FORAGING ECOLOGY OF ANTARCTIC SEABIRDS IN THE SCOTIA SEA

BY

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A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

2007

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This manuscript has been read and accepted for the
Graduate Faculty in Biology in satisfaction of the
dissertation requirement for the degree of Doctor of Philosophy.

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ABSTRACT

FORAGING ECOLOGY OF ANTARCTIC SEABIRDS IN THE SCOTIA SEA

By

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Adviser: Dr. Richard R. Veit

I studied the foraging behavior of seabirds near the western Antarctic Peninsula. The central questions in this study are: *Where do seabirds forage*? and *How do they respond to prey distribution*? I use a combination of field surveys and analytical techniques to examine the response of Cape Petrels (*Daption capense*) and Chinstrap Penguins (*Pygoscelis antarctica*) to changes in krill distribution (*Euphausia superba*). First, I present a study of satellite-tracking and ship-based survey for measuring the foraging distribution of penguins. I demonstrate that foraging distributions of penguins, measured by these two methods, are quite different. All satellite-tracked penguins foraged in a core area, whereas foraging penguins counted from ship were greater to the east and west of the core area. Penguins counted from ship were correlated with dense krill patches that were located 10-15 km from breeding colonies. Second, I investigate whether seabirds prefer to forage in locations on the basis of krill patchiness. Penguins prefer to forage in areas where krill are patchy at scales ranging from 1 to 5 km, whereas petrels preferred areas where krill was patchy at one particular scale (e.g. 1 or 5 km). Third, I establish a system for monitoring the association of foraging seabirds and krill near the Antarctic Peninsula. Over three years (2004-2006), I found that abundance of krill varied by more than 2 orders of magnitude, and there is a negative relationship between abundance and patchiness of krill. Penguins were only associated with krill when patchiness of krill was low (2004). Petrels were associated with krill when patchiness of krill was either high (2006) or low, but not at intermediate levels (2005). Fourth, I present a study on how changes in krill distribution, within a few days, affects seabird foraging distribution. After a gale, I found that krill abundance decreased by 50% and horizontal distribution of krill shifted between two hydrographic canyons. Foraging distribution of petrels were linked to changes in krill distribution, but penguins were not.

Acknowledgments:

This dissertation is dedicated to Jeffrey Santora and Arlene Parsons-Santora.

I am grateful for the excellent guidance and support of Dr. Richard R. Veit. This work would not have been possible without him.

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CHAPTER 1

INTRODUCTION

My objective in this dissertation is to investigate the foraging ecology of Antarctic seabirds in the Scotia Sea near the western Antarctic Peninsula (Fig. 1.1). Seabirds are an excellent group of species for studying foraging ecology because their foraging distributions can be measured simultaneously along with prey and oceanographic factors (Hunt 1990). This is a rare ability in studies of foraging vertebrates and was important in my decision to study them. I organized this dissertation around a framework of observations that I developed while at sea in the Southern Ocean. The central questions in this study of seabird foraging ecology are: (1) Where do they forage? and (2) How do they respond to prey distribution? I use a combination of field surveys and analytical techniques to address variations of these questions in subsequent chapters.

The majority of seabirds near the Antarctic Peninsula region eat krill. The Antarctic krill (*Euphausia superba*, Fig. 1.2) is integral to the food web in the western Antarctic Peninsula ecosystem. Krill are known to form dense swarms, and patches are distributed in a hierarchical fashion, where patches are nested within patches. I studied krill distribution using hydro acoustics and nets to determine how krill influences where seabirds choose to forage and potentially how they may locate krill patches. In each of the chapters to follow, I investigate the responses of seabirds to krill distribution, ranging from how different colonies of penguins may forage on different krill patches, to the effect of a storm event on the distribution of krill and consequent behavioral responses of petrels.

I studied the foraging ecology of penguins (Order: ***Sphenisiciformes***) and petrels (Order: ***Procellariiformes***). Penguins, probably the most familiar Antarctic seabirds are specially adapted for diving in search of prey. They are diurnal foragers, and during the breeding season make daily commutes to foraging locations. Their breeding populations have been routinely monitored for decades, and population growth and reproductive success is related to prey abundance. Yet, answers to "Where do they to forage?" and "How do they respond to prey distribution?" are not at all clear. I focus on answering these questions by studying the foraging ecology of the Chinstrap Penguin (*Pygoscelis antarctica*, Fig. 1.3). I show that: 1) foraging distributions of Chinstrap Penguins are different when estimated by satellite tracking and ship-based surveys, 2) penguins prefer to forage in areas where krill are patchy across a range of scales, 3) spatial association of penguins and krill patches is more probable when abundance of krill is high and patchiness of krill is low, and 4) foraging distributions of penguins were not altered by a short-term storm event.

The Cape Petrel (*Daption capense*, Fig. 1.4), probably the most conspicuous petrel of the Southern Ocean, is the other species I chose to study. I became fascinated with this species after viewing thousands of them on my first expedition to the Elephant Island area (61°S, 55°W, Fig. 1.1). After only a few days of observing their foraging behavior, I realized that they should be good indicators of the Antarctic marine environment. They are gregarious seabirds, routinely forming dense foraging flocks (Fig. 1.4), which are easy to monitor for behavioral changes (Fig. 1.5-1.6). Cape Petrels are restricted to feeding at the surface, but overcome this vertical constraint by the ability to sample a broad horizontal dimension through dynamic soaring to minimize energy expenditure during flight. In addition, petrels generally go on longer foraging trips than penguins, lasting for days and can forage day or night. The size and distribution of their breeding populations are poorly understood. In the Antarctic Peninsula region, they nest in small and scattered colonies along steep icy cliffs that are nearly inaccessible to humans. I examine the relationship between their foraging behavior and krill distribution. For Cape Petrels, I show that their: 1) feeding behavior is a good indicator of krill patchiness, 2) distribution patterns track changes in abundance and patchiness of krill, and 3) foraging behavior was affected by a short-term storm event, but they were able to track re-distribution patterns of krill within days of the event.

In subsequent chapters I examine foraging behavior of Cape Petrels and Chinstrap Penguins in response to krill distribution. Choice of feeding locations for petrels and penguins may differ primarily because of locomotion. Obviously, Cape Petrels are more restricted in the amount of prey they can detect in the water column, but they can overcome this constraint by sampling a broader horizontal dimension through dynamic soaring to minimize energy expenditure during flight. On the other hand, penguins must swim to reach foraging locations, and should therefore restrict the amount of horizontal space and maximize vertical coverage through diving. In addition, Chinstrap Penguins are diurnal foragers and return to land in the evening, whereas petrels generally go on longer foraging trips lasting for days and forage day or night. Nevertheless, because of differences in their locomotion, these predators represent two types of krill predators:

aerial surface-feeding petrels and pursuit diving penguins. Thus it is important to understand how these predators respond to krill distribution in their own respective ways.

Organization of Dissertation:

Chapter 2: Simultaneous satellite-tracking and ship-based surveys of foraging Chinstrap Penguins

If a seabird forages in the ocean and no one is around to observe it, does it really happen? In Chapter 2, I present the first ever synthesis of a simultaneous satellite-tracking and ship-based survey. I demonstrate that foraging distributions of Chinstrap Penguins, measured by these two methods, are quite different. I found that satellite-tracked penguins foraged in a “core area”, whereas penguin aggregations counted from ship were greater in size to the east and west of the “core area” used by satellite-tracked birds. In addition, I suspect that penguins from neighboring colonies might use separate areas to forage for krill. I recommend that future investigations track individual penguins from neighboring colonies to test whether this is true. There are many exciting directions to pursue after conducting this study. I suspect that my work will be helpful in constructing *realistic* models of foraging penguins in the Antarctic.

Chapter 3: Influence of krill patchiness on seabird foraging behavior near Elephant Island, Antarctica

Differences in the dispersion of krill should be expected to influence the effectiveness of foraging strategies employed by seabirds. In Chapter 3, I investigate whether Cape Petrels and Chinstrap Penguins prefer to forage in locations on the basis of krill patchiness. The study was unique because: 1) it involved measuring foraging behavior of seabirds while simultaneously estimating distribution of krill patches using a towed acoustic array, and 2) transects were repeatedly sampled during a 10 day period. I ask if petrels and penguins choose areas where krill are patchy across a range of scales or if they prefer areas where krill is patchy at one particular scale. I found that foraging behavior of seabirds is an excellent indicator of krill patchiness. Penguins prefer to forage in areas where krill are patchy at scales ranging from 1 to 5 km, whereas petrels preferred areas where krill was patchy at one particular scale (e.g. 1 or 5 km). The results from this study provided insight on where and why petrels and penguins choose to forage. In addition, this study provided me with a platform for addressing inter-annual changes in seabird foraging behavior in relation to krill patchiness.

Chapter 4: Annual Spatial Variability of Krill Influences Seabird Foraging Behavior near Elephant Island, Antarctica

My goal was to establish a system for monitoring the spatial association of seabirds and krill patches in the western Antarctic Peninsula region. There is a considerable amount of evidence suggesting that there are “good” and “bad” krill years in the western Antarctic Peninsula, but it is not known how this fluctuation affects seabirds. Following this rationale, I became particularly interested in addressing whether or not annual changes in krill patchiness influences patchiness of foraging predators. In Chapter 4, I present the first synthesis exploring annual variability of krill and seabird distributions near Elephant Island. I examined the annual spatial association of krill and seabirds over three years. I found that abundance of krill varied by more than 2 orders of magnitude, and there was a negative relationship between abundance and patchiness of krill. This means that when krill was less abundant, there were fewer patches available to predators. I tested whether patchiness of krill influences where seabirds choose to forage. I found that Cape Petrels are excellent indicators of krill abundance and patchiness and their foraging distributions track changes in krill remarkably. When krill patches were clumped and scarce, Cape Petrels were tightly associated with krill patches. I also found that spatial association between penguins and krill occurs only when abundance of krill was high, and patchiness of krill was low. The work I conducted in this chapter will be used as a framework for future assessments of the distribution of foraging seabirds and krill near Elephant Island.

