* concentrations (Fig. 4.6b) and chl *a* gradients (Fig. 4.7b), suggesting the birds followed a more contorted path within elevated productivity regions. In contrast, we detected a negative effect of wind speed on FPT, with the greatest values at the lowest wind speeds $< 5 \text{ m s}^{-1}$ (Fig. 4.6c). FPT showed no consistent trend with respect to SST (Fig. 4.6d) or gradient (Fig. 4.7c), except that FPT was shorter and less variable within the higher SST bin ($> 15^\circ\text{C}$). These results are supported by variables retained and their coefficients from the statistical modeling (Table 4.2). Our search-radius dependent subsampling procedure for FPT locations was successful in reducing autocorrelation in the response variable. Autocorrelation was low ($r < 0.20$) and attempts to model it (using harmonic terms) offered little improvement in overall fit, likely because periodicity was highly irregular within and among individuals at the various FPT radii (e.g., Fig. 4.4).

Chl *a* was greatest over the shelf ($\bar{X} = 1.44$, $SE = 0.23$) and declined linearly to oceanic waters ($\bar{X} = 0.73$, $SE = 0.06$). Areas of greatest concentrated search activity for albatrosses (identified as the upper quartile of FPT, 70 km radius) sometimes coincided with persistent chl *a* hot spots, particularly off the northeast coast of Japan, the Kuril Islands, Aleutian Islands, and southeastern Bering Sea shelf (Fig. 4.8). The Kuroshio Extension was not a prominent feature used by short-tailed albatrosses during their post-breeding season migration from Torishima. In May, some birds crossed the northern part of this region, especially those that moved northeast over oceanic waters when transiting to the Aleutian Islands (Fig. 4.9). However, these birds engaged in limited ARS behavior in this region (Fig. 4.8), as evidenced by the small FPT values along this portion of their tracks.

Discussion

Marine habitats

Bathymetric relief (e.g., banks, shelf-breaks) and hydrographic fronts (e.g., eddies, tidal fronts) are commonly associated with productivity hot spots. As such, these features are commonly sought by many foraging seabirds, including albatrosses (Hunt et al. 1996, Rodhouse et al. 1996, Hyrenbach et al. 2002, Yen et al. 2004). Our results suggest that during spring and summer (May – July) surface chl *a* standing stocks are greatest on the shelf and progressively decline with increasing water depth, with few exceptions depending on month. Primary production alone, however, does not explain short-tailed albatross hot spots, as areas of foraging do not always coincide with regions of greatest chl *a* (Fig. 4.8). This may be explained, in part, by time lags between increased primary productivity and associated increased availability of albatross prey, but also by habitat preferences of prey species consumed (Rodhouse et al. 1996, Waugh et al. 1999, Cherel et al. 2000).

What little information exists on short-tailed albatross diets comes exclusively from the breeding season and suggests that squids, crustaceans, and fishes are important prey (Hattori 1889, Hasegawa and DeGange 1982). The Japanese common squid, *Todarodes pacificus* (formerly *Ommastrephes sloani pacificus*), was a common diet item (Hattori 1889) for short-tailed albatrosses and is common, although variable in abundance, off Japan (Sakurai et al. 2000, Mokrin et al. 2002). *T. pacificus* is particularly abundant within the Kuroshio-Oyashio transition zone west of 160° E longitude (Mori et al. 2002), a region that was visited by all albatrosses tracked from Torishima. In the Bering Sea, midwater squid concentrations (primarily *Berryteuthis magister*, *Gonatopsis borealis* in the upper layer, 200 – 500 m) were greatest near the outer continental shelf and slope, with the standing stocks in these regions comprising one quarter of the mesopelagic squid biomass in the western Bering Sea (Sinclair et al. 1999). Midwater prey become available to albatrosses through: (1) scavenging on discards from subsurface predators and fisheries, (2) post-mortem individuals that are positively buoyant, and (3) vertical migration (Lipinski and Jackson 1989, Croxall et al.

1994). Therefore, the distribution of squids provides a plausible explanation for the association of short-tailed albatrosses with shelf break and slope regions, which are habitats frequented by other seabird species known to exploit similar niches (e.g., northern fulmar, *Fulmarus glacialis*; Shuntov 1972, Springer et al. 1999).

Wind speed is an important determinant of marine bird distributions at a variety of spatial scales (Spear and Ainley 1998, Spruzen and Woehler 2002). Our results underscore the significance of wind speed as an important habitat variable influencing short-tailed albatross movement patterns. The negative relationship between FPT and wind speed and interaction between wind speed and depth suggest that foraging albatrosses “trapped” by low winds slow down their progress, giving rise to tracks potentially indicative of ARS behavior. This is evident in Fig. 4.2a, with one of the upper 50 percentile locations showing little ARS activity, despite having a long FPT. This result is consistent with prior evidence that albatrosses will travel shorter distances and fly slower during high pressure conditions (Jouventin and Weimerskirch 1990), and they seem to concentrate in areas of low wind conditions (Spruzen and Woehler 2002). Thus, when attempting to define key foraging areas from residency time alone, it is important to also consider wind speed (e.g., Fig. 4.8a,b).

Hot spots

Our telemetry data demonstrate that short-tailed albatrosses did not disperse widely throughout the subarctic North Pacific and are consistent with infrequent ship-based observations in the gyres (Sanger 1972, McDermond and Morgan 1993). The primary hot spots for short-tailed albatrosses in the Northwest Pacific Ocean and Bering Sea occur where a variety of underlying physical processes enhance biological productivity or prey aggregations. Upon departing Torishima, all the tagged albatrosses traveled to the outer continental shelf off northeast Honshu, a convergence region of the Kuroshio and Oyashio currents, with some influence of the Tsugaru warm current (Qu et al. 2001, Shimizu et al. 2001, Qiu 2002). Albatross activity in this boundary region (36° – 40° N) was greatest in May and June along the shelf break. Primary production in this region was evident in chl *a* imagery for May and June, but it was not persistent

through the remaining study months. However, the northern convergence region to the east of northern Japan and the southern Kuril Islands was evident as a persistent chl *a* hot spot (Fig. 8) and a region of extensive use by albatrosses (Fig. 4.9). Such turbulent mixing and eddy formation within the Kuroshio and Oyashio convergence region extends into the western central gyre (Qu et al. 2001, Shimizu et al. 2001, Qiu 2002). However in our study, albatrosses made mainly transitory excursions along the northern boundary of the Kuroshio Extension and Oyashio Front while in-route to the Aleutian Islands and Bering Sea. It is intriguing that the satellite-tracked albatrosses did not venture into the sub-arctic gyre or forage along the Transition Domain, like other North Pacific pelagic predators including species known also to feed on squid, such as Dall's porpoises (*Phocoenoides dalli*), sperm whales (*Physeter catodon*), fur seals (*Callorhinus ursinus*), and Laysan albatrosses (*P. immutabilis*; Springer et al. 1999, Hyrenbach et al. 2002, Ream et al. 2005).

The Aleutian Islands, in particular, were a primary foraging destination for short-tailed albatrosses, with the maximum FPT for eight of the 14 birds occurring in this region. Passes within the Aleutian Islands with the greatest albatross ARS activity included Near, Buldir, Shumagin, and Seguam. Currents flowing through these relatively narrow and shallow passes cause localized upwelling, frontal zone formation, and eddies that enhance mixing, nutrient supply, and productivity (Shuntov 1993, Reed and Stabeno 1994, Lapshina 1996, Coyle et al. 1998). The significance of passes as feeding zones for breeding and migratory seabirds, is well documented (Springer et al. 1996b, Hunt et al. 1998) and their use by short-tailed albatrosses have been described from ship-based observations (Piatt et al., this volume) and historically by their prevalence in middens of native Aleut communities (Yesner 1976).

Within the Bering Sea, short-tailed albatross locations were most associated with the shelf break and slope, excursions over deeper water were typically transitory. The Bering Sea shelf break and slope and associated currents are well defined features of enhanced productivity and use by upper trophic level predators (Shuntov 1972, Springer et al. 1999, Robson et al. 2004). The intrusion of the Alaska Stream through the Aleutian Islands creates an along shelf current (Stabeno and Reed 1991, 1994) that

fuels elevated primary productivity, particularly in the early spring. The few excursions of albatrosses onto the Bering Sea shelf occurred in the region south of St. Matthew Island and in the southeast, both areas where frontal zones commonly occur (Hunt 1997, Belkin 2003). The fact that short-tailed albatrosses spent little time in the central Bering Sea is consistent with ship-based observations indicating low seabird densities over deeper waters of the central Bering Sea (Shuntov 1972, Wahl et al. 1989, Springer et al. 1999).

The scale of habitat associations and first-passage time analysis

Identifying the spatial and temporal scales at which animals respond to environmental cues is a central issue in ecology (Fauchald 1999, Fauchald et al. 2000, Schneider 2001). Our results confirm the use of FPT as a valuable analytical tool for identifying the spatial scales of foraging activities and habitat associations of continuously tracked, free-ranging animals. Habitat use models at a scale of 70 km search radius best explained variation in FPT of short-tailed albatrosses. Previous studies have documented strong seabird–habitat associations over 10s km, both in the sub-arctic North Pacific and the Bering Sea (Schneider 1991, Gould and Piatt 1993). The prevalence of spatial patterns over intermediate scales (e.g., shelf-breaks, frontal systems) may partly explain why our finer scale models (10 km and 40 km search radius) explained less variation in short-tailed albatross habitat associations (Table 4.2). It also is important to consider how the resolution of sampling instruments can affect these scale-dependent patterns; for example, a mean of 5 locations per animal-day obtained in this study vs. global positioning system receivers that provide up to tens of thousands of locations per day (Weimerskirch et al. 2002, Fritz et al. 2003). Nevertheless, FPT identified appropriate spatial scales for our application, which we used to create general habitat use models capable of explaining half of the variation in short-tailed albatross movements. These results are particularly encouraging given that we did not include other variables such as prey distribution and occurrence of fishing vessels, which are known to attract short-tailed albatrosses.

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Table 4.1. Summary of satellite tracking data for 14 short-tailed albatrosses tagged at Torishima, Japan, and Seguam Pass, Alaska, following the breeding seasons in 2002 and 2003.

Animal ID ^a	Gender	Age (yrs)	# Days Tracked	# Filtered Locations	Minimum Distance Traveled (km)	Deployment Date
Torishima						
B0963 ^{b,d}	F	-- ^h	104	664	11,732	10 May 2003
A0837 ^{c,e}	F	9	101	680	9,525	6 May 2003
A1034 ^{b,d}	F	6	113	634	13,661	6 May 2003
A1076 ^{c,e}	F	5	138	369	14,303	7 May 2002
B0899 ^{b,d}	M	-- ^h	54	400	8,454	6 May 2003
B0900 ^{b,d}	M	-- ^h	87	483	14,205	10 May 2003
B0962 ^{c,e}	M	18	74	437	9,749	10 May 2003
A1181 ^{b,d}	M	4	86	279	15,364	7 May 2002
A1311 ^{b,d}	M	4	51	131	5,869	10 May 2003
A1281 ^{c,f}	M	3	81	375	9,621	7 May 2002
A1291 ^{b,d}	--	3	120	427	16,863	7 May 2002
Seguam Pass						
A7040 ^{b,g}	M	2	81	513	13,264	17 August 2003
B2428 ^{b,d}	M	< 1	110	509	27,814	12 August 2003
B2493 ^{b,d}	M	< 1	102	808	24,251	12 August 2003

^aActual band # is preceded by 13, e.g., 13A0837.

^{b,c}Duty cycle: (b) 8 hr on and 24 hr off, (c) 6 hr on and 18 hr off.

^{d,e,f,g}Satellite transmitter brand: (d) Sirtrack, (e) Toyocom, (f) North Star, (g) Microwave Telemetry

^hUnbanded individuals, but all had adult plumage (≥ 8 yr old).

Table 4.2. Results from mixed effects linear models of the effect of marine habitat variables on first-passage time (FPT) for short-tailed albatrosses. Analyses were conducted for eight spatial scales (FPT radii) of 10 to 220 km, in 30-km increments, and results of four final models are presented (10-, 70-, 160-, and 220-km radii). Individual was included in all models as a random effect. Environmental variables of seafloor depth (log transformed), wind speed (wspd), chlorophyll *a* (chl), sea surface temperature (SST), plus gradients (g) of each (except wspd) and selected interactions^a were evaluated as fixed effects. ΔAIC is the change in Akaike's information criterion between the final and next best models. R^2 was calculated from log-likelihood ratios following Magee (1990).

Variable	10 km $R^2 = 0.30, n = 775,$ $\Delta AIC = 4.6$			70 km $R^2 = 0.40, n = 304,$ $\Delta AIC = 2.0$			160 km $R^2 = 0.51, n = 140,$ $\Delta AIC = 7.7$			220 km $R^2 = 0.49, n = 104,$ $\Delta AIC = 3.5$		
	β	<i>t</i>	<i>P</i>	β	<i>t</i>	<i>P</i>	β	<i>t</i>	<i>P</i>	β	<i>t</i>	<i>P</i>
wspd	-0.088	-6.78	<0.001	-0.660	-4.94	<0.001	-0.758	-2.98	0.004	-0.162	-3.89	<0.001
depth	-0.152	-4.84	<0.001	-0.907	-6.27	<0.001	-0.931	-3.23	0.002	-0.373	-3.63	<0.001
depthg	16.195	2.12	0.035	11.210	4.11	<0.001	27.846	5.04	<0.001	29.916	3.69	<0.001
chl	0.138	2.58	0.010				-1.557	-2.57	0.011	-2.131	-2.30	0.024
chlg				3.731	1.62	0.107	50.973	4.90	<0.001	50.877	3.02	0.003
SST							0.001	0.04	0.966	-0.008	-0.20	0.841
wspd*depth				0.066	3.88	<0.001	0.076	2.36	0.020			
depth*depthg	-1.666	-1.66	0.098									
chl*SST							0.217	3.28	0.001	0.238	2.38	0.020
chlg*SST							-5.984	-3.66	<0.001	-4.842	-1.76	0.082

^aInteractions tested: wspd*depth, wspd*chl, wspd*SST, SST*chl, SSTgrad*chl, SSTgrad*depth, chlgrad*depth, depthgrad*chl, depthgrad*SST, depthgrad*depth.

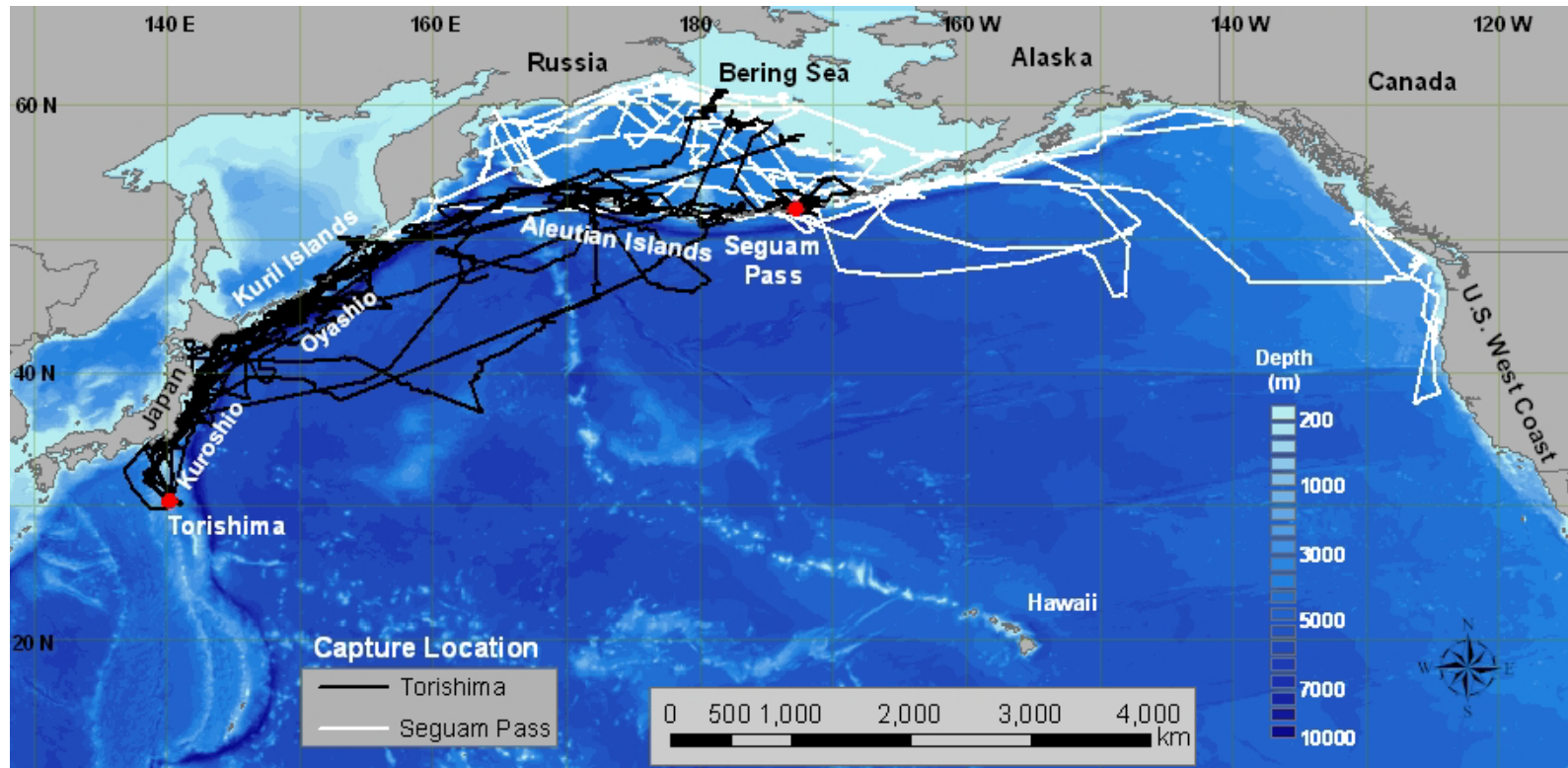


Figure 4.1. Flight paths of short-tailed albatrosses satellite-tracked from the breeding colony on Torishima, Japan ($n = 11$) and Seguam Pass, Alaska ($n = 3$, captured at-sea). Individuals were tracked May - November 2002 and 2003.

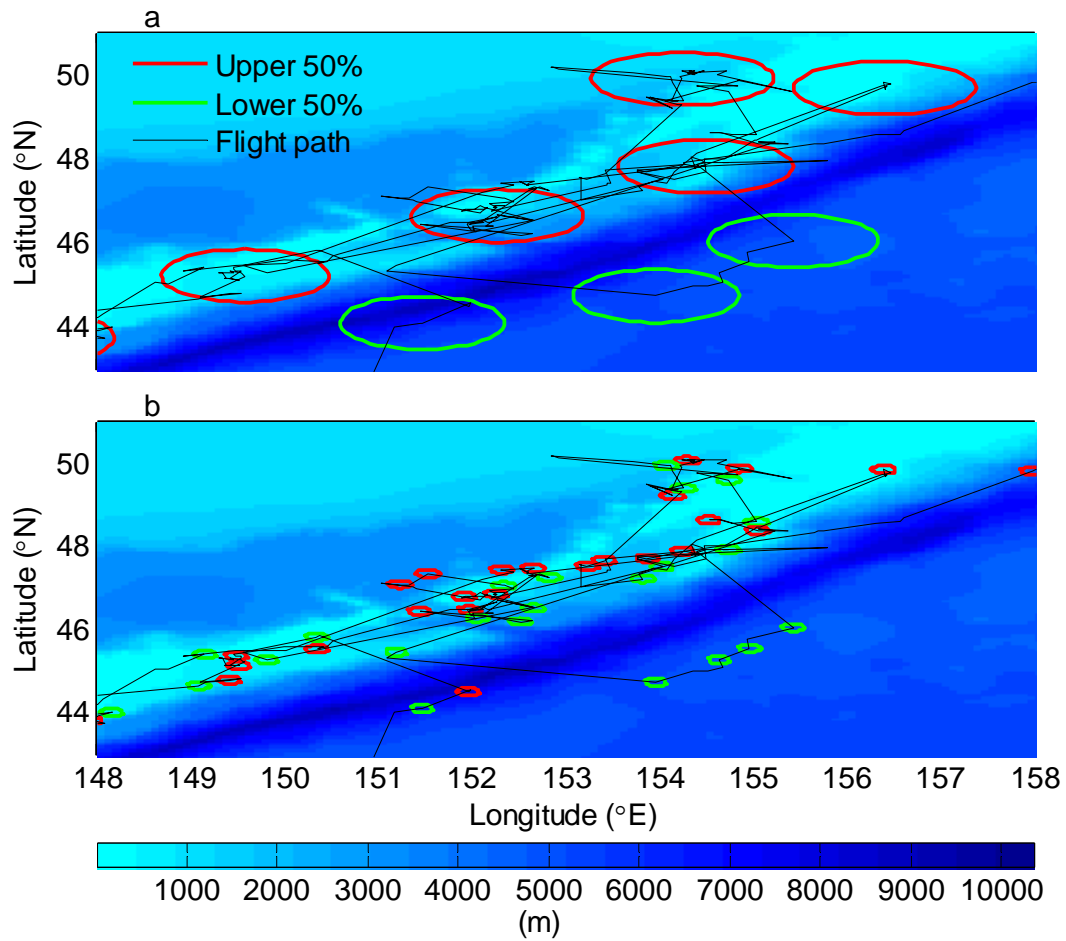


Figure 4.2. Locations and first-passage time (FPT) radii for a portion of the flight path of short-tailed albatross B2493, superimposed over a map of sea floor depth near the Kuril Islands, Russia. Regions of area-restricted search vs. more transitory movements are signified by longer (upper 50 %) and shorter (lower 50 %) FPT, respectively, for spatial scales of 70 km (a) and 10 km (b) radii.

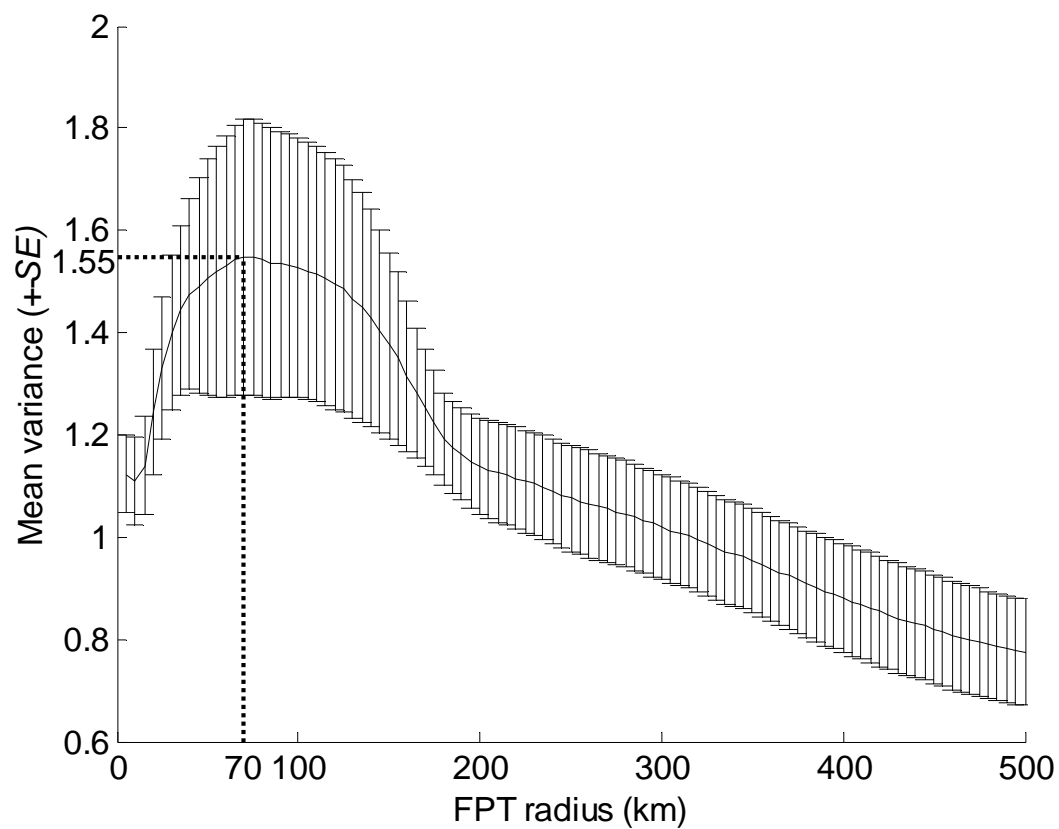


Figure 4.3. Mean variance ($\pm SE$) in log-transformed first-passage time (FPT) vs. FPT radius for 14 satellite-tracked short-tailed albatrosses. The peak in variance occurred at a search radius of 70 km.

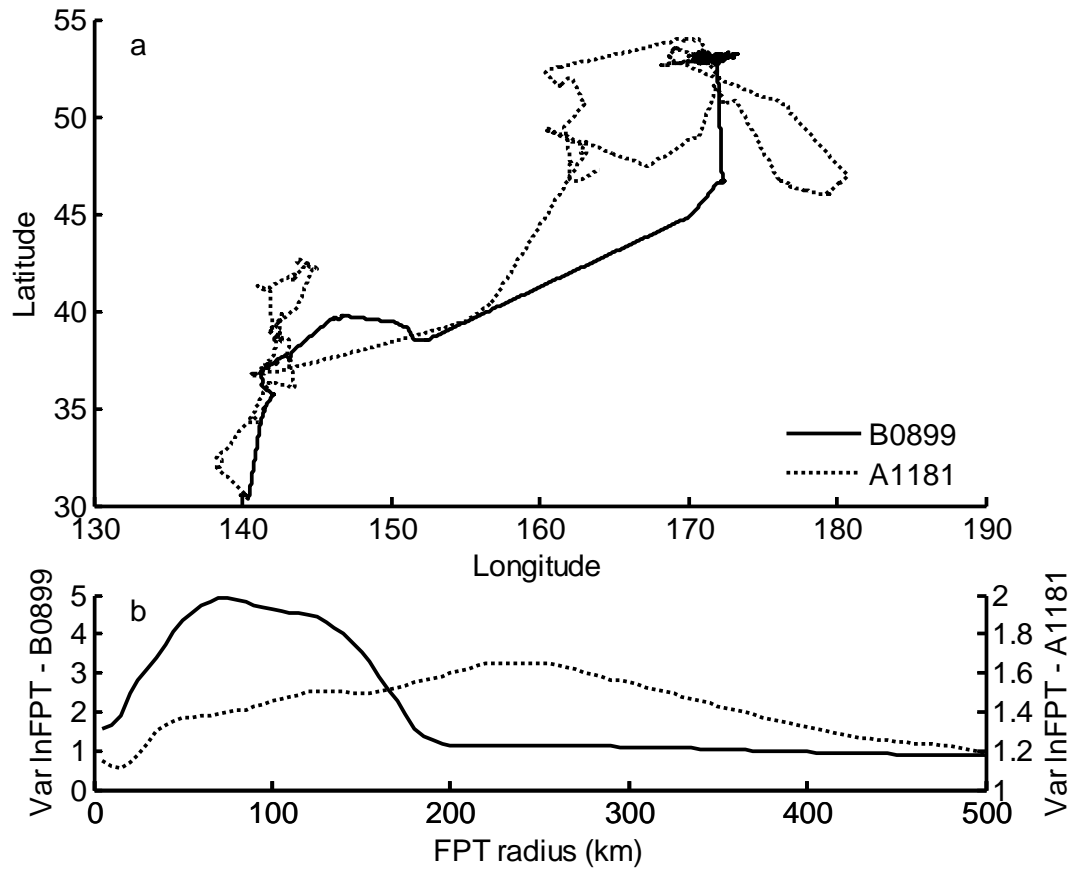


Figure 4.4. Flight paths of short-tailed albatrosses B0899 and A1181 showing differing spatial scales of area-restricted search (a) and corresponding differences in peaks in variance of the of first-passage time (FPT, log transformed) among various search radii (b). The single, well defined region of area-restricted search of albatross B0899 produced a well-defined peak in variance of FPT that occurred at a smaller spatial scale than for A1181.

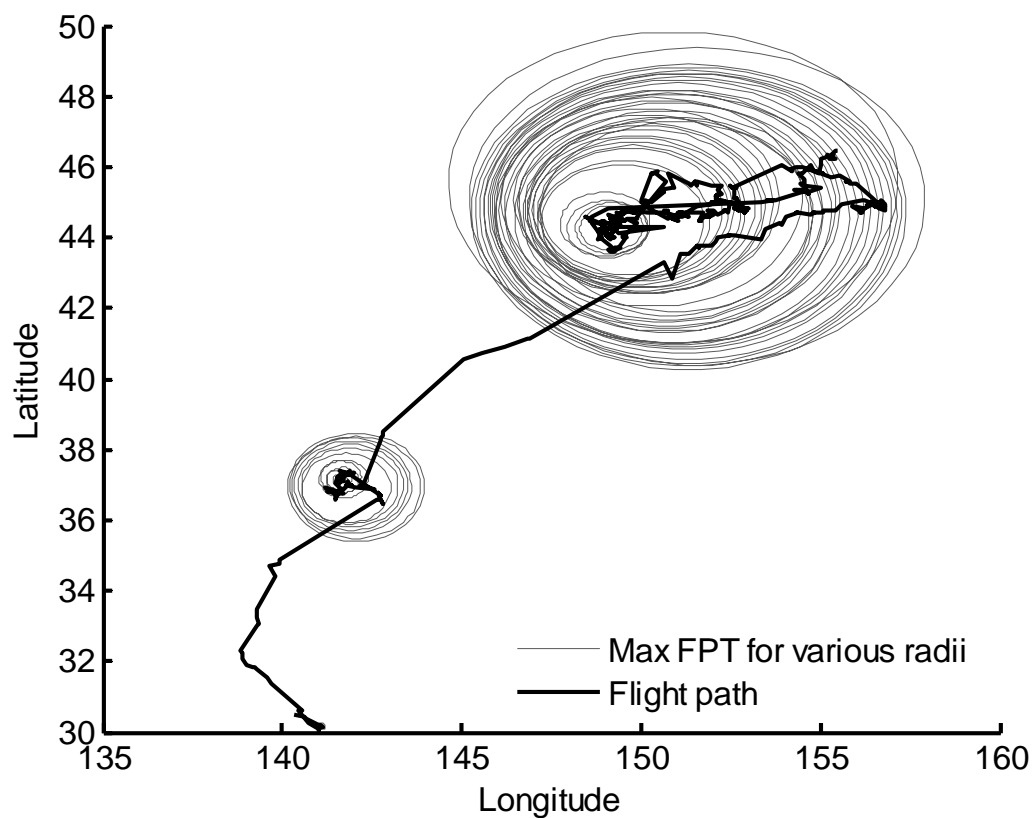


Figure 4.5. Locations of maximum first-passage time (FPT) for search radii from 10 km to 500 km, at 10-km increments along the flight path of albatross A0837. The locations of the 50 radii illustrate how various spatial scales of area-restricted search can occur at different locations along flight paths.