Chapter 5: Effect of a Near Gale on the Distribution of Krill and their Predators

There is little known about the response of predator foraging behavior to fine-scale changes in prey distribution. Changes in krill distribution, over a few days, likely have significant implications for predator foraging success. Moreover, different foraging strategies may allow some species to respond more quickly or be less affected by changes in the horizontal and vertical distribution of krill. In Chapter 5, I present a synthesis on how a gale influences the distribution patterns of krill and subsequent foraging behavior of petrels and penguins. The southern Drake Passage region (Fig. 1.1) is a notorious place for foul weather, and on average a storm passes through the region every 3-7 days. During a 10-day survey of the waters north of Livingston Island we experienced a gale in the middle of the survey that caused all ship operations to cease.

I conducted an analysis to determine if the gale altered krill distribution (vertically and horizontally) and how it influenced foraging birds. I found that krill abundance was halved and horizontal distribution of krill shifted from the east to the west canyon after the storm event. In addition, there were fewer krill closer to the surface after the storm. I found that Cape Petrels tracked changes in krill distribution. Cape petrels were more affected by changes in krill distribution than were penguins. Feeding aggregations of petrels were repeatedly detected in the eastern canyon prior to the storm event, but no feeding aggregations were found there in the post storm survey, with all feeding aggregations being located in the western canyon where krill biomass was greater. Thus, foraging petrels tracked the changes in their principal prey within the course of a few days. On the other hand, chinstrap penguins displayed little variation in their foraging distribution patterns with respect to the storm event. Chinstrap penguins routinely foraged closer to shore and at the heads of the canyons.

The variability of the krill-centered ecosystem is high within the spatial and temporal scales measured in this study ($10^2 – 10^3$ km^2, 10-10^2 hr). Thus, ecosystem surveys that visit a site or station only once, or multiple times separated by weeks or more may be biased as a result of recently or presently occurring mesoscale phenomena such as the passing of a low pressure system, as in this study.

Implications of Research on Antarctic Seabird Foraging Ecology:

Depletion of krill by commercial fisheries could potentially cause destabilizing effects in the zooplankton community whereby krill patches may become scarce. Consequently birds may have some difficulty acquiring enough energy to sustain basic metabolic activities, and provision resources for egg production, and chick rearing. Our survey occurred in January, when breeding Cape Petrels and Chinstrap Penguins are either incubating eggs or provisioning food for their chicks. If commercial krill fishing is conducted near Elephant Island during the breeding season, than conservation policies should be developed to sustain foraging requirements of predators. If krill patches become depleted by fisheries at a rate faster than foraging birds can adjust to, than there is good reason to expect that reproduction and survivorship of birds will decline. Moreover, if fisheries target sites that are important for feeding birds, such as krill patches in proximity to breeding colonies, than negative seabird-fishery interactions might occur.

Average air temperature in the western Antarctic Peninsula has increased dramatically by 6° C during the last 50 years (Weller 1992, Smith *et al.* 1996, Clarke *et al.* 2007). This warming has resulted in warmer surface waters, reduced ice cover in winter, melting glaciers and clearly detectable changes in ocean fauna (Croxall 1992, Hewitt 1997, Loeb *et al.* 1997, Wilson *et al.* 2001, Fraser and Hoffman 2003, Atkinson *et al.* 2004, Croxall *et al.* 2004, Moline *et al.* 2004, Clarke *et al.* 2007, Murphy *et al.* 2007). Furthermore, there is good reason to suppose that patterns of krill abundance might be linked to the large-scale climate variability of the El-Nino Southern Oscillation (ENSO), (Murphy *et al.* 2007).

Since seabirds are top predators, their foraging behavior should be a good indicator of climate change, and the food web of which they are a part (Hunt 1990, Veit *et al.* 1996, Ainley *et al.* 1998, Boyd and Murray, 2001, Thompson and Ollason 2001, Davoren and Montevecchi 2003, Fraser and Hoffman 2003, Croxall 2004). ENSO may influence population dynamics of seabirds by altering wind and sea currents, which in turn may affect food resources (Veit *et al.* 1996). The effect of climate variability on Antarctic seabird populations is likely to be indirect, through change in key foraging habitats and prey availability (e.g. SST, position of fronts and edge of pack ice). Since seabirds are downstream of the energy flow within an ecosystem (Hunt 1990), changes in energy flow through ecosystems should be reflected in the ecology of seabirds near the end of the food chain. Since the food chain in the western Antarctic Peninsula region is short (i.e. primary productivity → krill → birds), changes in seabird populations due to climate change could be rapid (Murphy *et al.* 2007). If krill distribution is influenced by climate variability, than krill-dependent seabirds will certainly be affected as well.

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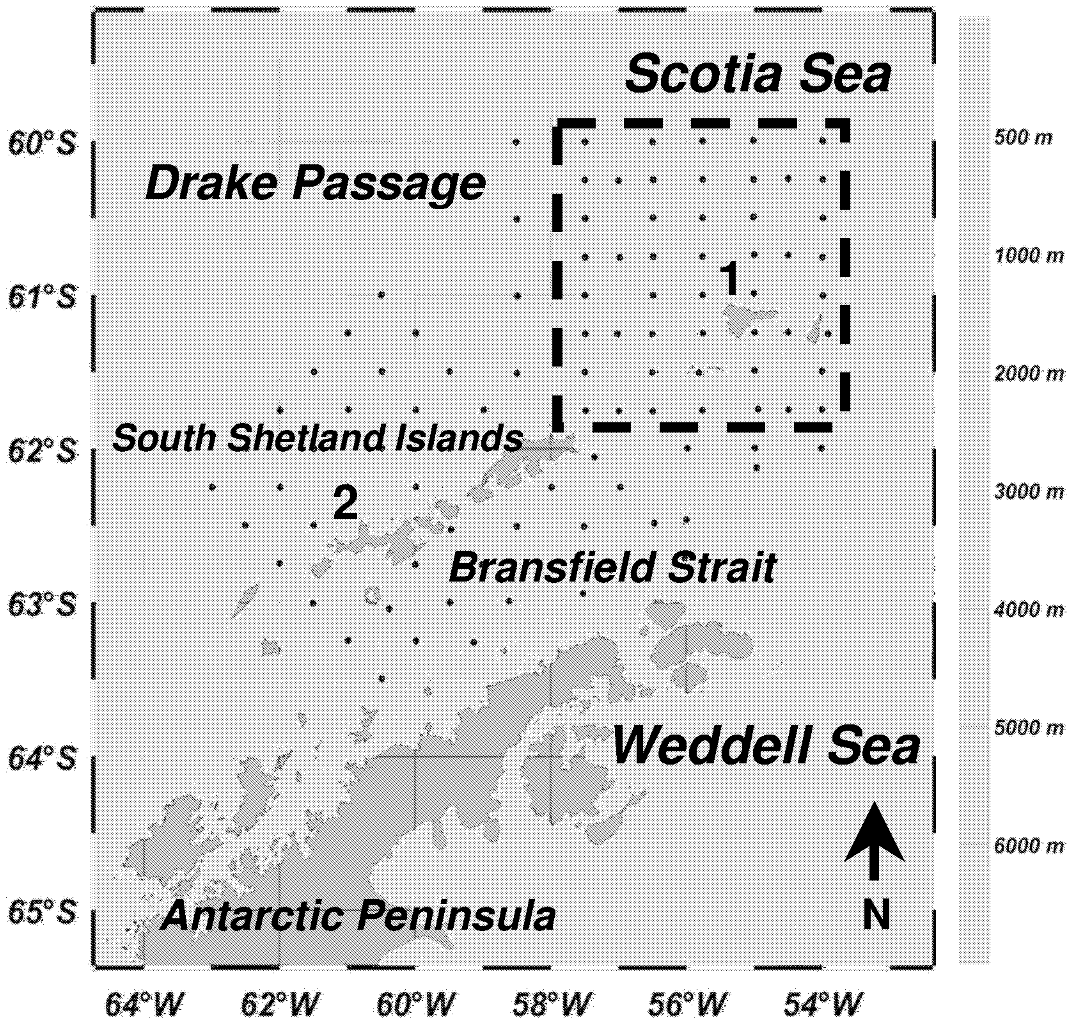


Figure 1.1: The western Antarctic Peninsula region lies between the Scotia and Weddell Seas. The region is an area of dynamic hydrographic variability that sustains one of the most abundant krill populations in the Southern Ocean. The research in this dissertation occurred near Elephant Island (**1**) and Livingston Island (**2**).

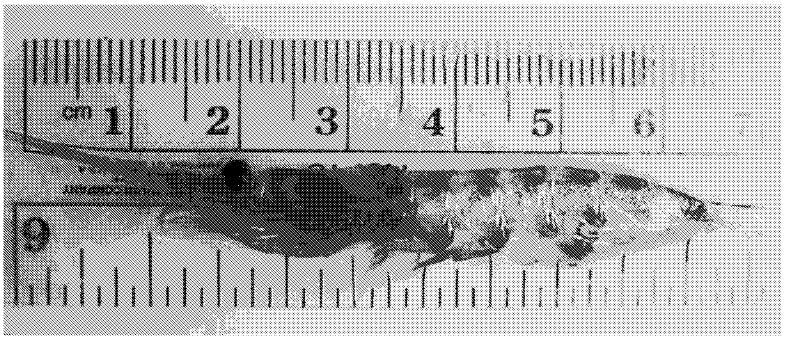


Figure 1.2: Adult Antarctic Krill (*Euphausia superba*), photograph taken during January 2004 near Elephant Island by JAS.