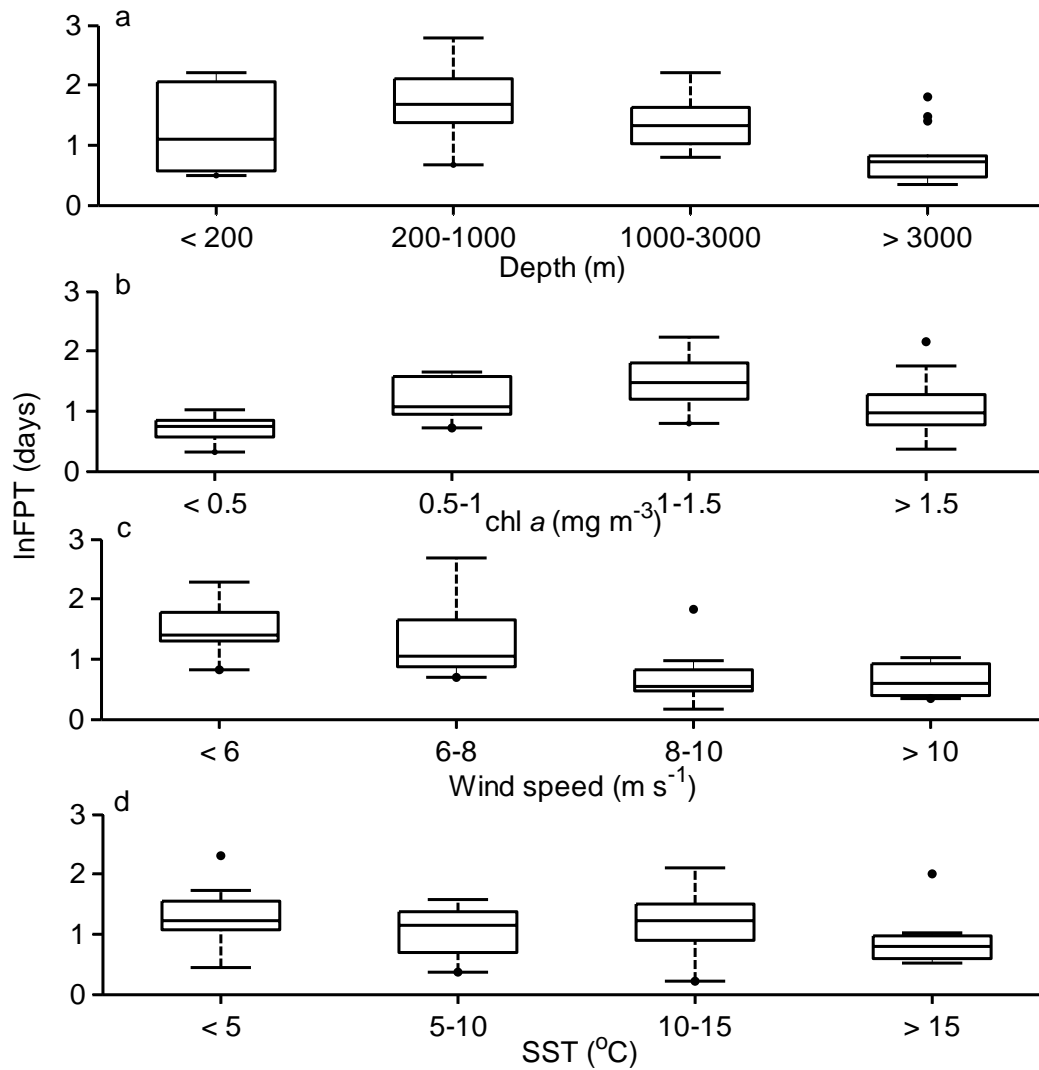


Figure 4.6. First-passage time of short-tailed albatrosses at a 70-km search radius in relation to marine habitat variables. Bin sizes represent specific depth domains (a) and equal sample sizes chl *a* (b), wind speed (c), and of sea surface temperature (d) among bins. Box plots depict median (horizontal line), interquartile range (box), 1.5*interquartile range (error bars), and outlying data (dots).

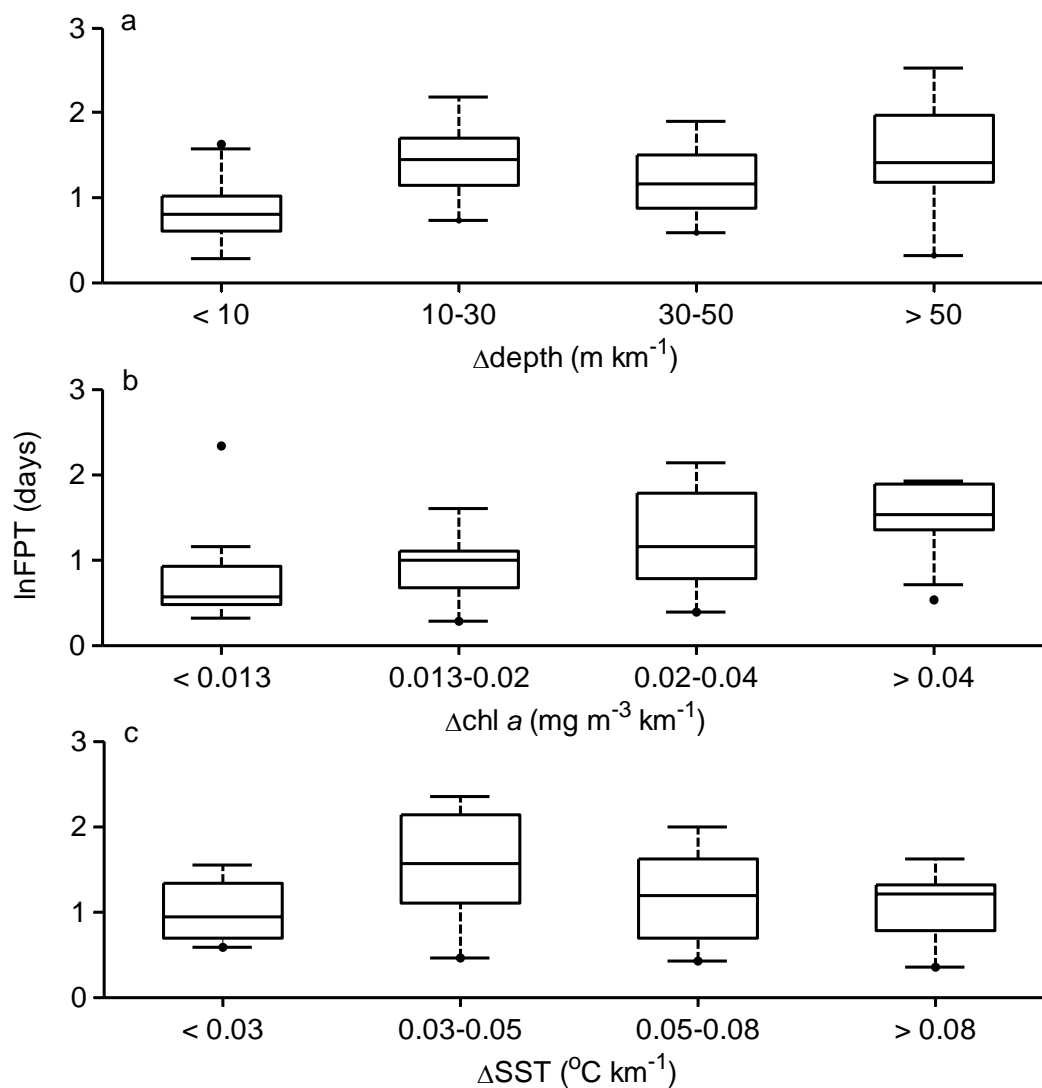


Figure 4.7. First-passage time of short-tailed albatrosses at a 70-km search radius in relation to gradients for marine habitat variables of depth (a), chlorophyll *a* concentration (b), and sea surface temperature (c). Bin sizes were selected for each metric to produce approximately equal sample sizes among bins.

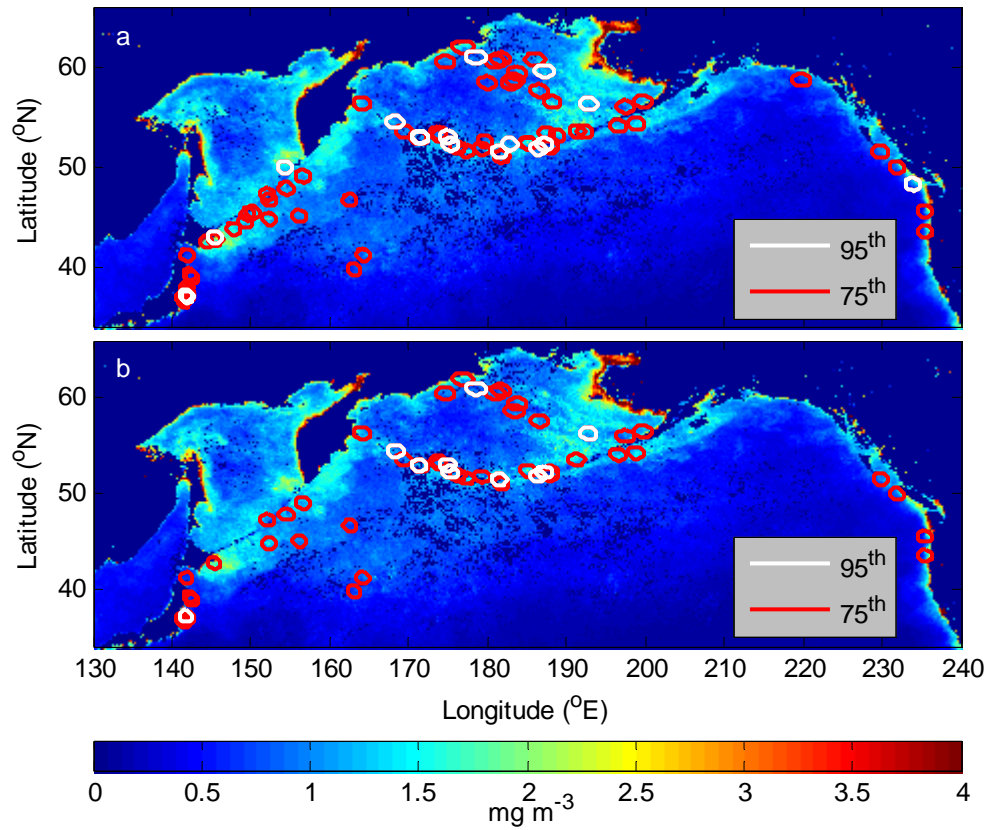


Figure 4.8. (a) Locations for 95th and 75th percentile of first-passage time at the 70-km search radius for each of the 14 short-tailed albatrosses tracked. Plot (b) includes only radii where wind speed was $\geq 4.4 \text{ m s}^{-1}$ (the lower quartile of wind speeds for locations in plot (a) and, therefore, area-restricted search activity was less likely to be limited by low wind speeds. Radii are superimposed over a composite image of chlorophyll *a* concentration for the study period (May – November, 2002 and 2003).

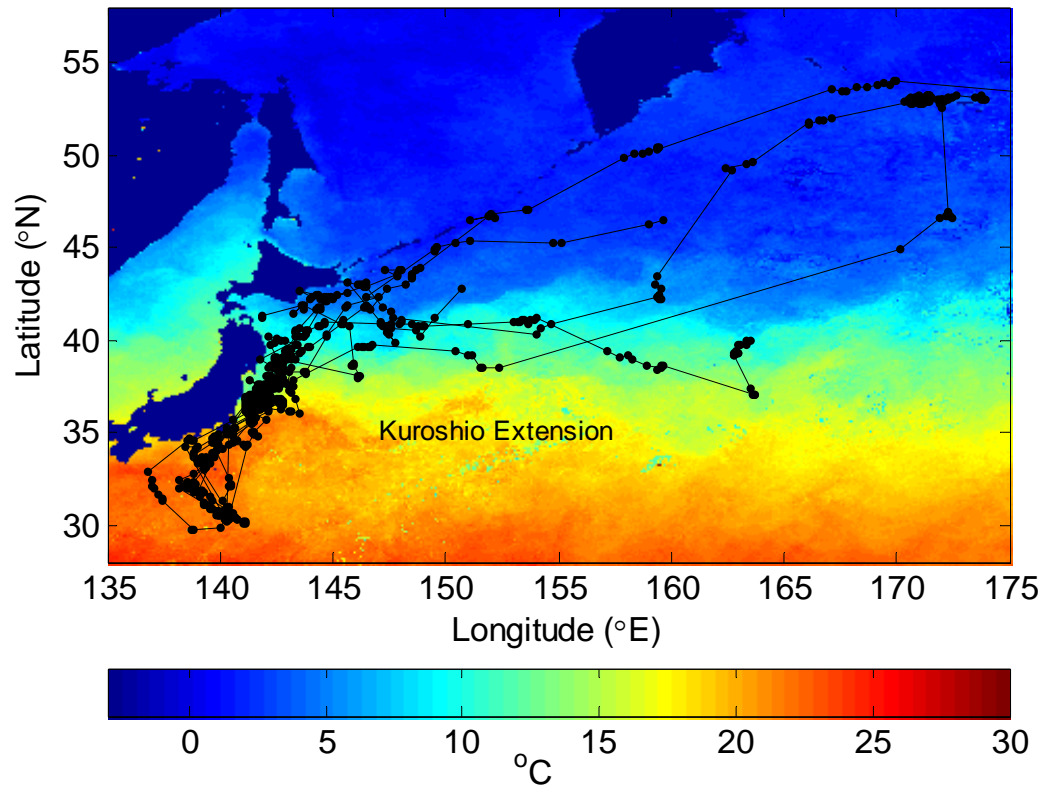


Figure 4.9. Average sea surface temperature and short-tailed albatross satellite telemetry locations in May, 2002 and 2003. Lines connect satellite fixes (points) of individual albatrosses. The confluence of the cooler Oyashio Current and warmer Kuroshio Current are evident and albatrosses tended to only use the northern portion of the Kuroshio Extension.

Chapter 5. Wind, Waves, And Wing Loading: Their Relative Importance To The At-Sea Distribution And Movements Of North And Central Pacific Albatrosses

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Abstract

Among the varied adaptations for avian flight, albatrosses possess morphological traits to capitalize on ocean surface wind and wave energy for efficient, long-distance travel. The four species of albatrosses that breed in the North and Central Pacific Ocean exhibit markedly different distributions at-sea, as well as different body morphologies. The two larger species, short-tailed albatross (*Phoebastria albatrus*; STAL) and waved albatross (*P. irrorata*; WVAL), nest closest (< 1,500 km) regions of productive coastal upwelling. However, STAL have 60% greater wing loading and 20-25% greater minimum sink and best glide velocities than WVAL. Aerodynamically, WVAL are more similar to the two smaller species, black-footed albatross (*P. nigripes*; BFAL) and Laysan albatross (*P. immutabilis*; LAAL), which breed much farther (> 3,000 km) from productive coastal upwelling and have greater foraging ranges than the two larger species. This apparent discrepancy for WVAL is explained by the consistently lower wind speeds and wave heights in the eastern equatorial region where this species occurs.

Even though STAL had the greatest wing loading and the potential to be within the regions of greatest wind velocity, they were often in regions where wind speed and wave heights were equal to or less than those encountered by BFAL and LAAL. Winds encountered by BFAL and LAAL were on average greater than those required for minimum sink velocity. This was not true for the two larger species, STAL and WVAL, which flew at faster ground speeds to possibly compensate for this. In contrast to the other species, WVAL rarely traveled through areas of greater wind speeds and wave heights than surrounding areas. Furthermore, WVAL was the only species in which long distance movement trajectories occurred into the wind. Our results support the hypothesis that aerodynamic disparities important to gliding flight are consistent with regional wind and wave patterns for North and Central Pacific albatrosses. We also demonstrate, however, that an albatross with relatively high minimum sink and best glide velocities (STAL) will regularly venture into regions of relatively slow wind speeds and low wave heights, apparently seeking preferred foraging opportunities.

Key words: aerodynamic theory, albatrosses, dynamic soaring, flight morphology, wave heights, wind velocity

Introduction

Albatrosses and petrels (Procellariiformes) are widely distributed throughout the world's oceans (Warham 1990). Many of the species within this order are well known for routinely traveling 100s to 1000s of km from their breeding colonies in search of food, as well as during post-breeding seasonal migrations (Jouventin and Weimerskirch 1990, Phillips et al. 2005). Success in exploiting resources in remote regions of the oceans is attributed to their ability to soar dynamically, thereby making efficient use of wind and wave energy to minimize energetic costs of flight (Pennycuick 1982, Costa and Prince 1987, Shaffer et al. 2001a). Among Procellariiformes, albatrosses (Diomedidae) best exemplify the morphological characteristics for gliding over vast expanses of open water, permitting them to circumnavigate the globe in just 46 days (Croxall et al. 2005).

Characteristics for gliding flight include high aspect ratio wings (long and narrow to maximize lift while minimizing induced drag), sufficient wing loading (wing area/weight) to overcome drag and maintain air speed for gliding (particularly in strong winds), and a shoulder lock tendon to hold the wings in gliding position with little or no muscle exertion (Pennycuick 1982, Norberg 1990). Moreover, albatrosses exhibit flight behavior that further capitalizes on wind and wave energy. Albatross flight has been characterized as dynamic soaring, i.e., flying along wave crests with their wing tips nearly touching the water, then “pulling up” to 15-20 m before beginning another glide cycle (Rayleigh 1883, Walkden 1925, Pennycuick 1982). By remaining close to the sea surface (generally < 15 m), albatrosses exploit wind velocity gradients and ground effect to increase airspeed and lift for prolonged gliding flight. During the “pull-up”, kinetic energy is both gained and traded for potential energy in the form of altitude. This type of pull-up flight behavior is exhibited by all albatrosses (but few other species) and may be a key behavioral trait in prolonged fixed-wing flight (Pennycuick 2002).

Even within this uniquely adapted group of birds, there is sufficient variation in body and wing morphology to have important implications for differential use of wind. For example, Pennycuick (1982) recorded differences in flight behavior and performance among nine species of Procellariiformes that were consistent with differences in body and wing morphologies that influence flight mechanics. Furthermore, even within a single species, Shaffer et al. (2001b) suggested that gender and age-related size dimorphism in wandering albatrosses (*Diomedea exulans*) may have a functional role in flight performance that explains the observed differences in their at-sea distribution and use of wind systems.

Of the 24 extant species of albatrosses (Robertson and Nunn 1997), only four species breed in the North and Central Pacific Ocean and they exhibit markedly different distributions at sea. Short-tailed albatrosses (STAL, *Phoebastria albatrus*) breed only in the northwest Pacific (Hasegawa and DeGange 1982) within close proximity (< 500 km) to the continental margin and forage within the productive waters of the Kuroshio and Oyashio Currents (Suryan et al. 2006). Waved albatrosses (WVAL, *P. irrorata*) occur solely in the equatorial eastern Pacific and travel moderate distances (< 1,500 km) from its nesting colonies in the Galápagos Islands to adjacent feeding grounds within the Humboldt Current region (Fernández et al. 2001). In contrast, the population center for black-footed albatrosses (BFAL, *P. nigripes*) and Laysan albatrosses (LAAL, *P. immutabilis*) is in the central North Pacific (Hawaiian archipelago; Tickell 2000) and breeding birds traverse over large expanses of open ocean (> 3,000 km) to feed in the subarctic transition zone and along continental shelf regions of the California and Alaska Currents (Fernández et al. 2001, Hyrenbach et al. 2002). In addition to differences in proximity of breeding colonies to continental margins, these four albatrosses also differ morphometrically with the two smaller species (LAAL and BFAL) nesting farthest from productive coastal regions. These morphometric disparities indicate potential adaptive significance for body size and flight energetics with respect to regional wind patterns.

Herein, we focus on the four species of Central and North Pacific albatrosses to address hypotheses related to at-sea movement patterns and the association with sea

surface winds and wave heights. We used satellite telemetry to track albatrosses at-sea and integrated tracks with remotely sensed wind data (speed and direction) and numerical models of surface wave heights. The primary hypotheses that we addressed were: (1) the two larger species with shorter flight distances to productive upwelling regions will have higher wing loading (potentially higher flight costs); (2) albatrosses with lower wing loading will occur in regions of lower wind speeds and wave heights; (3) when traveling long distances, albatrosses with higher wing loading are more likely to use regions of greatest wind speeds and wave heights; and (4) long distant movement trajectories will occur when albatrosses are traveling in the direction of prevailing winds.

Methods

We captured albatrosses to measure morphology ($n = 91$) and to attach satellite transmitters ($n = 61$) at three breeding colonies and one at-sea location, collectively including the North Pacific Ocean and the eastern equatorial Central Pacific Ocean. We captured STAL at their breeding colony on Torishima ($30^{\circ} 28.3' \text{ N}$, $140^{\circ} 18.6' \text{ E}$), Izu Islands, Japan and at-sea in Seguam Pass ($52^{\circ} 25.8' \text{ N}$, $172^{\circ} 46.4' \text{ W}$), Aleutian Islands, Alaska. All STAL were tracked during post-breeding migrations (Table 5.1) and, therefore, their tracks do not represent central-place trips of birds returning to a colony. WVAL were captured and tracked from their breeding colony on Isla Española ($1^{\circ} 22.2' \text{ S}$, $89^{\circ} 15.0' \text{ W}$), Galapagos Islands, Ecuador, and BFAL and LAAL from Tern Island ($23^{\circ} 52.2' \text{ N}$, $166^{\circ} 16.8' \text{ W}$), northwestern Hawaiian Archipelago and (Fig. 5.1). All WVAL, BFAL, and LAAL were tracked during the incubation period (Table 5.1); therefore, their tracks represent central place foraging trips. It was not feasible to adequately sample various age classes and both genders of all four species in this study. Therefore, our hypotheses focus on inter-specific differences and we do not consider age and gender effects in our analyses.

Morphometrics and flight mechanics

Albatrosses were weighed using spring balances to the nearest 100 g. In most cases, the elapsed time since a previous feeding was unknown, therefore the mass of some individuals may have included partially digested food. We measured culmen, bill width and height (immediately anterior of the nares), and tarsus using vernier calipers (± 0.5 mm). Tail length was measured (± 1 mm) from the insertion point to the tip of the longest central rectrix. Body girth (circumference) was measured (± 0.5 cm) at the widest point posterior to the wings; wing span was measured (± 1.0 cm) either from mid-body to the tip of one outstretched wing and then doubled or between the tips of both wings outstretched. To determine wing area, we traced the outline of one wing onto a sheet of paper (Pennycuick 1989). Measures of tarsus or a single wing, including tracings, were from the right side of the bird. We compared overall body size among species using principal components analysis to calculate a body size index (first principal component; Rising 1989) based on standardized measures of culmen, tarsus, body girth, and wing span (Manly 1994).

We followed procedures in Pennycuick (1989) for calculating flight performance metrics (Table 5.2). Body frontal area (S_b) was calculated from body girth. We measured root chord (chord at the most proximal end of wing) from each trace, then multiplied this by shoulder width to determine inter-wing area. We calculated wing area (S) as $2 \times \text{area of trace} + \text{inter-wing area}$. Wing traces were converted to area using a mass-to-area linear regression determined by weighing sheets of paper of known area (Shaffer et al. 2001b). Wing traces were copied to a clean sheet of paper, cut along the perimeter, then weighed (± 0.01 g). We then cut and weighed 22 rectangular sheets with areas spanning those of wing traces to develop the predictive linear equation of $\text{area} = 4.1394 + 148.2 \times \text{mass (g) of paper}$ ($r^2 = 0.999$, $P < 0.001$). Wing loading (W), a measure of force per unit area, and aspect ratio, a measure of aerodynamic efficiency, were calculated as described in Table 5.2.

Mechanical calculations of flight performance were conducted using computer program Flight v1.15, written by C. Pennycuick (<http://www.bio.bris.ac.uk/people/staff.cfm?key=95>; (Pennycuick 1998)). We calculated

minimum sink velocity (V_{ms}) and best glide velocity (V_{bg}), minimum sink rate, and best glide ratios for each bird. Program inputs for each bird included body mass, wing span, wing area, aspect ratio, air density at sea level, and body frontal area. We used program default values for the remainder of inputs needed to calculate glide polars.

Satellite tracking of albatrosses

We satellite-tagged 14 - 20 individuals per species and tracked individuals for 5 – 125 days (Table 5.1). Transmitters were 35-100 g and $< 2.5\%$ of body mass. Satellite-derived position fixes were provided through the Argos system (Service Argos, Inc.). Because Argos position fixes vary in accuracy, we used a forward-backward speed filtering algorithm to cull erroneous locations (McConnell et al. 1992). We used a maximum speed cut-off of 80 km h^{-1} , which is consistent with speed thresholds previously used to filter Argos locations for STAL (Suryan et al. 2006), BFAL, and LAAL (Hyrenbach et al. 2002). We used the same maximum speed value for WVAL for consistency in data filtering among species. After filtering, we retained 90% ($n = 17,061$) of all the locations obtained.

Transmitters deployed on STAL had duty cycles of either 8 hr on and 24 hr off or 6 hr on and 18 hr off, providing a mean of 5.3 (range 2.6 – 8.3) locations per individual per day after filtering. Transmitters deployed on BFAL and LAAL transmitted continuously, providing 12.7 and 13.7 (range 4.3 - 18.9) locations per individual per day, respectively. The duty cycle for WVAL was 8 hr on and 24 hr off, providing 2.3 (range 1.3 - 3.6) locations per individual per day. We compensated for the differing duty cycles by using a temporal resolution of one day and established minimum criteria that a series of position fixes on a given day must meet (see Analysis of Albatross Tracks and Wind and Wave Data below).

Wind speed and direction

We obtained QuikSCAT ocean wind data for 10 m above the ocean surface (a height consistent with observations of albatrosses soaring at-sea; Pennycuick 1982) from the SeaWinds sensor aboard the QuikBird satellite. These data were obtained

from Remote Sensing Systems (www.remss.com; sponsored by the NASA Ocean Vector Winds Science Team) and provided in a global coverage of 0.25 degree latitude / longitude (~ 23 km) spatial resolution grids of wind speed (m s^{-1}), direction, and a binary rain flag. To characterize monthly wind regimes within a 100 km radius of each colony, we averaged monthly composites over a 5-yr period (July 1999 to August 2004). Additionally, to characterize winds at varying distances from the colonies, we created a 5-yr composite wind grid and calculated average speed and direction at varying distances within the foraging range of albatrosses from each colony. For analysis of wind along albatross tracks, we used daily wind grids consisting of ascending and descending passes with 0600 hr and 1800 hr local time equator crossings, respectively. Because of incomplete coverage of the globe during each pass, we averaged speed and direction of the two passes to create a single composite for each day. Some data gaps still remained in daily averaged files (particularly at low latitudes); however, this had little effect on our analyses (sample sizes of albatross locations were sufficiently large).

Wave height

We obtained data on significant wave heights from the U.S. National Oceanic and Atmospheric Administration (NOAA), National Center for Environmental Prediction (<http://polar.ncep.noaa.gov/waves/Welcome.html>). Significant wave height represents the average of the highest 33% of all individual waves. We used data output from the NOAA Wavewatch III model (Tolman 1998, Tolman et al. 2002). Model inputs include wind speed, sea surface temperature, ice conditions, and land boundaries. We used wave height data provided at a spatial scale of 1° latitude by 1.25° longitude (ca. 55 – 134 km resolution within our study area) and a temporal scale of 3-hr intervals. From these data, we calculated 24-hr averages for determining wave heights encountered by albatrosses during daily movement trajectories and we averaged monthly composites over a 6-yr period (1999-2004) for determining overall wave heights within albatross foraging ranges.

Analysis of albatross tracks with wind and wave data

Our analysis of wind and wave heights encountered by albatrosses at-sea focused on three main questions: (1) what are the mean wind speeds and wave heights encountered by satellite-tagged albatrosses; (2) are albatrosses using winds of greater velocity or waves of greater height than the surrounding environment; and (3) what is the direction of net albatross movement relative to wind direction? Wind speeds and wave heights encountered by STAL relative to the other three species were not directly comparable given that satellite tracking occurred during the post-breeding summer months, in contrast to the other three species, which were tracked during the breeding months in winter. Therefore, to determine potential wind speeds and wave heights encountered by STAL during the winter breeding season, we repeated the analysis but used data from November and December of the respective breeding season. For this analysis, we assumed the birds flew the same path from Torishima to local foraging areas; however, we restricted tracks to the first 15 days of departure from the breeding colony (the maximum time period of an outbound flight for the other three species during incubation). This assumption is valid based on recent satellite tracking of breeding birds (R.M. Suryan and F. Sato, unpubl. data).

Albatross locations for a given day were used if there were two or more locations separated by at least one hour. We extracted wind speed and direction data within a 15-km buffer along the albatross flight path to represent local wind conditions encountered for a given day. Because the resolution of wave data was approximately five times less than that of wind data, we used a 75-km buffer to represent local wave conditions. We next calculated mean wind speed and wave height among locations, net distance traveled and net movement direction between the first and last albatross location of each day. To determine if albatrosses were using regions of favorable wind speeds or wave heights, we also extracted wind and wave data at 100, 500, and 1000 km buffers around the travel paths. We used a one-sample t-test (one-tailed) to determine if the local wind speed or wave heights along the travel path were significantly greater than those available within the three radial distances from the travel path.

Statistical tests were performed using Matlab (The MathWorks, Inc.) or Systat (Insightful Corp.) software. Results of statistical tests were considered significant if $P \leq 0.05$. All remote sensing data processing and analysis of albatross satellite tracking data were performed using purpose-built programs written in Matlab. Multi-sample comparisons were conducted using Analysis of Variance with a Tukey post-hoc test. If necessary, data were \log_{10} transformed to meet conditions of normality or a Kruskal-Wallis non-parametric test was used.

Results

Morphometrics and flight mechanics

WVAL had the largest body frame, yet they were slender in build relative to STAL, which are the next closest in body size, followed by BFAL and then LAAL. Culmen, tarsus, and wing span were significantly greater for WVAL; however, WVAL were 25% lighter than STAL (Table 5.3). Body size index to mass relationships demonstrated that WVAL were outliers to a highly significant linear trend ($R^2 = 0.76$, $P < 0.001$) among STAL, BFAL, and LAAL (Fig. 5.2). For WVAL, the combination of the largest wing area among the four species and a low mass for its size, resulted in wing loading similar to LAAL, the smallest and lightest of the four species. STAL had the greatest wing loading. BFAL had significantly lower wing loading than STAL, but greater than WVAL and LAAL (Table 5.3). Glide polar calculations reflected these differences in flight morphometrics, with STAL having the highest minimum sink and best glide velocities, and WVAL having low values, comparable to BFAL and LAAL (Table 5.3).

Wind patterns near albatross colonies

Five-year average wind speeds were greatest within the foraging range of STAL and lowest within the foraging range of WVAL (Fig. 5.3a). During their respective breeding seasons, monthly mean wind speed within 100 km of the colonies were greatest for STAL, moderate for BFAL and LAAL, and lowest for WVAL (Fig. 5.4a).

At consecutive radial distances from the breeding colonies, STAL would encounter the consistently highest wind speeds and WVAL the lowest. BFAL and LAAL would encounter moderate wind speeds until reaching a distance of ~1,500 km when foraging ranges overlap with STAL and wind speeds encountered were similar (Fig. 5.5).

Wind direction within 100 km of the colonies and during the first eight months of breeding was consistently from the east for BFAL and LAAL at Tern Island and from the south and southeast for WVAL at Española. Wind direction for STAL at Torishima was predominantly from the northwest or southeast, but also was more variable compared to Tern Island and Española (Fig. 5.4b). Wind direction.

Travel speeds and wind encountered by albatrosses at sea

When moving distances greater than 100 km, STAL had the greatest travel speeds (Kruskal-Wallis $\chi^2_3 = 13.1$, $P = 0.004$), even though wind speeds encountered were significantly less than for BFAL and LAAL (Kruskal-Wallis $\chi^2_3 = 35.0$, $P < 0.001$; Fig. 5.6). Average travel speeds of WVAL, BFAL, and LAAL were not significantly different from each other even though wind speeds encountered by WVAL, like STAL, were significantly less than encountered by BFAL and LAAL. When including only outbound flights for WVAL, BFAL, and LAAL (to simulate non-central place trips of STAL), the results were similar, although differences among albatross travel speeds were not significant, possibly because of smaller sample sizes (Kruskal-Wallis $\chi^2_3 = 4.8$, $P = 0.188$).