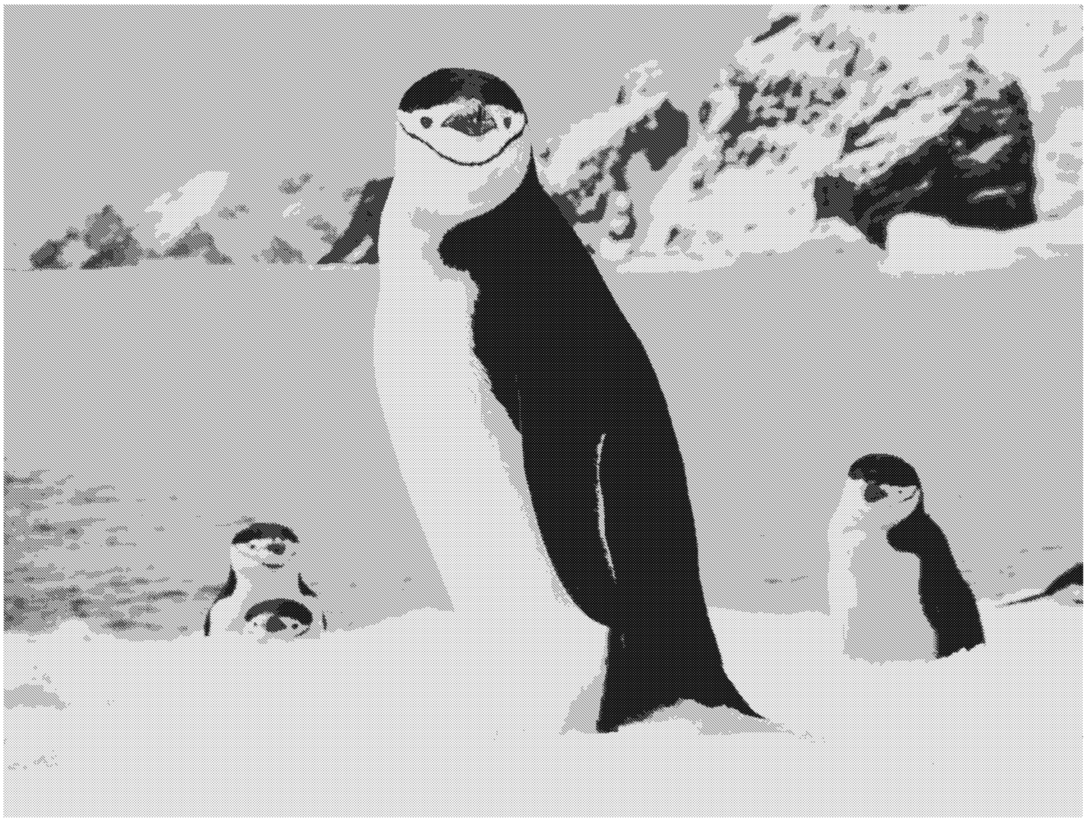
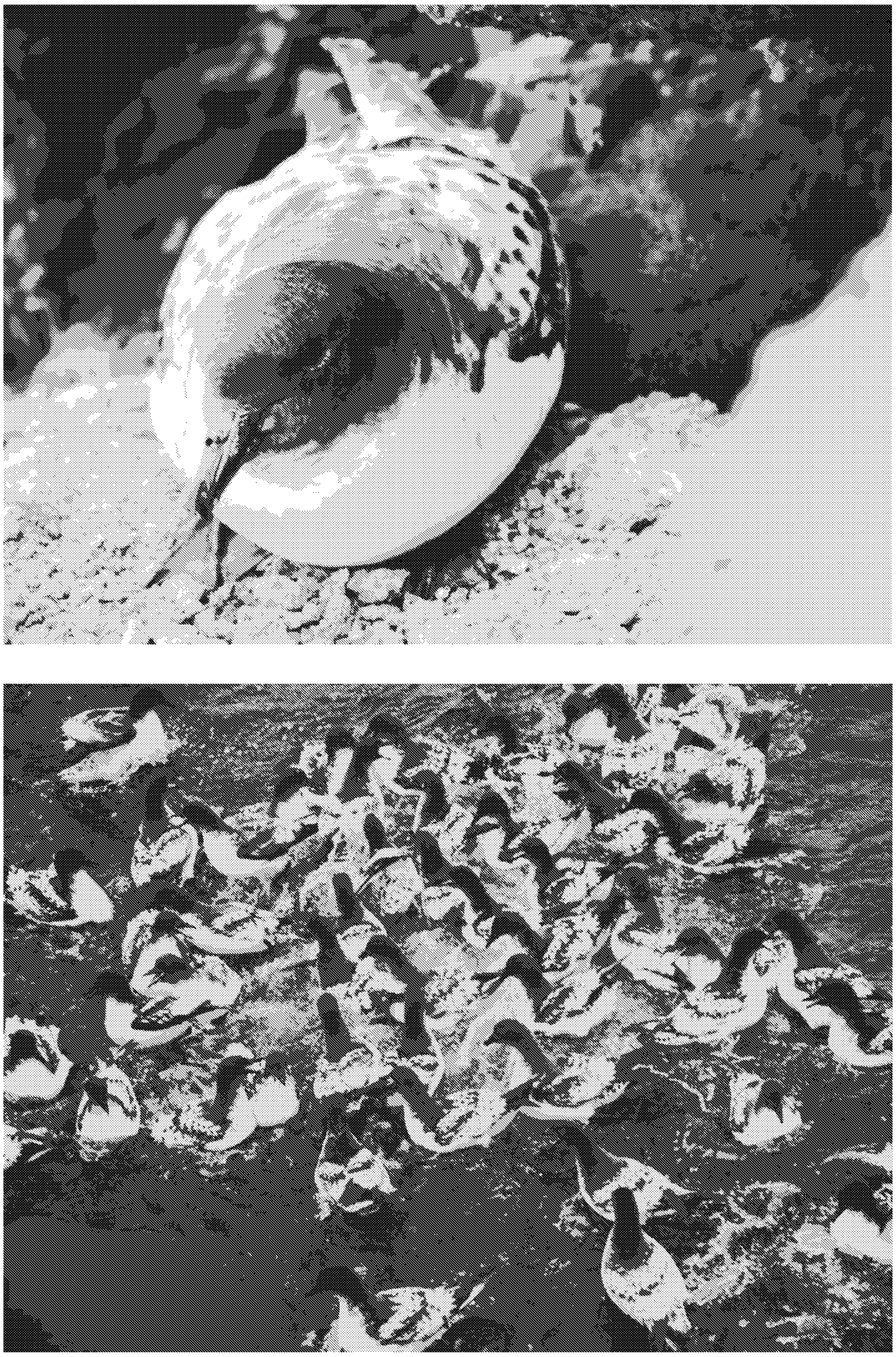


Figure 1.3: Chinstrap Penguin (*Pygoscelis antarctica*) near its nest at Point Wild, Elephant Island during December 2003. Photograph by JAS

Figure 1.3b: Adult Chinstrap Penguin (*Pygoscelis antarctica*) and its chick in a breeding colony at Penguin Island near King George Island, during late February 2003. Photograph by JAS



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CHAPTER 2

Simultaneous Satellite Tracking and Ship-Based Surveys of Foraging Chinstrap Penguins (*Pygoscelis antarctica*)

INTRODUCTION

Two methods have been used to determine habitat use and foraging range by marine birds. The first method is ship-based strip-transects to map spatial abundance (Tasker et al. 1984). This method has the advantage of large sample sizes, but suffers from lack of knowledge of the breeding status of birds seen (Table 2.1). The second method is to track with radio or satellite telemetry, GPS receivers or geolocators (Trivelpiece et al. 1986, Prince et al. 1992, Davis and Miller 1992, Ostrand et al. 1998, Ryan et al. 2004, Schaffer et al. 2006). With tracking, one knows the breeding status of the tagged individuals, but sample size is limited due to the small number of tags usually deployed (Table 2.1). The goal of measuring foraging distributions is to determine which resources are important for seabirds and how they locate them. Our objective is to test if distributions of foraging Chinstrap Penguins (*Pygoscelis antarctica*) measured by satellite tracking and strip-transects differ.

The objective of this study is to compare the two methods. We will use the novel approach of combining both methods to improve estimation of the foraging areas chosen by Chinstrap Penguins (*Pygoscelis antarctica*). We had the unusual opportunity in February 2005 to directly compare data from satellite-tracked birds to distributions measured by shipboard. In addition, we collected data on distribution of krill patches to determine why penguins aggregate where they do. An unknown proportion of penguins seen at sea could be immatures, non-breeders or breeders from distant colonies. Therefore, we wanted to determine if the distribution of traveling penguins, counted from shipboard, indicate probable locations on land. We show that penguin foraging distributions estimated by the two methods differ drastically and present evidence that penguins from different colonies might account for differences between methods.

Other benefits of ship-based surveys are that they provide information on the distribution of prey sought by birds and physical environment (e.g. location of fronts), (Hunt 1990, Hunt et al. 1992, Veit et al. 1993, Fauchald et al. 2000, Davoren et al. 2003). Another benefit of ship-based surveys is that they can measure several species simultaneously (i.e. seabirds and mammals). Such information has been used to quantify community composition and feeding assemblages in response to prey distribution and physical features (Harrison et al. 1991, Silverman and Veit 2001, Silverman et al. 2004).

Other benefits of tracking include year-round, global coverage and the ability to measure small-scale behavior like turning rates (Trivelpiece et al. 1986, Trathan et al. 1998, Nel et al. 2000, Klomp and Schultz 2000, Nicholls et al. 2002, Barlow and Croxall 2002, Catry et al. 2004, Wilson et al. 2005, Schaffer et al. 2006). A drawback of tracking studies is the difficulty of directly linking where the bird foraged with the distribution and quality of prey. Nevertheless, data gathered from tracking studies provide information on movements of individuals, which is important for understanding how individuals make decisions on where to forage. Unfortunately, there are potential adverse effects on foraging behavior due to instrument attachment (Croll et al. 1991, 1996).

METHODS

Penguins were fitted with satellite transmitters from a colony at Cape Sherriff, Livingston Island (62°36'S, 60°30'W), (Fig. 2.1). Simultaneously, the research vessel R/V Yuzhmorgeologiya surveyed 10 transects, each 45 km long to measure the distribution of penguins, krill and other physical and biological variables (Fig. 2.1).

Ship-Based Survey

Transects were conducted north of Livingston Island (62°36'S, 60°30'W), Antarctica from 2 to 10 February 2005. Krill abundance was measured using acoustic transducers (Simrad EK60) operating with 38, 70, 120, and 200 kHz transducers mounted on the hull. During the survey, pulses were transmitted every 2 seconds at 1 kW for 1 ms. Backscattering was averaged over 1 km bins to produce NASC (Nautical Area Scattering Coefficient) values, which are proportional to the density (g/m^2) of krill (Hewitt et al. 2003). Additionally, NASC values were integrated over 10 m depth bins down to either 200 m, or the sea floor, whichever was less. These values of NASC were then converted to estimates of krill biomass (g/m^2) using the length-frequency distribution of krill caught in nets and a theoretical acoustic scattering model (Demer and Conti 2005).

Data on Chinstrap Penguin abundance and behavior were collected continuously by 2 observers using binoculars along strip transects during daylight hours. Counts were made within an arc of 300 m from directly ahead to one side of the ship while underway

(Tasker et al. 1984). Each record was assigned a time to the nearest second and a spatial position from the ships global positioning system. Individual penguins, or flocks of penguins, were assigned a behavioral code. The behaviors were either sitting, or porpoising. We recorded travel direction on an 8-point compass (i.e. 45° groupings) for all porpoising penguins. We wanted travel direction in order to determine if penguins were commuting to feeding areas from colonies using shipboard data. Differences in travel direction were tested using circular statistics and Goodness of Fit tests (Zar 1999).

In total, 1203 km of transect were obtained during 2 to 10 February. Of these, 67 km had sitting penguins, and 38 km had porpoising penguins. We determined the spatial distribution of krill to locate the densest patches and to measure correlation with penguin abundance.

Satellite-Telemetry Survey

Penguins from a colony at Cape Sherriff, Livingston Island, were fixed with satellite platform tracking transmitters (PTT). All PTT's were Wildlife Computers, Spot 3 & 4 transmitters, and weighed approximately 60g. The units had a cross-sectional area of approximately 5cm^2 and were on a continuous duty cycle with a conductivity switch that allowed the unit to turn off when dry to conserve battery life. Penguins with live chicks were selected for instrumentation. The birds chosen for instrumentation were sexed by size and culmen measurements and weighed. PTT transmitters were attached to the lower back to minimize the effects of drag (Bannasch et al. 1994). Epoxy (Loctite 401) was applied to the penguin's back feathers. Instruments were deployed on 8 individuals for 7-10 days each. The animals were then recaptured, weighed and the PTT transmitter removed. Locations from the Argos satellite system and Class 1 or higher were used in this analysis. These are accurate to within 100 m -1 km (Argos 1989, Hays et al. 2001).

We tested whether the total number of satellite uplinks, and number of uplinks per day differed among individuals using Goodness of Fit tests (Zar 1999). For each uplink, we determined the approximate sea depth (from a nautical chart) and distance from the breeding colony at Cape Sherriff, Livingston Island. Distance from the colony was used as an index of foraging range. From these data, we calculated the daily mean foraging position, sea depth, and distance.

Assessment of Spatial Overlap of Satellite-Tracking and Ship-based Surveys

We constructed maps by plotting penguin position from PTT's, and strip-transect data to map the distribution penguins (#/km). To contrast distributions, we tested if mean penguin concentration differed along north-south and east-west axes.

RESULTS

Foraging Distribution and Range based on Satellite Tracking

There were 106 satellite uplinks from 8 birds recorded during the survey period (Fig. 2.1). The number of satellite uplinks did not differ among individuals ($\chi^2_{0.05, 7}$ = 11.6, p = 0.11), but number of uplinks differed among days ($\chi^2_{0.05, 49}$ = 68.57, p = 0.03). Penguins foraged 15.2 ± 9.2 km away from the breeding colony at Cape Sherriff, in areas where sea depth averaged 185.6 m (Table 2.2). Fig. 2.1 shows the presence of 2 'core' foraging areas utilized by penguins breeding at Cape Sherriff, during February 2005. The primary 'core' foraging area, approximately 274 km^2, is where 80% of all satellite uplinks were recorded (shown by polygon on Fig. 2.1), (hereafter "core area"). The distance from the Cape Sherriff colony to the core was approximately 5 km. The second core area was located in offshore waters near the 500 m shelf-break.

Foraging Distribution based on Ship-Based Survey

Penguin distribution recorded from ship was different from that shown by satellite tracking (Fig. 2.2). Penguins were concentrated along the edges of the 100 and 200 m isobaths (ANOVA: $F_{3,63}$ = 4.18, p = 0.009), (Fig. 2.2). The largest aggregations of Chinstrap Penguins were located to the east and west of Cape Sherriff (Fig. 2.2). In addition, penguins counted from ship foraged 30.6±11.6 km from the breeding colony at Cape Sherriff (Table 2.2).

Penguin Traveling Directions

Penguins traveled on a north-south axis (Rayleigh's z-test = 10.97, $p<0.0001$, and $\chi^2_{0.05,7} = 104.12$, $p < 0.0001$), (Fig. 2.3), which suggests that they were transiting to and from Livingston Island. The mean and median traveling vectors are 152.16°±113.1°SD and 180° respectively. Spatial distribution of traveling penguins indicate that they were probably commuting to and from 3 colonies: 1) Cape Sherriff, and 2) Byers Peninsula, Livingston Island and 3) Desolation Island (Fig. 2.3).

Spatial Overlap of Distributions Measured with each Method

By comparison, the distribution of foraging penguins measured by each method was quite different (Fig. 2.4). Penguins counted from shipboard were more abundant to the east of the core area utilized by the satellite-tracked birds ($t = -6.83$, $P <0.00001$, Fig. 2.4), whereas penguins tracked by satellite displayed a more northerly distribution ($t = 4.48$, $P<0.00001$, Fig. 2.4). In addition, penguins counted from shipboard were utilizing foraging habitat that was a greater distance from Cape Sherriff than penguins tracked by satellite ($t = -4.97$, $P<0.0001$, Figs. 2.1, 2.2).

Distribution of Krill Patches:

The distribution of krill patches is shown in Fig. 2.5. Penguin abundance estimated from shipboard was correlated with krill biomass ($r_S = 0.2$, $p<0.05$, Table 2.4). There are 6 regions (labeled A-F in Fig. 2.5) where there were dense krill patches. The densest krill patches were on the edges and heads of both west and east submarine canyons (Fig. 2.5). The biggest krill patches (E and F), located 5-7 km north if

Desolation Island, were located ≈20 km east of the area visited by satellite-tracked birds. However, these patches were not outside the estimated foraging range of penguins from Cape Sherriff (Table 2.2, Fig. 2.5). Krill patches C and D, which coincided with the location of the core area, were approximately 12 km from Cape Sherriff.

DISCUSSION

The two methods we used to find where penguins forage yielded dramatically different results. Satellite tracked penguins were found within a limited area 15 to 20 km north of Livingston Island. By contrast, penguins counted from ship were distributed over a much broader area. Penguins counted from ship were more numerous to the east of the core area, and clustered over canyon heads. All of these locations were outside the area encompassed by the satellite-tracked penguins. Satellite-tracked penguins traveled farther north than the largest aggregations detected from the ship.

The directional preference of porpoising penguins indicated that they orientated along a north-south axis. That axis is consistent with travel to and from colonies. A possible explanation for the dense aggregations of penguins recorded east of Cape Sherriff is the penguin colonies at Desolation Island (62°28’S, 60°22’W), which has large Chinstrap Penguin colonies (Ainley et al. 1995, Woehler and Croxall 1997, W.Z. Trivelpiece and J.A. Santora, pers. obs.). The similar sized aggregations of penguins west of Cape Sherriff may represent birds from colonies along Byers Peninsula, Livingston Island (62°45’S, 60°07’W), (Fig. 2.1), (Woehler and Croxall 1997).

The transect data showed why penguins were aggregated in certain areas. Satellite-tracked penguins foraged in the vicinity of the closest and densest krill patches to their colony (C and D, Fig. 2.5). However, the densest krill patches (E and F) were located to the east of Cape Sherriff near Desolation Island. Here, we found the largest penguin aggregations that may have been traveling from colonies on Desolation Island.

Theoretical studies of foraging seabirds provide field testable foraging rules (Alonzo *et al.* 2003, Grünbaum and Veit 2003). We suspect that Chinstrap Penguins may constrain commuting distance from colonies in order to maximize energy intake (i.e. encounter with krill patches), (Fig. 2.6). This rule works best when there are sufficient krill resources closer to shore (as showed in our study). In our field study, satellite tracked birds were utilizing a core area that was 5-10 km from their colony (Cape Sherriff), and our transect data showed numerous dense penguin aggregations 5-10 km north of penguin colonies on Desolation Island. We suggest that when there are dense krill patches close to colonies, penguins constrain commuting distance to maximize energy intake and to minimize length of foraging bouts (Fig. 2.6). Using satellite tracking and ship-based surveys, future investigations ought to confirm if Chinstrap Penguins from other colonies use different krill patches.

ACKNOWLEDGEMENTS

We would like to thank the officers and crew of the R/V Yuzhmorgeologiya, and members of the Antarctic Marine Living Resources (AMLR) program team during the 2004/2005-field season. D. J. Futuyma helped collect data on birds. A. Cossio and C. Reiss managed the data on krill. This project was generously supported by the AMLR program and the following NSF-OPP grants to J. D. Warren and D.A. Demer (OPP-0338196 and OPP-063393) and to R. R. Veit (OPP-9983751)

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Two Methods for Estimating Penguin Foraging Distribution

- **<u>Satellite-Tracking</u>**
  - Individual-Based (8)
  - Origin of penguin known
  - Can determine daily foraging distance and location
  - Breeding Status

- **<u>Ship-Based Surveys</u>**
  - Population Level (1000's)
  - Origin Unknown
  - Counts of penguins coincide with:
    - acoustic estimation of krill
    - oceanographic features

Table 2.1: A comparison of the benefits of estimating penguin foraging distribution from satellite-tracking and ship-based surveys.

Table 2.2. Average daily foraging location and range of Chinstrap Penguins determined by satellite telemetry.