When accounting for seasonal differences by having STAL travel the same routes during the winter incubation period (November – December), wind speeds encountered would be comparable to those of BFAL and LAAL during the same season (Fig. 5.6). When comparing wind velocity at colonies during the breeding season (Fig. 5.4) vs. wind velocity encountered by albatrosses at-sea (Fig. 5.6), all species except for WVAL tended to move into regions of equal or greater wind speeds than conditions near their respective colonies. Moreover, when traveling distances greater than 100 km in a day, all species except WVAL transited under windier conditions compared to more local movements ($< 100 \text{ km day}^{-1}$; Fig. 5.6). Indeed, when traveling $> 100 \text{ km day}^{-1}$, wind

speeds along travel paths of WVAL were more often similar to surrounding regions compared to other species (Fig. 5.7a). When moving distances of $> 100 \text{ km day}^{-1}$, movement trajectories were generally downwind ($135 - 225^\circ$ relative to albatross trajectory) for STAL or at 90° to the wind for BFAL and LAAL (Fig. 5.8). In contrast, WVAL often flew within a 45° angle into the wind.

Ocean surface wave heights

Wave heights in the Central and North Pacific and within albatross foraging ranges were mostly consistent with wind patterns (Fig. 5.3a,b), but a couple of exceptions were evident. Wave heights were smaller and less variable within the foraging range of WVAL compared with the three North Pacific species (Fig. 5.9a). Within the STAL foraging range, even though the median wave height was higher than that of WVAL (and comparable to heights within BFAL and LAAL ranges), actual wave heights encountered by STAL were small and most similar to WVAL (Fig. 5.9b). Unlike results of wind speeds encountered by STAL, the small wave heights encountered relative to BFAL and LAAL were not a seasonal effect. Wave heights encountered if STAL flew similar routes within the Kuroshio/Oyashio Current regions during the winter would still have been relatively small, similar to those in summer (Fig. 5.9b). The fact that STAL encountered waves smaller than BFAL and LAAL is consistent with smaller wave heights within shelf break and slope regions frequented by STAL (Piatt et al. 2006, Suryan et al. 2006) compared to oceanic domains (Kruskal-Wallis $\chi^2 = 13.71$, $P = 0.003$, $n = 4$; Fig. 5.10). Wind speeds also differed among bathymetric domains in this region (Kruskal-Wallis $\chi^2 = 10.88$, $P = 0.012$, $n = 4$), with a trend similar for wave heights; Foraging STAL, however, more often used regions of greater wind speeds than wave heights relative to surrounding areas when net movement trajectories were $\geq 100 \text{ km day}^{-1}$ (Fig. 5.7a,b). Moreover, reduced wave heights off Japan and the Kurile Islands, Russia, relative to north of Hawaii were also evident in the 6-yr composite image of mean wave heights (Fig. 5.3b). This regional difference in wave heights was not as evident for wind speeds (Fig. 5.3a.).

Discussion

Hypothesis 1: Larger species living closest to productive upwelling regions would have the highest wing loading.

Results of STAL flight morphometrics supports this hypothesis, however, results from WVAL are contrary to this hypothesis. WVAL had low wing loading and low V_{ms} and V_{bg} , despite having large body size and the most restrictive range. This apparent discrepancy can be explained by the reduced wind speeds and wave heights within the low-latitude distribution of WVAL compared to the other three species. For smaller and farther ranging BFAL and LAAL, low wing loading, V_{ms} , and V_{bg} relative to STAL were consistent with this hypothesis.

Hypothesis 2: Albatrosses with higher wing loading would occur in regions of greater wind speeds and wave heights

At a coarse scale, our results support this hypothesis. However, STAL, having the greatest wing loading, often occurred in regions where wind speed and wave heights were equal to or less than those encountered by BFAL and LAAL, even when the seasonal component was considered. Winds encountered by BFAL and LAAL were on average greater than that required for V_{ms} . This was not true for the two larger species, STAL and WVAL. However, as noted for other Procellariiforms (Pennycuick 1982), larger species tend to fly at faster ground speeds, which was true in our study even though they encounter slower wind speeds than the smaller species (Fig. 5.6). The greater travel speeds of STAL and WVAL may help to maintain sufficient airspeed, which is far more critical than ground speed in maintaining kinetic energy for gliding (Pennycuick 2002). Furthermore, the fact that albatrosses often fly at low velocities relative to their V_{ms} , is consistent with wave slope soaring (Pennycuick 1982).

Wave slope soaring and the benefit of wind gradients near the sea surface for albatrosses have been well documented (Rayleigh 1883, 1889, Irdac 1925, Wood 1973, Wilson 1975). However, because wind gradients sufficient to benefit albatross airspeed and lift occur only within 3 m of the ocean surface (Pennycuick 1982) and the shape of

near-surface wind profiles may be irregular due to the effects of waves (Shearman 1985), there is disagreement over the dominant beneficial mechanism for soaring in albatrosses. Pennycuik (2002) suggested that albatrosses gain less kinetic energy from a uniform wind gradient and up to 14 times more from gusts received on their ventral surface at the crest of a wave after passing through a low wind speed “separation bubble” on the leeward side. Alternatively, Sachs (2005) noted that maneuvering at the upper turn of the “pull-up” provides a substantial gain in kinetic energy for continued soaring. Regardless of the dominant mechanism, the importance of waves to albatross soaring is unequivocal. Moreover, even in the absence of surface winds, a traveling swell can generate up-currents of approximately 1 m s^{-1} (Froude 1888). This is greater than the minimum sink rate calculated for all four species in our study ($\leq 0.6 \text{ m s}^{-1}$) and greater than the lowest up-current of 0.6 m s^{-1} calculated for the much larger wandering albatrosses to maintain level flight (Wood 1973). Hence, even at low or negligible wind speeds, soaring for some albatrosses can be maintained by wave energy alone (Pennycuik 1982). Furthermore, if waves are traveling perpendicular to the bird’s line of flight, waves alone can carry a bird long distances depending on the speed of the wave.

Hypothesis 3: Albatrosses with higher wing loadings are most likely to use regions of greatest wind speeds and wave heights

In general, results support this hypothesis. Depending on radial distance considered, 31 - 59% of the time STAL, BFAL, and LAAL transited through greater wind speeds and wave heights compared to the surrounding areas (Fig. 5.7). The observation that WVAL less frequently transited within areas of greater wind speeds (23 - 26% of transits) or wave heights (8 – 9% of transits) was likely due to the limited availability of greater wind speeds or wave heights within foraging range of their breeding colony. (c.f., Figs. 5.4 and 5.5, Fig. 5.9a and 5.9b). In considering solely aerodynamic theory, we would expect STAL, compared to BFAL and LAAL, to more frequently transit areas of greater wind speed and wave heights. STAL, however, often encountered wind speeds and wave heights more similar to WVAL. This counter-

intuitive result is most likely explained by the oceanographic regions used by STAL relative to BFAL and LAAL (Fig. 5.1). Wind speed and wave height along the continental margins where STAL and WVAL were tracked were less than in the open ocean regions where BFAL and LAAL often occurred (Figs. 5.3 and 5.10).

Hypothesis 4: Long distant movement trajectories occur when albatrosses fly with a following wind

Results for all species except WVAL support this hypothesis. WVAL net movement trajectories frequently occurred at 45° to the wind and is best explained by the prevailing southeast winds that force these birds to fly into the wind when traveling between the Galapagos Islands and their feeding areas off the coast Peru (Figs. 5.3b, 5.7; Fernández et al. 2001, Anderson et al. 2003). Given this restriction, the low average wind speed in this region is beneficial in reducing energy costs when forced to fly into a headwind (e.g., (Weimerskirch et al. 2000)). Indeed, Alerstam et al. (1993) noted that black-browed albatrosses (*Thalassarche melanophrys*) and grey-headed albatrosses (*T. chrysostoma*) flew in all directions relative to light winds, perpendicular to moderate winds, and downwind in strong winds. In our study, the three species other than WVAL encountered winds from more variable directions and their trajectory was most often either perpendicular or downwind.

Although albatrosses gain airspeed, and therefore lift, when flying into a headwind, a headwind can actually be problematic for dynamic soaring. Wood (1973) noted that a shallow dive, for example after the upper turn of a “pull-up”, against the wind is unfavorable. Instead, the albatross must dive steeply to avoid serious loss of airspeed in a surface wind gradient. This is not true for downwind flight, however, where descending through a surface wind gradient is actually favorable in maintaining lift. Thus, in descending downwind flight, it is possible either to maintain airspeed in a very shallow glide or to gain speed very rapidly by diving (Wood 1973)

It is important to note that our analyses of albatross movements relative to wind focused on rather coarse, linear movement trajectories, whereas albatross fine-scale flight paths are rarely linear. Wandering albatrosses have been recorded flying in a

looping pattern as they move away from their breeding colony on Crozet Island (Weimerskirch et al. 2002) and, therefore, the ultimate trajectory is a result of many changing angles (Reinke et al. 1998).

Comparisons with other albatross species

The importance of wind on the at-sea distribution of albatrosses is well documented. However, it is unknown what combination of minimum wind speeds and wave heights present a physical or physiological barrier to the existence of various sized albatrosses. BFAL and LAAL are comparable in size and aerodynamic values to light-mantled sooty albatross (*Phoebastria palpebrata*). This species also tends to commute fairly rapidly from nesting areas to specific foraging areas in Subantarctic or Antarctic, where they spend most of their time and only rarely undertake long, looping tracks typical of several larger albatross species (Weimerskirch 1997). Although larger in size, WVAL have V_{ms} and V_{bg} values similar to light-mantled sooty albatrosses and exhibit similar foraging behavior during the breeding season. Overall, the WVAL is fairly unique among albatrosses in flight morphometrics and aerodynamic values, which may reflect an adaptation as the only albatross that exists exclusively in the relatively low wind speed regimes of a tropical region.

Although considered a medium-sized albatross, the rather bulky STAL has minimum sink and best glide velocities approaching that of the much larger wandering albatross (11.2 and 14.7, respectively, for STAL vs. 11.9 and 15.7, respectively, for wandering albatrosses), which is purported to be restricted to only the windiest regions of the southern hemisphere (Pennycuik 1982, Weimerskirch et al. 2000, Shaffer et al. 2001b). However, we found STAL to occur in regions of wind speeds and wave heights as low as those encountered by WVAL. During the STAL winter breeding season, the greater wind speeds within their foraging range are likely important for efficient flight during the more energy demanding task of reproduction compared to the post-breeding, non-central-place migrations in our study. Nonetheless, our results demonstrate that an albatross with high wing loading and high V_{ms} and V_{bg} , will regularly venture into regions of relatively slow wind speed and low wave heights to

seek their apparently preferred foraging areas (Piatt et al. 2006, Suryan et al. 2006). This also is likely true for those southern hemisphere albatrosses that forage in productive continental margins, such as portions of the Humboldt Current and Patagonia shelf where wind stress can be less on average than surrounding areas (Chelton et al. 2004). It has been suggested that the minimum speed near the sea surface for dynamic soaring could be as low as 5 m/s (Irdac 1925, Pennycuick 2002, Sachs 2005). Furthermore, the presence of swells to enhance dynamic soaring maneuvers may permit albatrosses to effectively travel in regions of relatively low wind speeds. However, this should only be beneficial if the region is sufficiently productive to compensate for the increased cost of flight relative to traveling in windier regions.

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Table 5.1. Summary of satellite tracking data for short-tailed, black-footed, Laysan, and waved albatrosses during 2001 to 2004. Ranges presented for # tracking days, # filtered locations represent minimum and maximum values for individuals from a given species, with the total combined in parentheses.

Species	# Individuals	# Tracking Days	# Filtered Locations	Months Tracked
Short-tailed	14	51 - 125 (1262)	131 - 808 (6709)	May - Sep 2002 May - Nov 2003
Waved	14	7 - 38 (288)	11 - 105 (717)	May - Jul 2001 May - Jul 2002
Black-footed	19	6 - 24 (279)	43 - 354 (3690)	Dec - Feb 2002/03 Nov - Jan 2003/04
Laysan	20	5 - 33 (407)	52 - 566 (5945)	Dec - Feb 2002/03 Nov - Jan 2003/04

Table 5.2. Summary of metrics and calculations relevant to avian flight mechanics following Pennycuick (1989). Table is modified from Shaffer et al. (2001b).

Variable	Formula (units)	Description
N	$\text{mass} \cdot 9.81$ (kg m s^{-2})	Weight: bird mass converted to weight by including gravitational acceleration and expressed in Newtons (N)
C	- (cm)	Body girth: circumference measured at the widest point posterior of the wings
S_b	$C^2/4\pi$ (cm^2)	Body frontal area: the cross-sectional area of the body at the widest point
-	- (cm)	Root chord: chord measured at the most proximal end of wing
b	- (m)	Wing span: total distance between wing tips
S	- (m^2)	Wing area: area of both wings including the inter-wing area of body (root chord*shoulder width)
c	b^2/S (cm)	Wing chord: mean wing width
W	N/S (N m^{-2})	Wing loading: force per unit wing area. Greater wing loading requires greater air speed to remain aloft
A	b/c	Aspect ratio: a dimensionless index of wing shape that is directly proportional to its aerodynamic efficiency (lift/drag ratio)

Table 5.3. Mean (SE , *n*) body morphometrics and glide polar values for three species of North Pacific and one species of Equatorial Pacific albatrosses. Like symbols denote significant differences ($P < 0.05$).

	Short-tailed	Waved	Black-footed	Laysan	<i>F</i>	<i>P</i>
Morphometrics						
Mass (kg)	4.68 ^{*,+} (0.13, 25)	3.51 [*] (0.95, 19)	3.17 ⁺ (0.76, 29)	2.77 ^{*,+} (0.89, 18)	69.2	< 0.001
Culmen (mm)	138.6 ^{*,+} (1.4, 22)	148.8 ^{*,+} (1.8, 19)	107.3 ⁺ (1.0, 30)	111.7 [*] (1.2, 23)	239.5	< 0.001
Bill height (mm)	41.7 ^{*,+} (0.5, 22)	37.4 [*] (0.4, 19)	37.4 ⁺ (0.5, 29)	34.4 ^{*,+} (0.3, 23)	44.5	< 0.001
Bill width (mm)	28.4 ^{*,+} (0.4, 19)	25.2 ^{*,†} (0.4, 19)	27.4 ^{†,‡} (0.3, 26)	25.3 ^{†,‡} (0.2, 23)	27.3	< 0.001
Tarsus (mm)	103.1 [*] (1.4, 22)	120.6 [*] (1.8, 19)	98.0 [*] (0.9, 29)	91.5 [*] (0.7, 23)	98.9 ^a	< 0.001
Tail (cm)	15.9 ^{*,+} (0.1, 18)	13.7 ^{*,+} (0.1, 19)	14.9 ⁺ (0.1, 26)	15.1 [*] (0.1, 23)	58.8	< 0.001
Girth (cm)	60.3 ^{*,+} (1.7, 6)	54.9 ^{*,+} (0.6, 19)	49.9 ⁺ (0.6, 29)	47.8 [*] (0.6, 23)	39.4	< 0.001
Body Frontal Area (cm ²)	291 ^{*,+} (17, 6)	241 ^{*,+} (6, 19)	199 ⁺ (5, 29)	183 [*] (5, 23)	37.2 ^a	< 0.001
Shoulder width (cm)	19.2 (5.4, 6)	17.5 (2.0, 19)	15.9 (1.8, 29)	15.2 (1.9, 23)	- ^b	-
Wing span (cm)	228 [*] (2, 10)	238 [*] (2, 19)	221 [*] (2, 29)	209 [*] (1, 23)	59.1	< 0.001
Wing chord (cm)	15.6 ^{*,+} (0.5, 5)	14.7 ^{*,†} (0.2, 19)	15.4 ^{†,‡} (0.1, 29)	14.3 ^{†,‡} (0.1, 23)	13.0 ^a	< 0.001
Wing area (cm ²)	3406 [*] (91, 5)	3858 ^{*,+} (60, 19)	3170 ⁺ (39, 29)	3065 [*] (33, 23)	57.4	< 0.001

Table 5.3. Continued

Aspect ratio	14.8 [*] (0.4, 5)	16.2 ^{*,+,†} (0.2, 19)	14.4 ⁺ (0.1, 29)	14.6 [†] (0.1, 23)	32.7	< 0.001
Wing loading (N m ⁻²)	141.2 ^{*,+} (13.9, 5)	89.2 ⁺ (2.0, 19)	99.3 [*] (2.6, 28)	88.7 [*] (3.3, 18)	16.8 ^a	< 0.001
Glide polar V _{ms} (m s ⁻¹)	11.22 ^{*,+} (0.51, 5)	8.95 ⁺ (0.10, 19)	9.44 [*] (0.12, 28)	8.93 [*] (0.17, 18)	16.99 ^a	< 0.001
Minimum sink (m s ⁻¹)	0.60 ^{*,+,†} (0.03, 5)	0.49 [*] (0.004, 19)	0.50 ⁺ (0.01, 28)	0.49 [†] (0.01, 18)	12.51	< 0.001
V _{bg} (m s ⁻¹)	14.70 ^{*,+,†} (0.55, 5)	12.29 [*] (0.10, 19)	12.77 ⁺ (0.14, 28)	12.43 [†] (0.23, 18)	13.37	< 0.001
Best glide ratio	20.80 [*] (0.25, 5)	21.04 ⁺ (0.13, 19)	21.55 ^{*,+,†} (0.12, 28)	20.95 [†] (0.10, 18)	6.07	0.001

^aLog transformed^bShoulder width was approximated by calculating body diameter from girth measurements

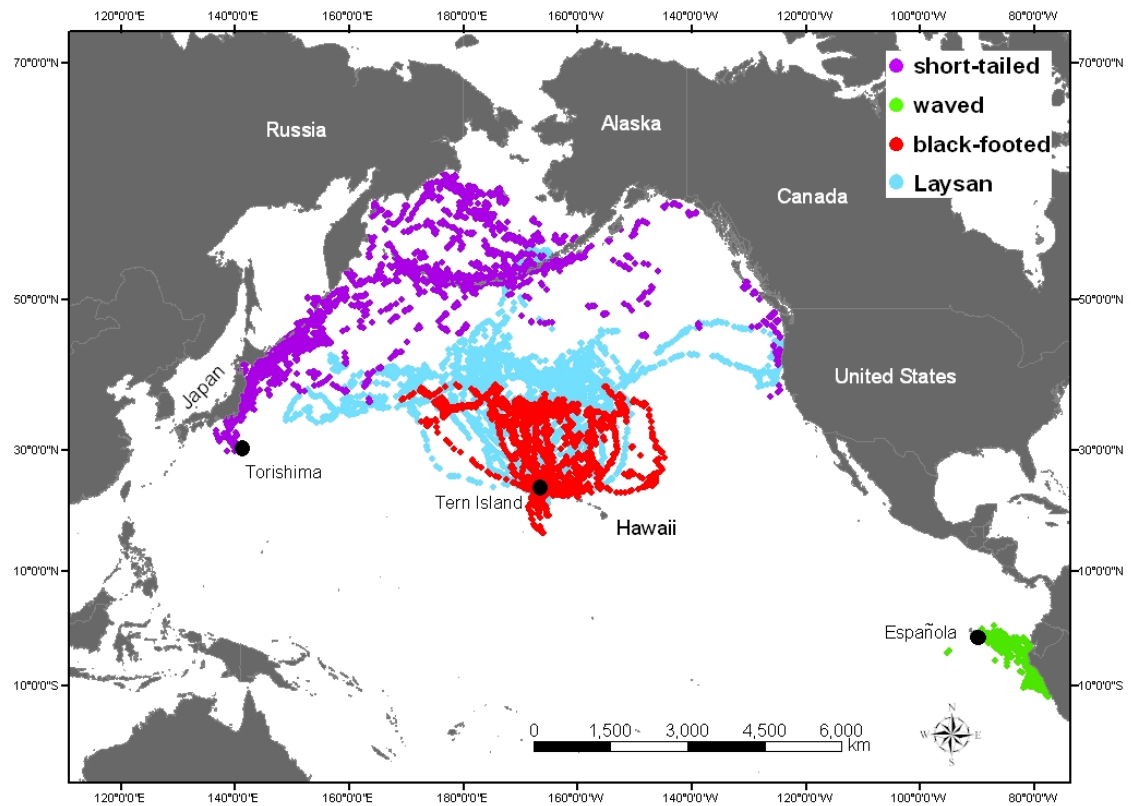


Figure 5.1. Locations of study colonies and satellite-tracking locations for four species of North and Central Pacific albatrosses, including two years of data for each species between 2002 and 2004.

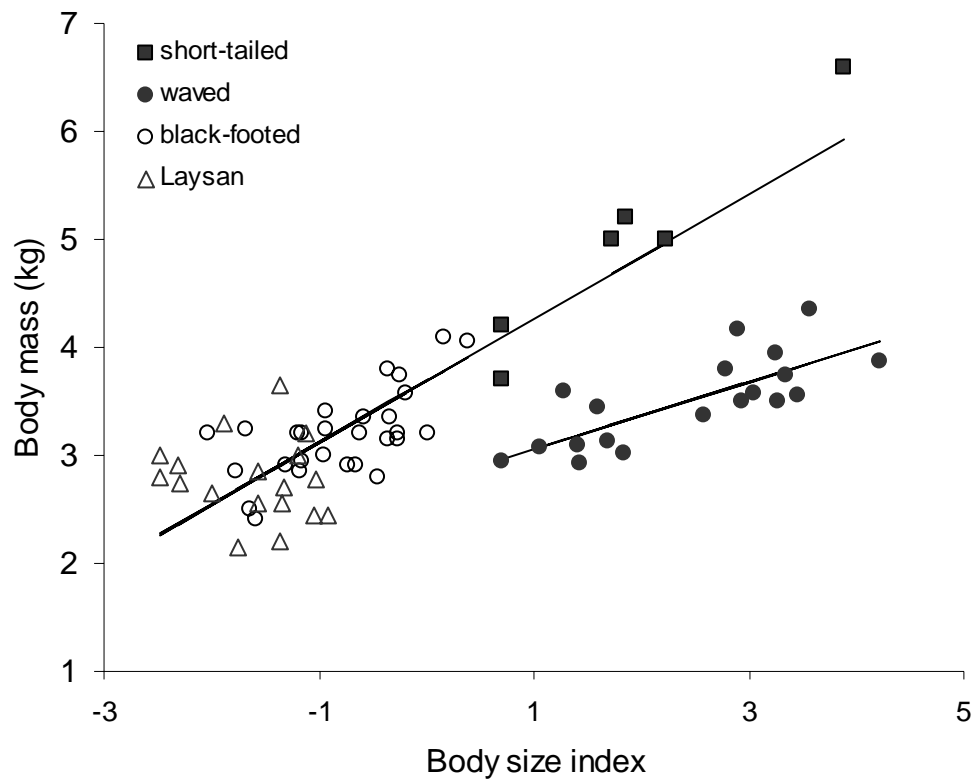


Figure 5.2. Body mass vs. body size index for short-tailed, black-footed, and Laysan albatrosses ($R^2 = 0.76$, $F_{1,50} = 154.3$, $P < 0.001$) and waved albatrosses ($R^2 = 0.76$, $F_{1,17} = 23.5$, $P < 0.001$). Body size index is the first principal component for measurements of culmen, tarsus, body girth, and wingspan, which collectively explained 82% of the variance in body measures.

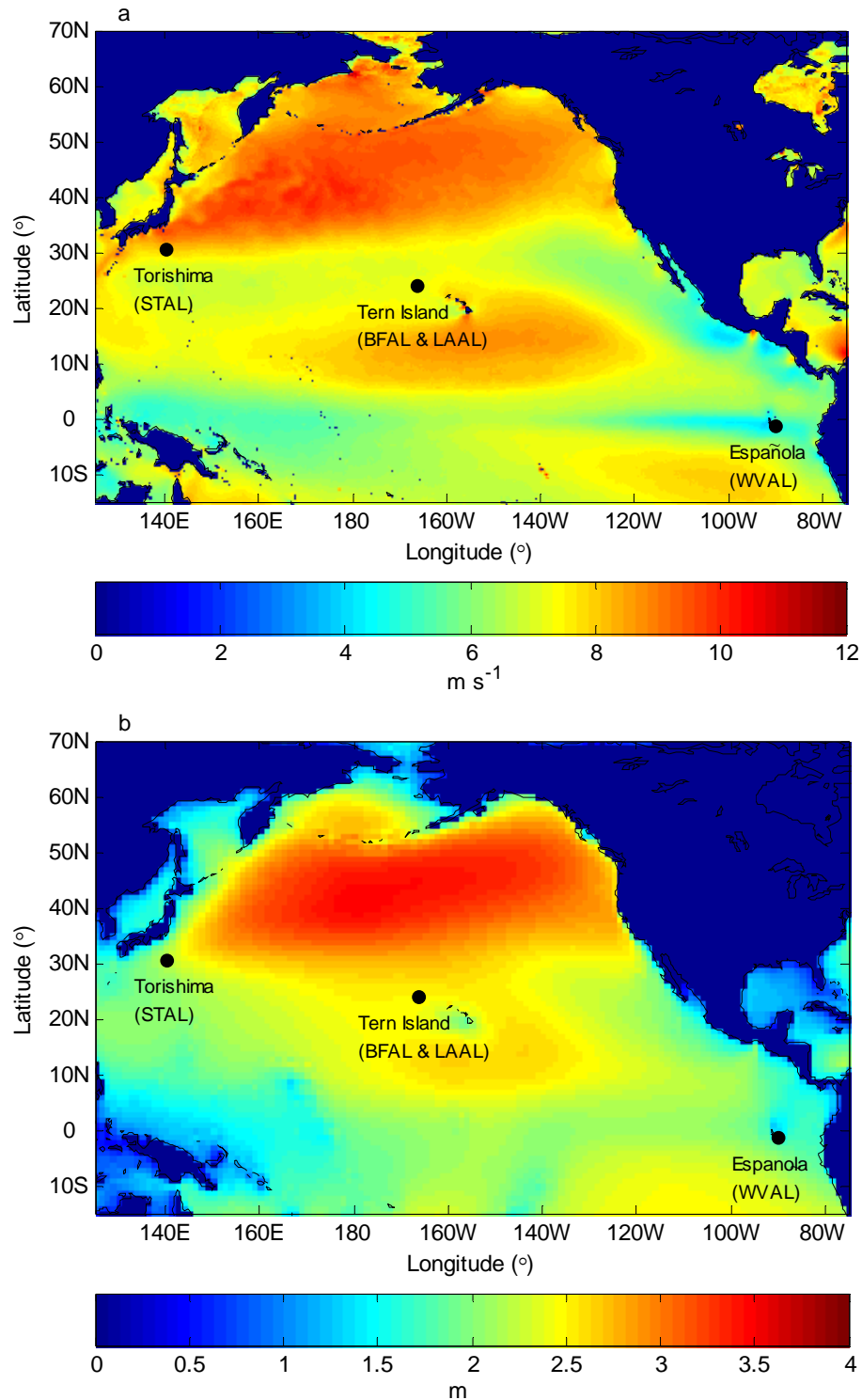


Figure 5.3. Five- and 6-yr average (1999-2004) wind speed (a; 0.25° resolution) and wave height (b; 1° latitude X 1.25° longitude resolution), respectively, and location of study colonies (dots) for North and Central Pacific albatrosses (short-tailed, STAL, waved, WVAL, black-footed, BFAL, and Laysan, LAAL).

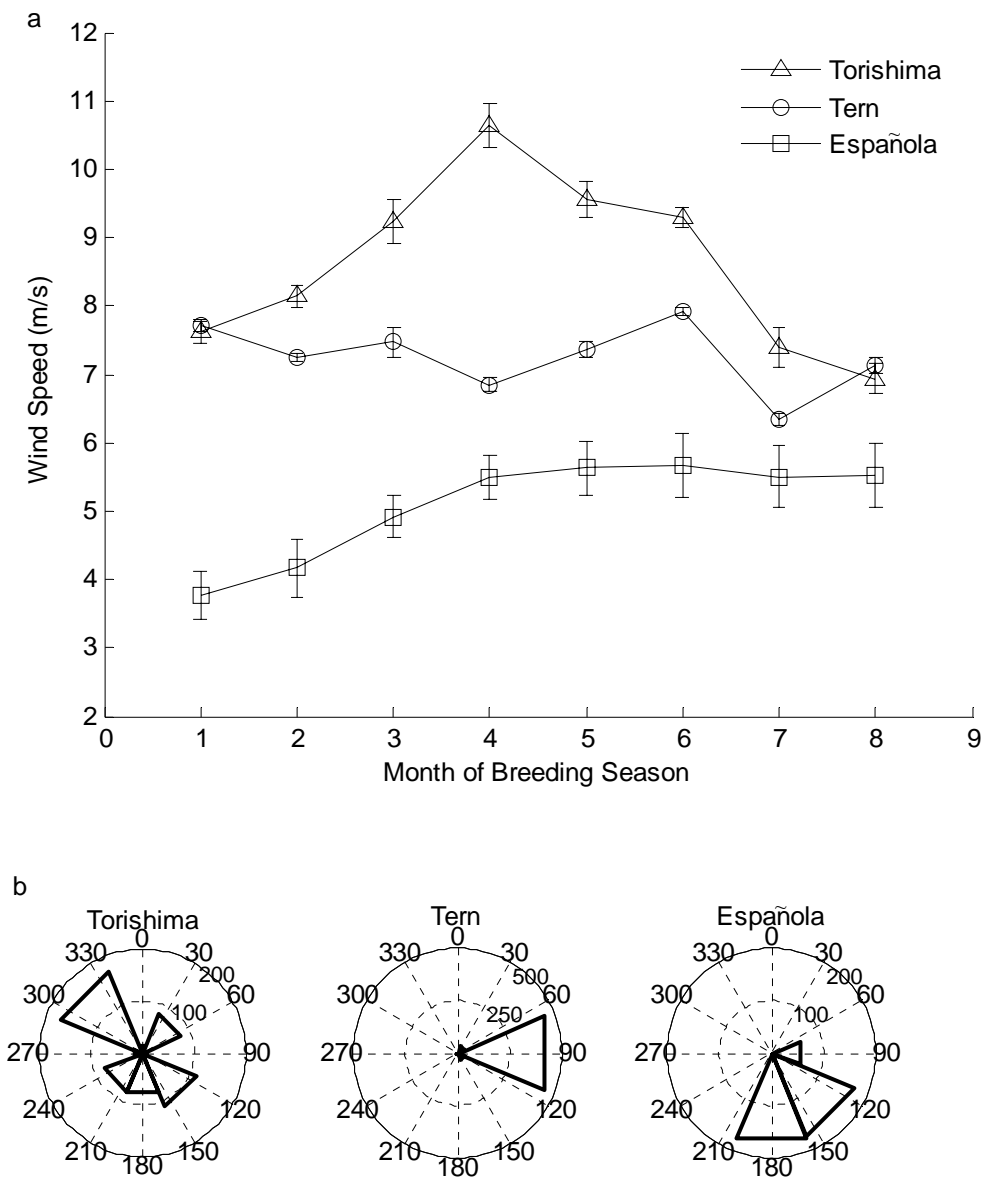


Figure 5.4. a) Average (± 1 SD) wind speeds within 100-km of breeding colonies during the first eight months of the breeding season at Torishima (short-tailed albatross), Tern Island (black-footed and Laysan albatrosses), and Española (waved albatross). b) Polar histogram of wind direction during the first eight months of the breeding season. Values on concentric rings denote number of observations per bin (8 bins of 45° each). Wind data are monthly averages over a 5-yr period (July 1999 – August 2004).