Penguin	**Sea Depth**		**Distance[2]**		**Latitude**		**Longitude**		**N Day Trips[1]**
	Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	
1	97.0	12.9	10.8	2.6	-62.41	0.02	-60.91	0.09	7 (18)
2	107.6	41.2	13.6	6.7	-62.37	0.06	-60.82	0.06	5 (5)
3*	440.1	492.5	23.4	16.6	-62.28	0.15	-60.86	0.12	5 (7)
4*	720.7	832.9	30.2	16.7	-62.26	0.09	-61.10	0.29	2 (10)
5	111.4	22.1	12.7	4.5	-62.38	0.03	-60.82	0.13	6 (14)
6	104.7	37.8	12.2	5.4	-62.39	0.03	-60.84	0.14	6 (13)
7	117.8	34.3	15.7	6.8	-62.35	0.05	-60.87	0.06	7 (12)
8*	196.3	260.6	14.5	9.6	-62.37	0.07	-60.87	0.13	7 (27)
ALL	185.6	268.9	15.2	9.2	-62.36	0.07	-60.87	0.12	(106)

Sea Depth (m) is approximated sea depth where penguin was located; Max Distance is distance from the breeding colony at Cape Sherriff, Livingston Island; [1] = number of days in which penguins went on foraging trips; [2] Distance is the mean distance a penguin traveled during the 8 day study; parentheses indicate the number of satellite uplinks recorded during 2 to 9 February, * indicates penguins that went on an overnight foraging trip

Table 2.3: **Descriptive statistics for Chinstrap Penguins observed during the ship-based survey.**

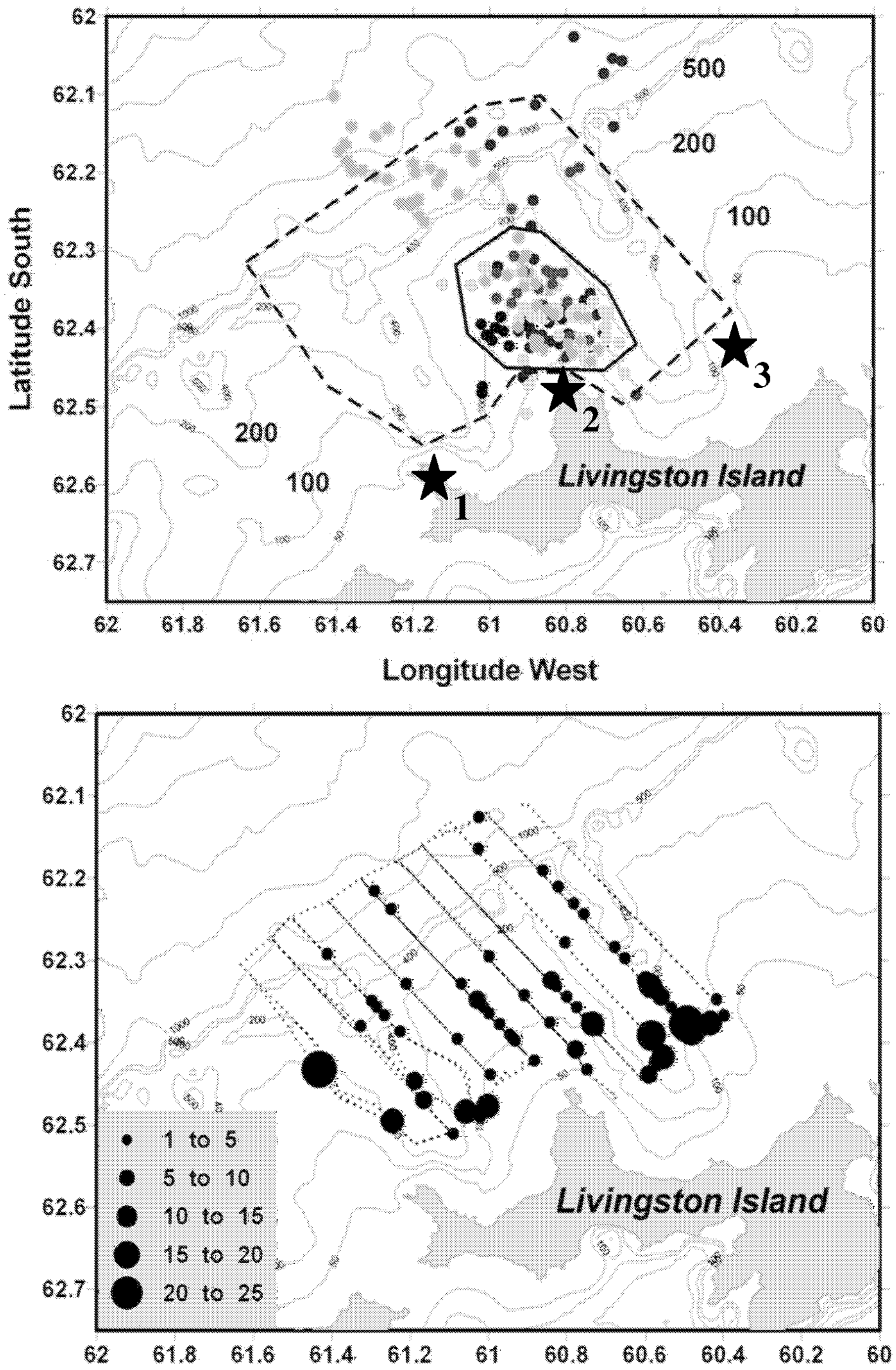
Ship-Based Survey		
	Sitting	**Porpoising**
[1]N (#/km)	67	38
Mean±SD	5.25±4.98	16.65±33.93
Min-Max	1 - 21	1 - 192

[1]N = number of 1 km intervals, SD = Standard Deviation, Min-Max = Minimum and Maximum.

Table 2.4: Utilization of krill biomass (g m^2) by Chinstrap Penguins estimated during the ship-based survey.

Krill	
	Ship-based Survey
[1]N (#/km)	67
Mean±SE	475.68±72.57
Min-Max	2.77 – 2813.09

[1]N = number of 1 km intervals, SD = Standard Deviation, Min-Max = Minimum and Maximum.



Figures 2.1 and 2.2: Foraging distribution of Chinstrap Penguins measured by Satellite-tracking (top) and Strip-transects (bottom). Stars indicate known penguin breeding colonies at (1) Byer's Peninsula, (2) Cape Sherriff, and (3) Desolation Island

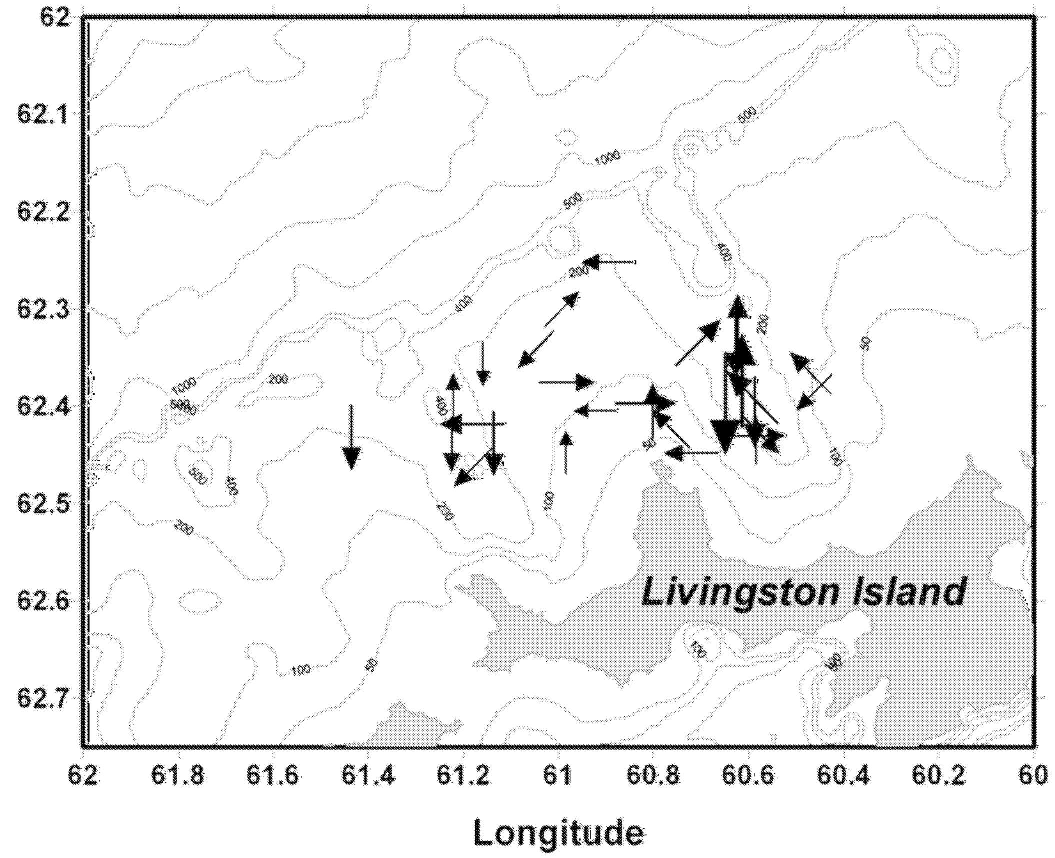


Figure 2.3a: (a) Distribution, direction and magnitude of observed 'Porpoising' Chinstrap Penguins (#/km) recorded during the ship-based survey; temporal resolution 9 days. The actual position is located in the center of the arrow.