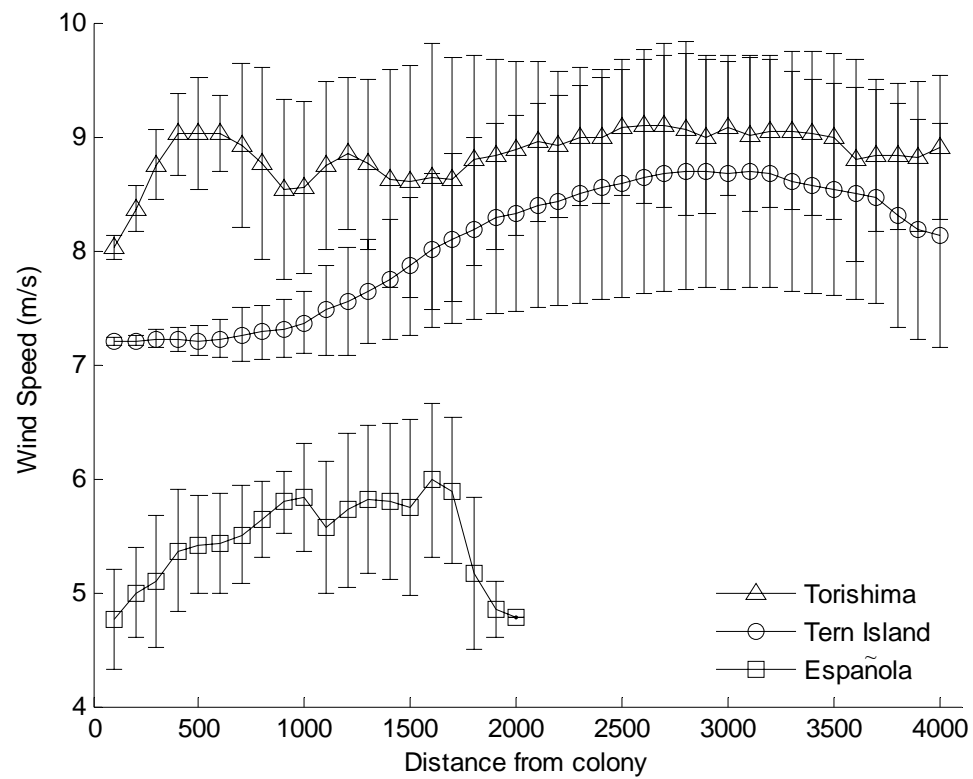


Figure 5.5. Average (± 1 SD) wind speeds at 100-km increments for radial distances within foraging areas up to 4,000 km from the breeding colonies at Torishima (short-tailed albatross), Tern Island (black-footed and Laysan albatrosses), and Española (waved albatross). Wind data are 5-yr averages (July 1999 – August 2004).

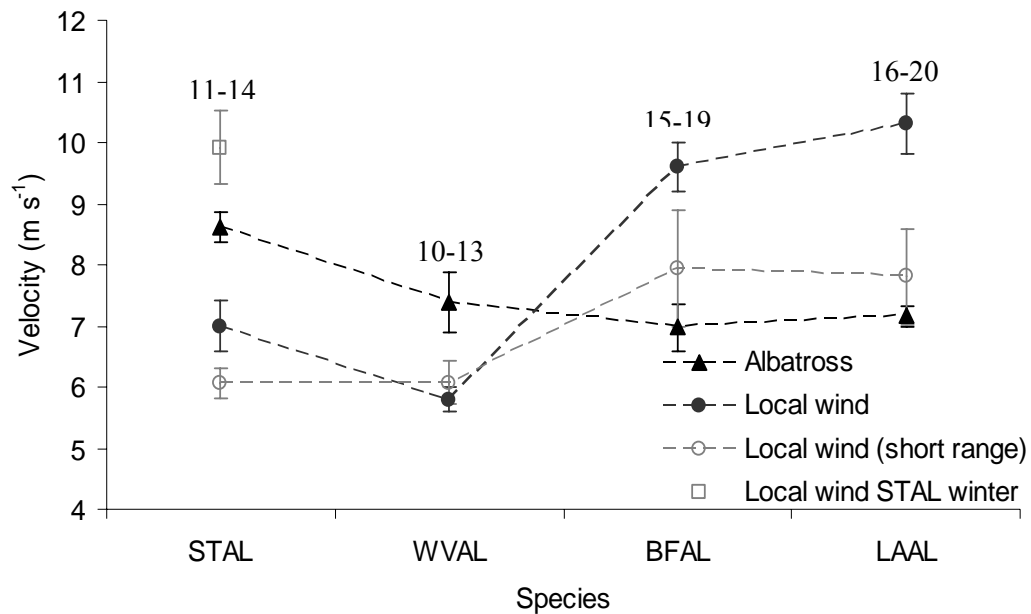


Figure 5.6. Travel speeds of albatrosses and local (≤ 15 km from trackline) wind speed encountered along flight paths for four species of Pacific albatrosses (short-tailed, STAL, waved, WVAL, black-footed, BFAL, and Laysan, LAAL). Speeds are means (\pm SE) among individuals (n is noted above symbols) for each species. Data for albatross flight speed and local wind were conducted on daily albatross movement trajectories of greater than 100 km. Data for local wind short range were wind speeds encountered when net distance traveled was < 100 km day⁻¹. Wind speed encountered during winter for STAL assume the birds flew the same flight path as the post-breeding season during the first 15 days after departing Torishima (see METHODS).

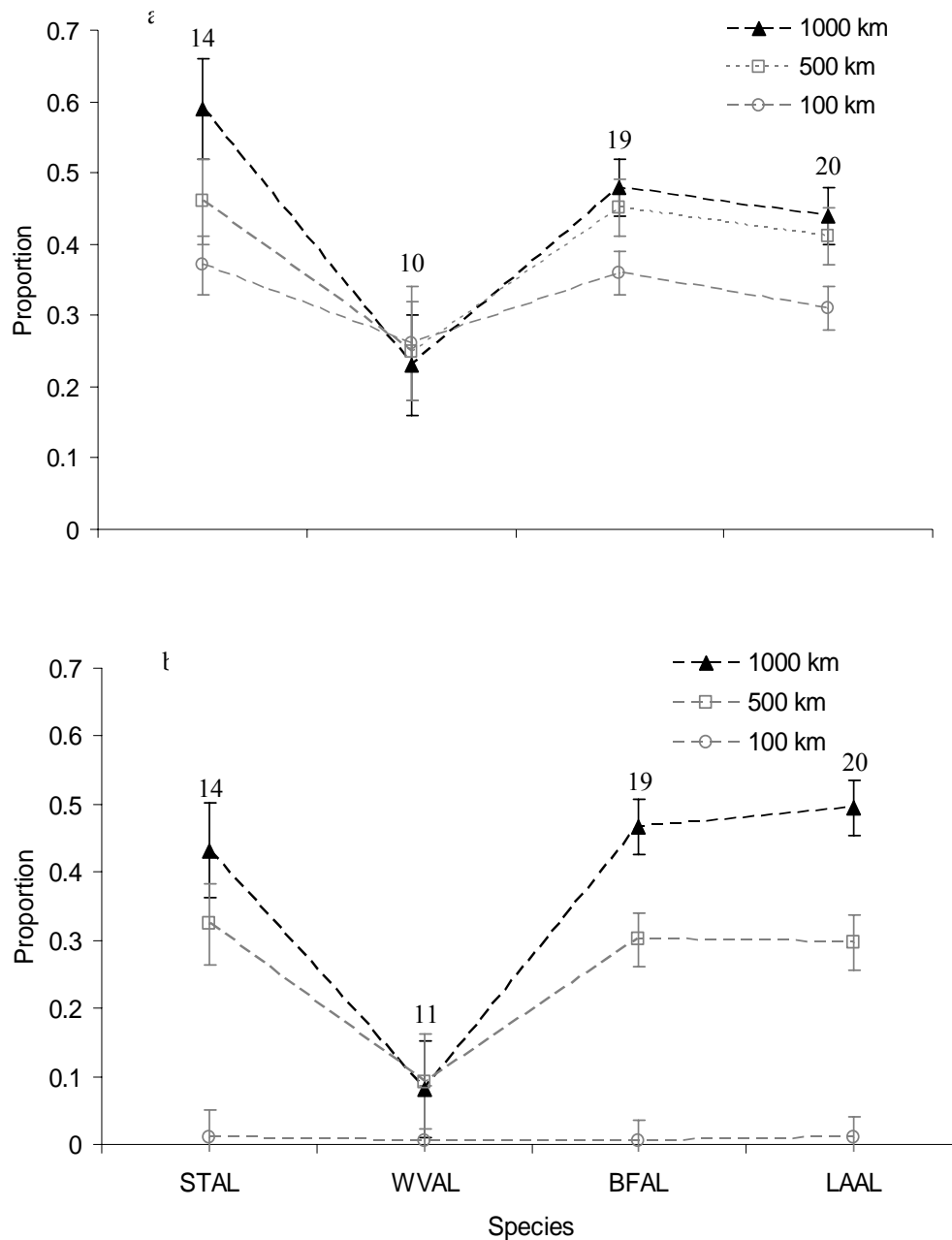


Figure 5.7. Proportion of time that wind speed (a) and wave height (b) along albatross flight paths were significantly (t -test, $P \leq 0.05$) greater than those of surrounding areas at radial distances of 100, 500, and 1000 km. Proportions are means (\pm SE) among individuals (n is noted above symbols) for each species (short-tailed, STAL, waved, WVAL, black-footed, BFAL, and Laysan, LAAL). Analyses were conducted on daily albatross movement trajectories of greater than 100 km. Note the proportion of P -values is essentially zero for the 100 km radius in b because this is approximately the spatial resolution of the wave height data and the distance used for determining local wave heights along the trackline (see METHODS).

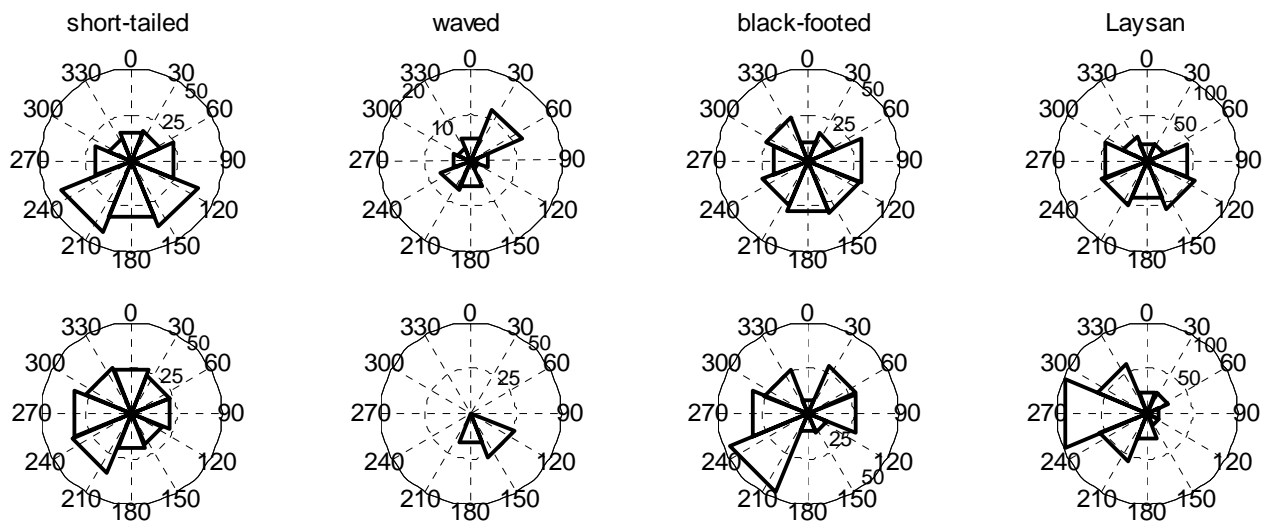


Figure 5.8. Polar histograms of wind direction relative to albatross heading (top row) and wind direction encountered (bottom row) along albatross flight paths when moving ≥ 100 km. Values adjacent to concentric rings denote number of observations per bin (8 bins of 45° each). Wind direction encountered during winter for short-tailed albatrosses is predominantly NW.

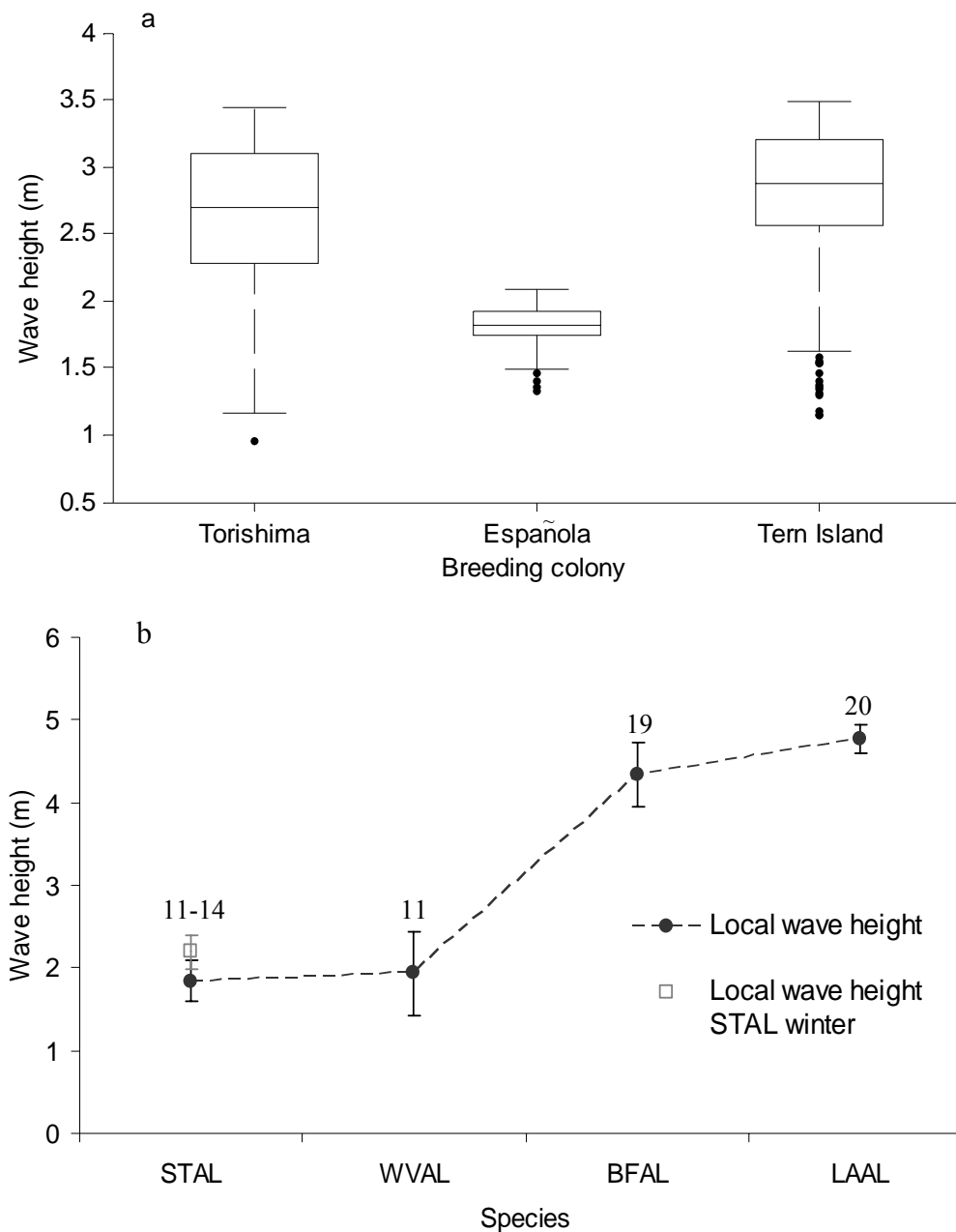


Figure 5.9. (a) Mean wave heights for a 6-yr period (1999-2004) within foraging range of albatrosses from Torishima (short-tailed albatross, STAL), Española (waved albatross, WVAL), and Tern Island (black-footed, BFAL, and Laysan albatrosses, LAAL). (b) Local (≤ 75 km from trackline) wave heights encountered by satellite-tagged albatrosses when net daily movement trajectory was ≥ 100 km. Wave height encountered during winter for STAL assume the birds flew the same flight path as during the post-breeding season within the first 15 days after departing Torishima (see Methods).