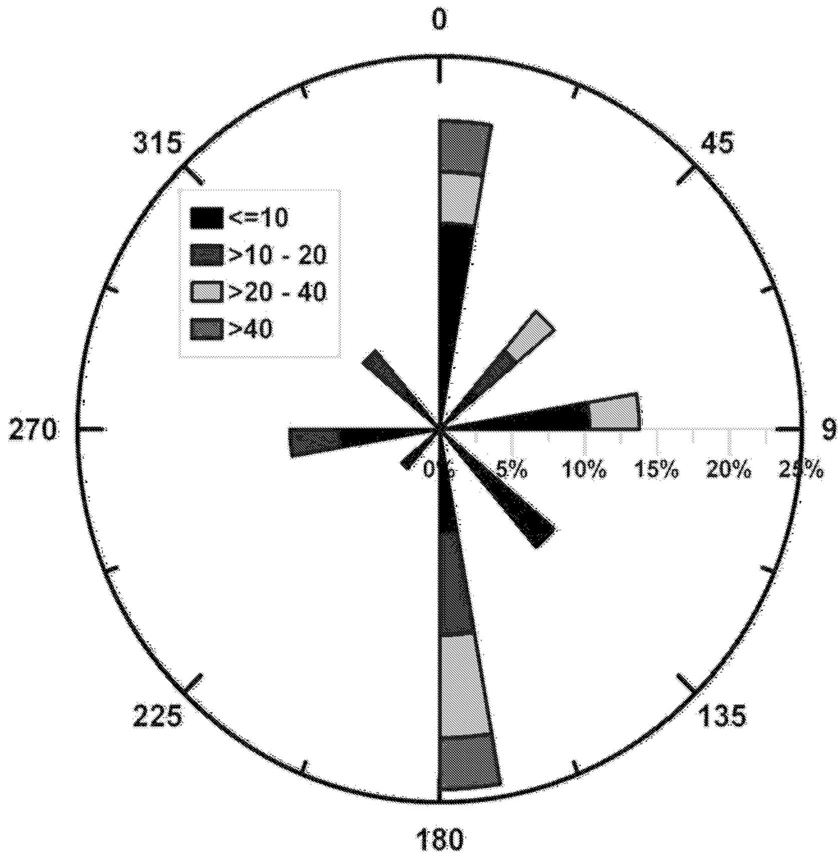


Figure 2.3b: Compass and frequency histogram plot of observed 'Porpoising' Chinstrap Penguins recorded during the ship-based survey 2 to 9 February 2005.

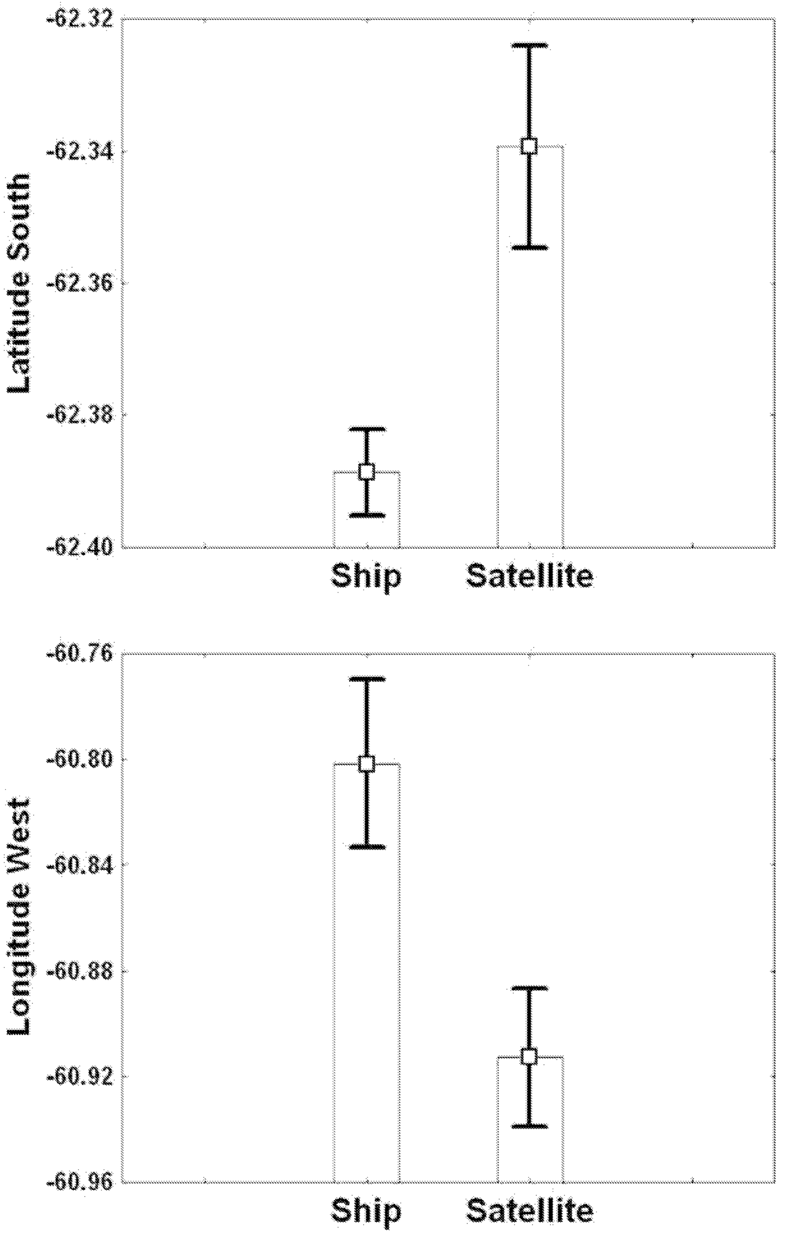


Figure 2.4: Comparison of foraging distributions of Chinstrap Penguin estimated by shipboard and satellite. Difference in (a) latitude and (b) longitude

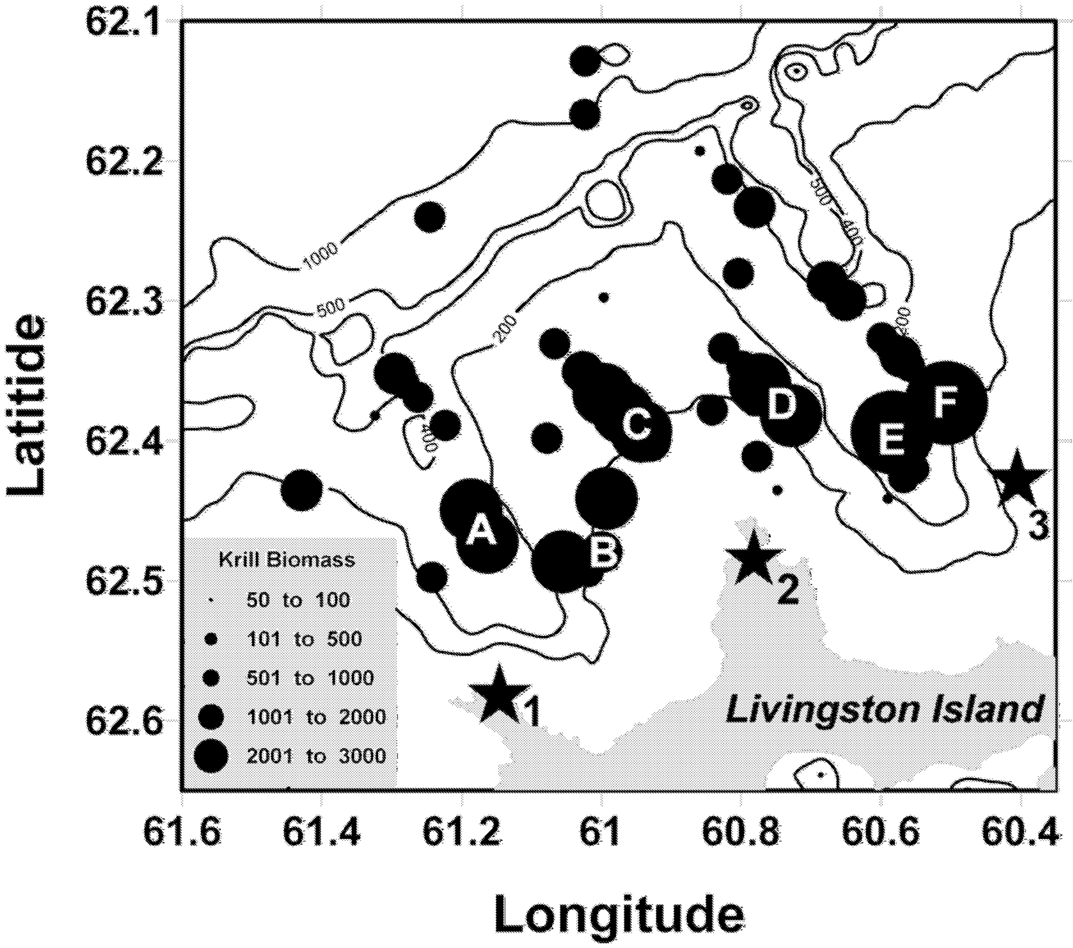


Figure 2.5: Distribution of krill patches during the ship-based survey. Krill is presented as biomass (g/m^2) per km. There were 6 dense patches (labeled A-F). Stars indicate the location of 3 known penguin colonies.

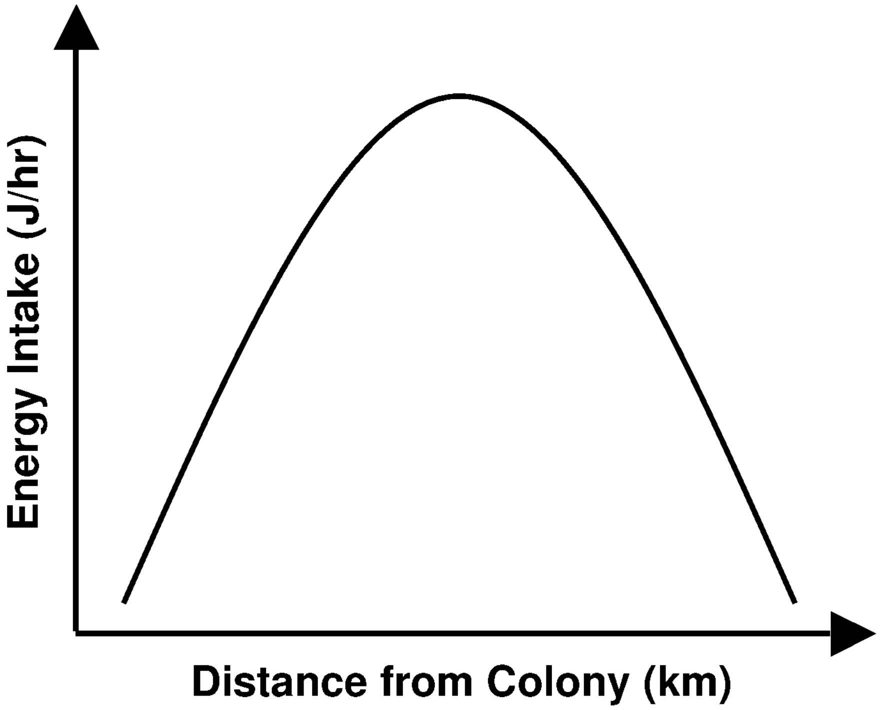


Figure 2.6: Theoretical relationship between distance from colony (km) and energy intake (J/hr) for penguins constraining time and space during foraging bouts.