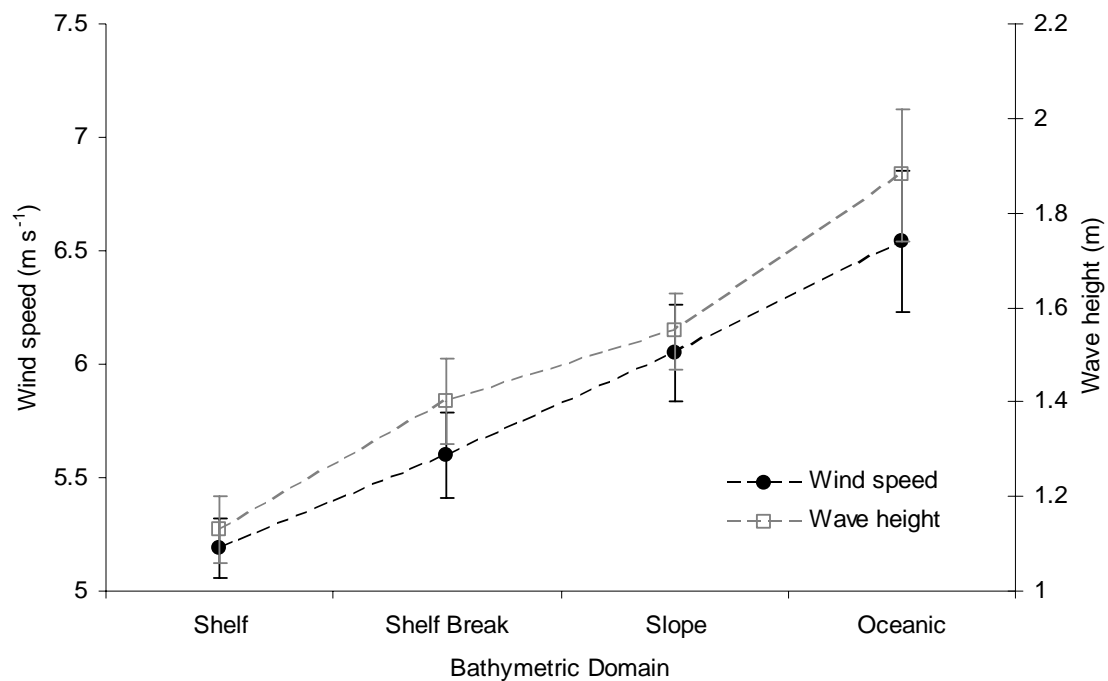


Figure 5.10. Mean (\pm SE) wind speed and wave height among bathymetric domains within the Kuroshio and Oyashio Current regions (ca. 30 – 50° N latitude, 137 – 176° E longitude) during post-breeding season dispersal (May – August) of short-tailed albatrosses from Torishima, Japan. Bathymetric domains categories are < 200 m (shelf), 200 – 1000 m (shelf break), 1000 – 3000 m (slope), and > 3000 m (oceanic).

Chapter 6. Conclusions Of The Dissertation

Using continuous tracking data from a diverse group of marine birds, I demonstrated that a variety of intrinsic (e.g., flight morphology) and extrinsic factors (e.g., availability of prey species or age classes) affect the distribution, habitat use, and spatial scale of foraging by seabirds. For albatrosses, wind and waves were important determinants of at-sea movements, but apparent habitat preferences resulted in birds sometimes traveling to regions despite relatively low wind speeds and wave heights (Chapters 4 and 5). For black-legged kittiwakes (*Rissa tridactyla*), it was clear that differences in foraging strategies, whether facultative or obligatory, had significant effects on reproduction (Chapters 2 and 3). Although I didn't test optimal foraging models explicitly, these results strongly support the Hughes' (1993) premise that optimal foraging and diet theory must incorporate considerations of functional anatomy, life history, and a variety of other even finer resolution variables (e.g., early vs. late chick-rearing stages) to effectively describe foraging activities of free-ranging animals.

Both species of seabirds for which I evaluated the spatial scale of foraging activity (Chapters 3 and 4) exhibited some consistent patterns, despite considerable variation among and within individuals. Not surprisingly, the dominant spatial scale of search activity was two orders of magnitude larger for short-tailed albatrosses (*Phoebastria albatrus*; 70 km) vs. black-legged kittiwakes (~ 0.8 km; Fig. 6.1). For short-tailed albatrosses, we did not have sufficient data to identify variables that might explain this variation, such as prey concentration or fisheries discards. Nonetheless, I was still successful in creating a general habitat use model that explained half the variation in movement patterns with a suite of marine habitat variables. Fortunately for studies involving kittiwakes, detailed diet and forage fish distribution data provided insight to observed variation in foraging strategies and demonstrated that even within prey types considered "high quality" schooling forage fishes, differences among species, age classes, and presence of seabird feeding flocks can significantly affect the duration of search and prey capture, and, thereby, affecting reproductive success. This has important implications regarding the applicability of captive feeding studies aimed

at testing the “junk food hypothesis” (Trites and Donnelly 2003, Trumble et al. 2003) that do not also consider the accessibility or ease of capture of various prey species and age classes by the predator. For example, mounting evidence indicates that abundant 1-yr-old herring (*Clupea pallasii*), specifically, leads to efficient foraging and maximum breeding success of kittiwakes at particular colonies in Prince William Sound (Suryan et al. 2000, Jodice et al. 2006, Suryan et al. 2006).

A primary purpose in using analytical techniques such as first-passage time analysis is to quantitatively differentiate between regions of area-restricted search vs. more transitory activity along the movement path. In discussions of foraging areas, I am assuming that the most sinuous portions of the track designate the regions of most intense foraging activity. For short-tailed albatrosses, I received position only data from the satellite tags; therefore, I cannot confirm this assumption. Fortunately, by directly observing kittiwakes throughout their foraging trips, we recorded behavior for every location and I could, therefore, test the assumption that the majority of foraging occurred within regions of greater first-passage time. Indeed, first-passage time was significantly longer in regions where one or more feeding attempts occurred vs. no feeding attempts (Fig. 6.2). These results were statistically significant for all spatial scales considered. Additionally, first-passage time predicted search and feeding duration within a 0.6 km radius with ~67% accuracy, whereas the relationship between first-passage time and travel duration was poor ($R^2 = 0.032$).

I next created a subsampling routine following first-passage time analysis that allowed me to model habitat use as a continuous process along the movement path, as opposed to use vs. availability approaches where identifying what habitat is truly available to an animal is often equivocal (Johnson 1980, Porter and Church 1987, Millspaugh and Marzluff 2001). This approach is consistent with Millspaugh and Marzluff's (2001) recommendation that the preferred alternative is to focus analyses on resources used by animals and to characterize animal behavior within particular habitats. This novel habitat use analysis provided a multi-scale perspective of the post-breeding season range and foraging hot spots for the short-tailed albatross, a highly migratory, upper trophic-level marine predator. The approach of subsampling first-

passage time radii by iteratively searching for maximum first-passage time and excluding overlapping radii, allowed inclusion of the entire track when modeling marine habitat use of an upper trophic-level predator. This subsampling technique could also be applied to other approaches (e.g., fractal analysis) for analyzing continuous tracking data.

Previous studies have documented strong seabird–habitat associations over 10s km, both in the sub-arctic North Pacific and in the Bering Sea (Gould and Piatt 1993). The prevalence of spatial patterns over intermediate scales (e.g., shelf-breaks, frontal systems) may partly explain why my finer scale model (10 km search radius) explained little variation in short-tailed albatross habitat associations. It also is important to consider how the resolution of sampling instruments can affect these scale-dependent patterns; for example, a mean of five locations per animal-day obtained in this study vs. global positioning system receivers that provide up to tens of thousands of locations per day (Weimerskirch et al. 2002, Fritz et al. 2003). Nevertheless, first-passage time identified appropriate spatial scales for our applications and proved to be sufficiently robust to accommodate data of varying accuracy and from two widely different methods of tracking free-ranging animals.

These results demonstrate that habitat selection within a heterogeneous landscape is a hierarchical process in which a forager relies on physical and biological cues at multiple scales when seeking productive foraging areas. For kittiwakes, those processes that influence the distribution and abundance of forage fishes create a complex environment whereby foraging conditions among relatively closely spaced colonies can vary dramatically. The efficient use of wind and wave energy by albatrosses allows them to travel throughout ocean basins to locate productive foraging areas. However, variation in weather systems and physical forcing affecting biological productivity and flight likewise create a complex foraging environment for albatrosses, but over much larger spatial scales.

Conservation Implications

Black-legged kittiwakes in Prince William Sound were not designated as injured species following the *Exxon Valdez* oil spill in 1989. There is evidence, however, that breeding conditions deteriorated between the late 1980s (pre-spill) and 1990s (post-spill) and that this occurrence may be linked to a declining herring population (Irons 1996, Suryan and Irons 2001). We found 1-yr-old herring to be strongly associated with successful reproduction in kittiwake colonies that were near herring nursery bays and farthest from areas where alternate prey may be advected from the Gulf of Alaska. These colonies also exhibited the highest reproductive success and most rapid growth for colonies in Prince William Sound during the 1970s and 1980s (Suryan and Irons 2001). The herring population in Prince William Sound fell to very low levels in years following the *Exxon Valdez* oil spill and never recovered through the 1990s. It remains equivocal, however, whether the population decline was caused by the spill or coincidental (Norcross et al. 2001). Our results suggest that reduced herring abundance is a plausible explanation for the decline in kittiwake reproductive success, especially at large, fjord colonies throughout most of the 1990s. Golet et al. (2002) also found a reduction in the breeding success and population size of pigeon guillemots (*Cephus columba*) and their prey, Pacific sand lance (*Ammodytes hexapterus*), in Prince William Sound during the same time period. In both cases, it is evident that seabird populations have changed in response to prey abundance, but, particularly for kittiwakes, it is unclear whether the indirect effects were caused by natural environmental change, the oil spill, changes in kittiwake predator populations and their impacts at the breeding colonies, or, most likely, a combination of these variables.

For the endangered short-tailed albatross, we documented the post-breeding season migration routes and provided the first description of marine habitat use for free-ranging individuals. Short-tailed albatrosses spent the majority of time along continental shelf break and slope regions within territorial waters of Japan, Russia, the United States, and Canada. Our results demonstrate strong habitat affinities of the short-tailed albatross throughout its migratory range and compliment similar habitat associations identified for this species determined from 16 years of ship-board sightings

in the Gulf of Alaska and Bering Sea (Piatt et al. 2006). As Piatt et al. (2006) noted, such apparently predictable “hotspots” for short-tailed albatrosses should facilitate the at-sea conservation of this species. During the nonbreeding season, satellite-tagged short-tailed albatrosses spent the greatest proportion of time within the United States exclusive economic zone off Alaska, regardless of whether they were tagged in Japan or Alaska (Suryan and Balogh 2005). Fortunately, seabird bycatch mitigation studies have been conducted for Alaskan longline fleets (Melvin et al. 2001) and seabird deterrent regulations are currently in place in Alaska. Our data, however, support the need for such efforts to be more widespread among regions and nations of the Pacific Rim, especially given potential differences in post-breeding distributions between genders and age classes. Females may have a prolonged exposure to fisheries in Japanese and Russian waters compared to males and juvenile birds may have greater exposure to fisheries off the west coast of Canada and the United States (Suryan and Balogh 2005). Opportunistic sightings of short-tailed albatrosses off the west coast of North America confirm the prevalence of juvenile and subadult age classes (Hasegawa and DeGange 1982 and recent unpublished sightings).

The United States Short-tailed Albatross Recovery Team has identified colony re-establishment on a safe, non-volcanic island as a requirement for down- or delisting of this endangered species (USFWS 2005). Probable sites for re-colonization efforts include Japanese islands where this species historically bred (especially the Ogasawara [Bonin] Islands). Short-tailed albatrosses have infrequently been observed in the Hawaiian Archipelago, including one individual that has periodically laid an apparently unviable egg on Midway Island (USFWS 2005). Although there are no confirmed records of short-tailed albatrosses breeding on the Hawaiian Islands, Midway has been suggested as a potential site for a new colony establishment. Analyses in Chapter 5 indicate that albatrosses foraging from the northwestern Hawaiian Islands during the breeding season could encounter wind and wave conditions comparable to those for birds breeding among historical sites in Japan. Wind and wave conditions, therefore, appear adequate for foraging flights of this relatively large-bodied albatross. However, the strong association of short-tailed albatrosses with continental shelf-break

and slope habitats calls into question whether islands in the central North Pacific, > 3000 km from continental margins, are appropriate breeding habitat for this species.

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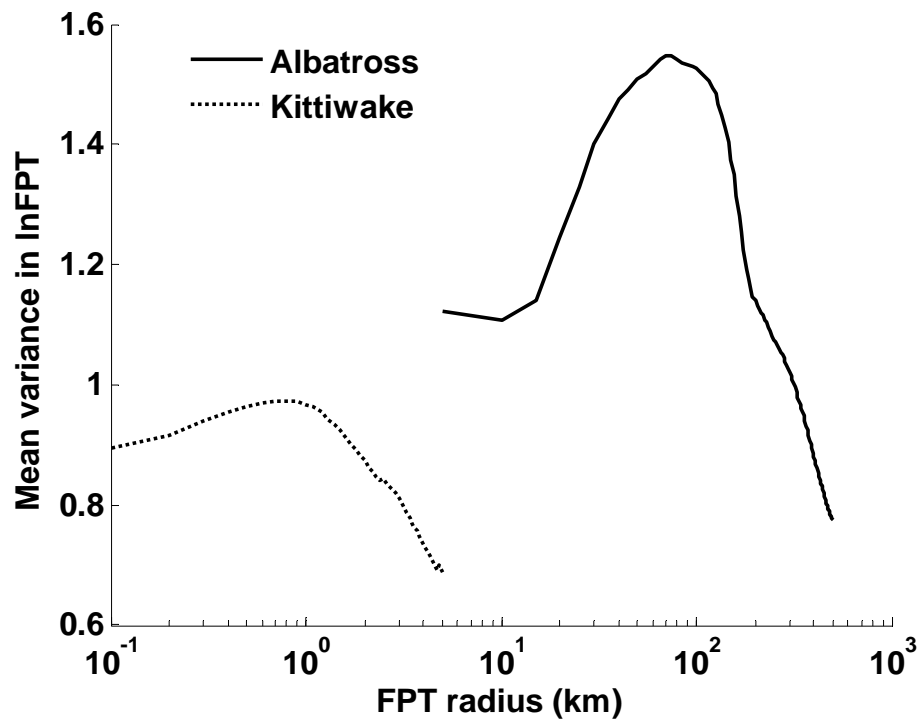


Figure 6.1. Results of first-passage time analysis for black-legged kittiwake and short-tailed albatross tracking data. Peak spatial scales of area-restricted search activity for kittiwakes was ~ 0.8 km vs. 70 km for albatrosses.

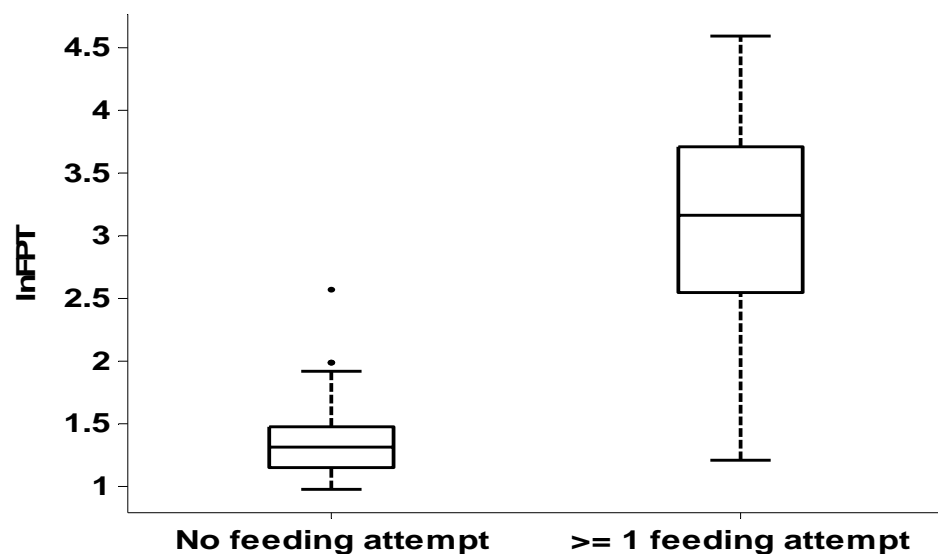


Figure 6.2. Comparison of mean first-passage time for black-legged kittiwakes where no feeding vs. ≥ 1 feeding attempt occurred within a 0.6-km search radius ($P < 0.001$, $Z = -5.42$, $n = 46$). First-passage time was significantly greater where feeding occurred vs. non-feeding areas at all spatial scales considered.

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