CHAPTER 3

Influence of krill patchiness on seabird foraging behavior near Elephant Island, Antarctica

INTRODUCTION

In order to understand foraging behavior of Antarctic seabirds as a response krill, one must determine how they search for and detect suitable patches (Veit 1999, Grunbaum and Veit 2003, Alonzo *et al.* 2003). During the breeding season, when birds are acting as central place foragers, they must make foraging trips to collect enough prey for chicks and themselves (Davoren *et al.* 2003a-b). Clearly, abundance of prey is a critical factor influencing where birds choose to forage, but the dispersion of prey patches may be important as well (Hunt *et al.* 1992, Veit *et al.* 1993, Fauchald 1999). For example, if prey patches are arranged in a hierarchical fashion, than foraging seabirds may search for prey patches by tracking prey at several scales (Hunt and Scheider 1987, Russell *et al.* 1992, Fauchald 1999). The decision by birds on where to forage should be made to maximize detection or encounter rate with prey patches, and minimize the amount of space and time spent while foraging (Mangel and Clarke 1986, Alonzo *et al.* 2003, Pinaud and Weimerskirch 2007). We examine the response of foraging birds to krill patchiness.

Krill are social creatures and spend nearly their entire lives in schools or swarms (Ritz 2000). Swarming reduces the risk of predation, enhances success of food capture and reproduction, while minimizing costs involving energy loss through swimming (Quentin *et al.* 1994, Ritz *et al.* 2001). In the Antarctic, krill (*Euphausia superba*) swarms are often distributed in a complex hierarchical fashion, where patches of swarms are arranged within patches of swarms (Macaulay *et al.* 1984, Weber *et al.* 1986, Miller and Hampton 1989, Hewitt and Demer 1993). Thus, patches of swarms could be defined as a measure of krill patchiness in relation to spatial scale (Rose and Leggett 1990).

Previous studies revealed that seabirds are dependent on abundance of their prey (Obst 1985, Hunt and Schneider 1987, Hunt 1990, Hunt *et al.* 1992, Russell *et al.* 1992, Veit *et al.* 1993, Croxall *et al.* 1999), and that measurement scale is important in interpreting the response of foraging seabirds to prey patches (Hunt 1990, Schneider 1990, Piatt 1990, Faulchald *et al.* 2000). Generally, the correlation between birds and prey are scale dependent, and correlation is usually higher at large scales (e.g. ~50 to 100 km) (Hunt and Schneider 1987, Hunt et al. 1992, Russell et al. 1992, Fauchald *et al.* 2000). For example, at large scales, prey patches may be aggregated in predictable locations that might enable easy exploitation by predators, whereas at small scales, prey may form high density swarms that may last for short time periods (e.g. minutes), but might be more difficult for predators to locate (Rose and Leggett 1990, Fauchald 1999). In the western Antarctic Peninsula region, correlations between densities of seabirds and krill have been variable and generally weak. For example, Obst (1985) found that high densities of birds at sea was a good indicator of krill density, but correlation was only evident at spatial scales greater than a nautical mile. Given that krill swarms are patchy, the association of birds with krill may be better understood by exploring the response of foraging birds to krill patchiness. That is, patchiness of krill may be more important than abundance of krill for predicting where birds choose to forage. More importantly, evidence that feeding behavior is linked to krill dispersion has not yet been demonstrated.

We investigate whether or not seabird foraging behavior differs in response to differing levels of krill patchiness. Specifically, we focus on measuring the response of foraging Cape Petrels (*Daption capense*), and Chinstrap Penguins (*Pygoscelis antarctica*) to krill patchiness. There are differences between the modes of search for penguins and petrels. Since penguins swim while searching for prey patches, they should be better at detecting prey patches below the surface and over short distances, but are probably poor at detecting distant feeding groups of predators (Hunt *et al.* 1992). By comparison, Cape Petrels are not as efficient as penguins in detecting subsurface prey patches, but are certainly better at obtaining information from other foragers as visual cues to the presence of prey (Hoffman *et al.* 1981, Harrison *et al.* 1991, Silverman *et al.* 2004). We investigate whether the responses of petrels and penguins differ in relation to krill patchiness.

We present an analysis of strip-transect data of estimates of Cape Petrel, Chinstrap Penguin, and krill distributions collected near Elephant Island. Transects were grouped according to krill patchiness and we asked whether abundance and behavior of penguins and petrels differed between those groups.

METHODS

Data were collected on board the R/V Laurence M. Gould during 10 to 20 December 2001. Six transects were situated north of Elephant Island (61°S, 55°W), extending over the insular shelf (Fig. 3.1), (Hewitt and Demer 1993). For each transect, data collection consisted of recording seabird abundance and behavior (#/km) while simultaneously integrating sonar volume backscattering as an index of krill abundance (log#/km). Since nearly all transects were sampled twice, except for D due to weather restrictions, we were able to assess the usefulness of having sampled transects twice.

Krill Patch Estimation

Distribution of krill patches was assessed using a hydroacoustic echosounder (Hydroacoustic Technology, Inc, Split Beam Model DES244), towed approximately 2 m below the surface, and was coupled with a computer so that estimates of krill biomass were directly digitized and stored in a database. Acoustic transducers were operated continuously at 38 and 120 kHz (6° beam angle and 2 pps) during transects, and estimates of krill abundance were based on measurements of volume back scattering over a depth range of 3-200 m for the 120 kHz transducer. The average ship speed during sampling was 9.2 km hr^{-1}. Krill abundance, represented as volume backscattering, was averaged at horizontal intervals of 1 km, and aligned with estimates of seabird abundance and behavior. Of course some plankton other than krill must be included in our estimates of krill abundance. Nevertheless, we are confident, based on net sampling, that *E. superba* was the numerically dominant zooplankton detected by the echosounder.

Classification of Krill Patchiness

We describe the patchiness of krill along transects by calculating: (1) the relationship between mean abundance (#/km) and Coefficient of Variation (CV) of 1 km bins of each transect, and (2) the spatial autocorrelation function for each transect (Legendre and Legendre 1998).

We classified transects of acoustically determined krill abundance as uniform or patchy using spatial autocorrelation (Weber *et al.* 1986, Rose and Legget 1990). From perusal of autocorrelation functions, some transects had distinct scale of patchiness. For example, on some transects there was a distinct peak at one 1 km spatial lag. On others, there was no such peak. We defined the first group as “patchy” and the second as “uniform”. The “uniform” transects did not lack patchiness, but lacked the distinct scale of patchiness of the “patchy” transects. We then measured the response of foraging seabirds to uniform vs. patchy krill.

Seabird Observations

Data on bird abundance and behavior were collected using binoculars along strip transects continuously during daylight hours. We counted birds within an arc of 300 m directly ahead to one side of the ship while underway (Tasker *et al.* 1984). Each record was assigned a time and a spatial position acquired by the ships global positioning system. Individual birds, or flock of birds, were assigned a behavioral code. The behaviors were: flying, sitting on water, feeding, porpoising (penguins only), and ship following (Veit 1999). Travel direction was entered for flying and porpoising birds. Ship followers were entered when first encountered and ignored thereafter. Only observations of sitting penguins were used in the subsequent analyses because sitting penguins are assumed to be feeding more so than traveling birds.

Cape Petrels and Chinstrap Penguins were chosen because they are the most abundant breeding predators encountered near Elephant Island, and they predominantly feed on krill (Croxall *et al.* 1997). In addition, Chinstrap Penguins forage for krill via pursuit diving, and Cape Petrels feed at the surface (Bengston *et al.* 1993, Warham 1990). In this study an important distinction is made between flying and feeding Cape Petrels. We used spearman rank correlation to test if bird and krill abundance were related at the transect scale (1 to 40 km).

RESULTS

Transect Scale Analysis

To begin, we calculated mean density and patchiness (CV) of krill abundance for 11 transects (Fig. 3.2). We then used spatial autocorrelation as a second measure of krill patchiness on each transect. Spatial autocorrelation revealed that there were 6 transects where krill abundance was correlated across a range of scales (uniform), in contrast to 5 that were patchy, as defined above (Fig. 3.3). Patchy transects displayed irregular functions, suggesting that there were similar sized krill patches at a single or few spatial scales. Krill abundance was significantly greater on patchy than on uniform transects (Mann-Whitney test: $U = 4904$, $Z = -8.03$, $P<0.00001$). Both the highest abundance and patchiness of krill were on Transect B (Fig. 3.2).

Our study assessed the novel use of repeatedly sampling the same transects for distributions of krill and seabirds. We found that the abundance and patchiness of krill was somewhat consistent along transects during the course of this study. The clearest case for comparison was the repeated sampling of Transect B, where krill abundance and patchiness was remarkably similar (Fig. 3.2). Nearly all transects sampled twice were classified consistently as uniform or patchy krill distributions except for transects A and F (Figs. 3.1-3.3). Transects A and F were initially classified as uniform and no less than 24 hours later they were sampled again and krill distribution was patchy. All transects were sampled during morning daylight hours so effects of vertical migration by krill could probably be ruled out. Future studies ought to examine patch dynamics of seabirds and prey by sampling repeatedly sampling transects within hours and days to examine persistence of prey patches and foraging birds.

Response of Seabirds to Krill Patchiness

In Figures 3.4 and 3.5, the distribution of feeding Cape Petrels and Chinstrap Penguins shows the different response by birds to a “uniform” and a “patchy” transect. Cape Petrels and Chinstrap Penguins differed in their response to krill patchiness (Table 2.1). *Flying* Cape Petrels were negatively correlated with krill abundance on uniform transects (r_p = -0.17, P = 0.02), but positively correlated with krill on patchy transects (r_p = 0.21, P = 0.03), (Table 3.1). *Feeding* Cape Petrels, on the other hand, were positively correlated with krill abundance on patchy transects (r_p = 0.23, P = 0.01), but were not correlated on uniform transects (r_p = 0.10, P = 0.17), (Table 3.1). There was no difference in abundance of feeding Cape Petrels between uniform or patchy transects (t = -0.27, P = 0.78), whereas flying Cape Petrels were more abundant on patchy rather uniform transects (t = -4.83, P <0.0001).

Chinstrap Penguins were positively correlated with krill on uniform (r_p = 0.18, P = 0.014), but not, patchy transects (r_p = -0.03, P =0.78). In addition, Chinstrap Penguins were significantly more abundant on uniform transects (t = 2.14, P = 0.03), (Table 3.1).

DISCUSSION

Krill patchiness influenced the foraging behavior of Cape Petrels and Chinstrap Penguins at Elephant Island in 2001. We found that the response of petrels was diametrically opposed to that of penguins (Table 3.1). Abundance of *flying* Cape Petrels exhibited a negative response when distribution of krill patches was uniform, whereas the abundance of *feeding* Cape Petrels feed was greatest on transects where krill was patchy. Moreover, petrels were more abundant on transects where krill was patchy, but not uniform. On the other hand, Chinstrap Penguins clearly preferred uniform transects. That is, they were more abundant and more likely to be associated with krill abundance on transects where the distribution of patches was uniform.

The behavioral response of Cape Petrels has been linked to the presence of krill swarms (Veit 1999). In this study, *flying* Cape Petrels preferred areas where krill were patchy. Since Cape Petrels are restricted to searching for krill patches that are close to the surface, their feeding behavior is probably a good indicator of the presence of prey that is close to the surface. Even though we were unable to measure krill patches at the surface, there is good reason to suppose that feeding petrels are associated with surface krill patches (Veit et al. submitted). Given the ephemeral nature of surface krill swarms, petrels probably spend a lot of time searching for surface patches. Thus, petrels may choose foraging areas where the detection of prey is coupled with the percent of prey patches that are close to the surface. However, Cape Petrels may also use other foragers, such as other birds, seals or whales as cue to the presence of prey (Davoren *et al.* 2003, Grunbaum and Veit 2003, Silverman *et al.* 2004). The few large (200 to 600) feeding aggregations of Cape Petrels we encountered were attending Long-finned Pilot Whales (*Globicephala melas*), so petrels may have found prey driven to the surface (Harrison *et al.* 1991).

In this study, Chinstrap penguins were more likely to forage in more uniform krill distributions. Chinstrap Penguins clearly have an advantage over Cape Petrels owing to their ability to exploit krill patches throughout the water column. Thus, they should choose areas based on a tradeoff between diving times and encounter rate with krill patches (Alonzo *et al.* 2003). Penguins could then effectively increase their encounter rate with krill patches and minimize the amount of time spent diving.

During the breeding season, Chinstrap Penguins act as central place foragers, and usually forage during daylight hours, and return to their colony to roost at night (Bengston *et al.* 1993). This tie to land may also pressure them to select areas where krill patches are uniform. This is would facilitate their ability to maximize their encounter rate with krill patches, in order to minimize time spent away from the breeding colony. Thus enabling them to repeatedly deliver a profitable amount of food to theirs chicks per foraging bout.

ACKNOWLEDGEMENTS:

This study was supported by and NSF-OPP grant (OPP-9983751) awarded to R.R. Veit. Richard S. Heil, and Andrew J. Bernick assisted in data collection of birds and Bala Sundaram assisted in managing acoustic data. We are grateful to the crew of the RV Laurence M. Gould for assistance at sea.

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Table 3.1: Summary of results for association of seabirds with krill patchiness.

RESULT	Cape Petrel "Flying"	Cape Petrel "Feeding"	Chinstrap Penguin
Association with krill on Uniform Transects	NO	NO	YES
Association with krill on Uniform Transects	YES	YES	NO

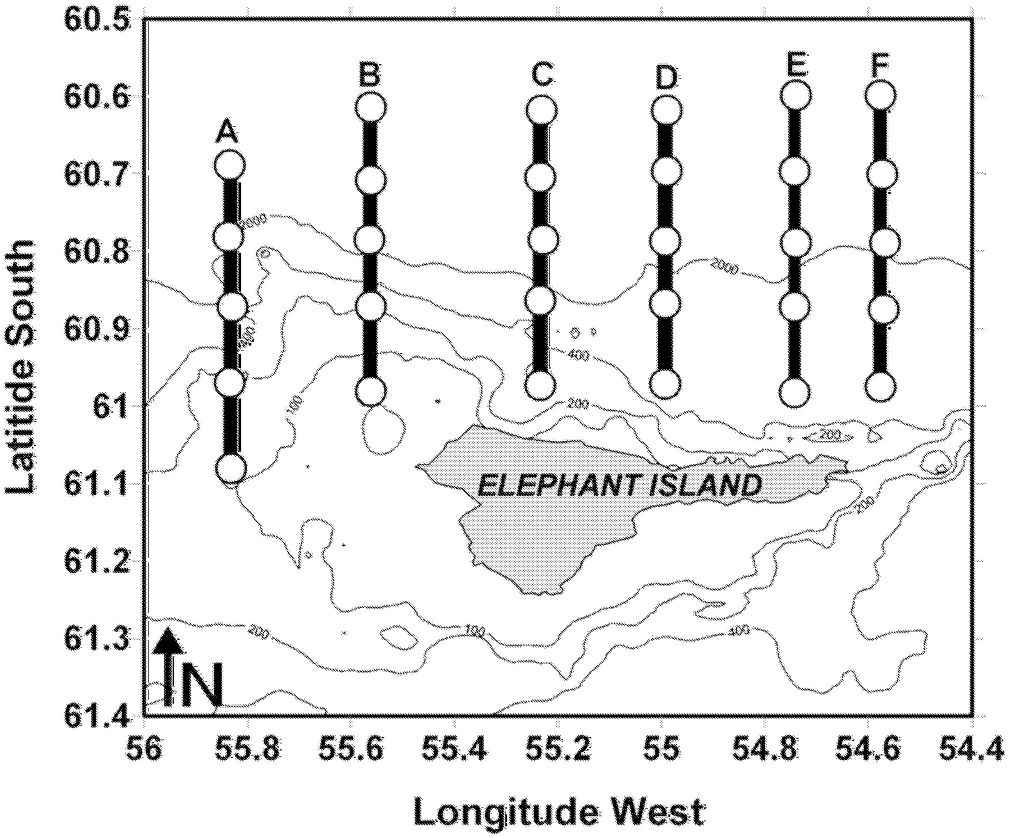

Figure 3.1: Bathymetric map (m) of the insular shelf around Elephant Island, and location of transects sampled for seabirds and acoustically determined krill swarms

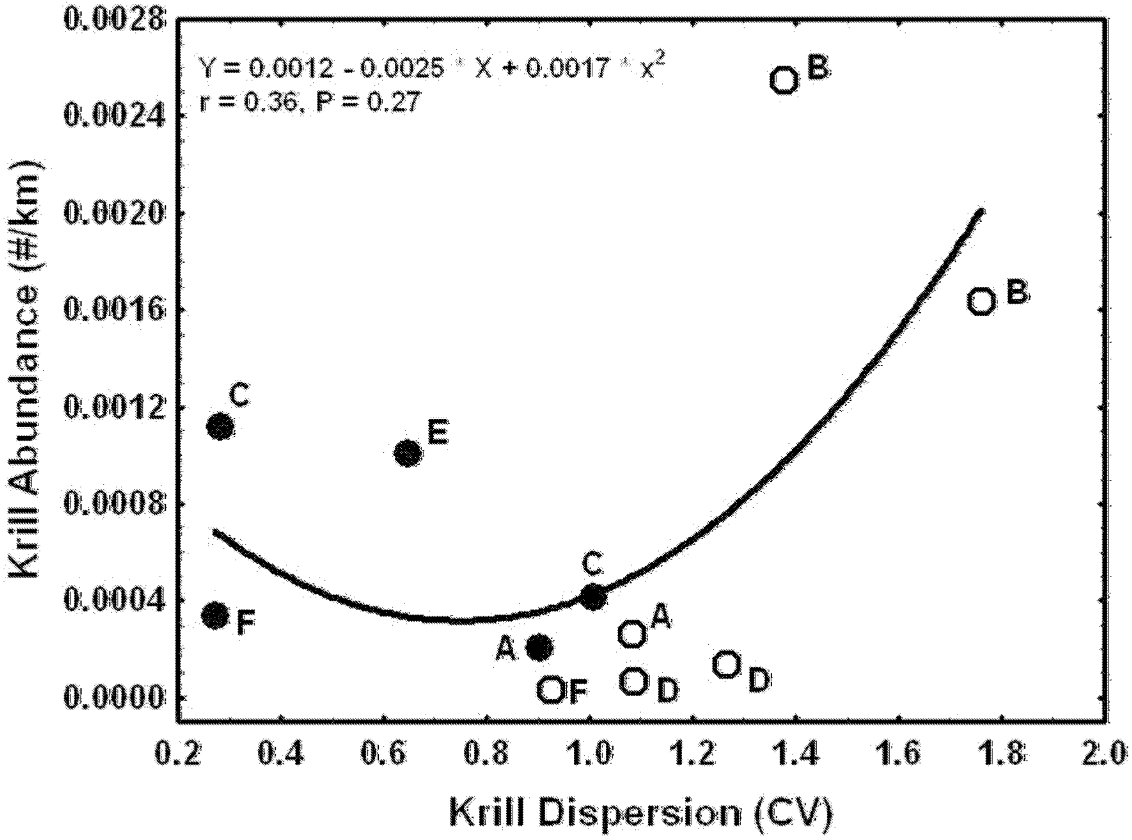

Figure 3.2: Relationship between mean krill abundance (#/km) and dispersion (CV) for transects (labeled A-F, see Figure 1) characterized as either Uniform (filled dots) or a Patchy (open circles).

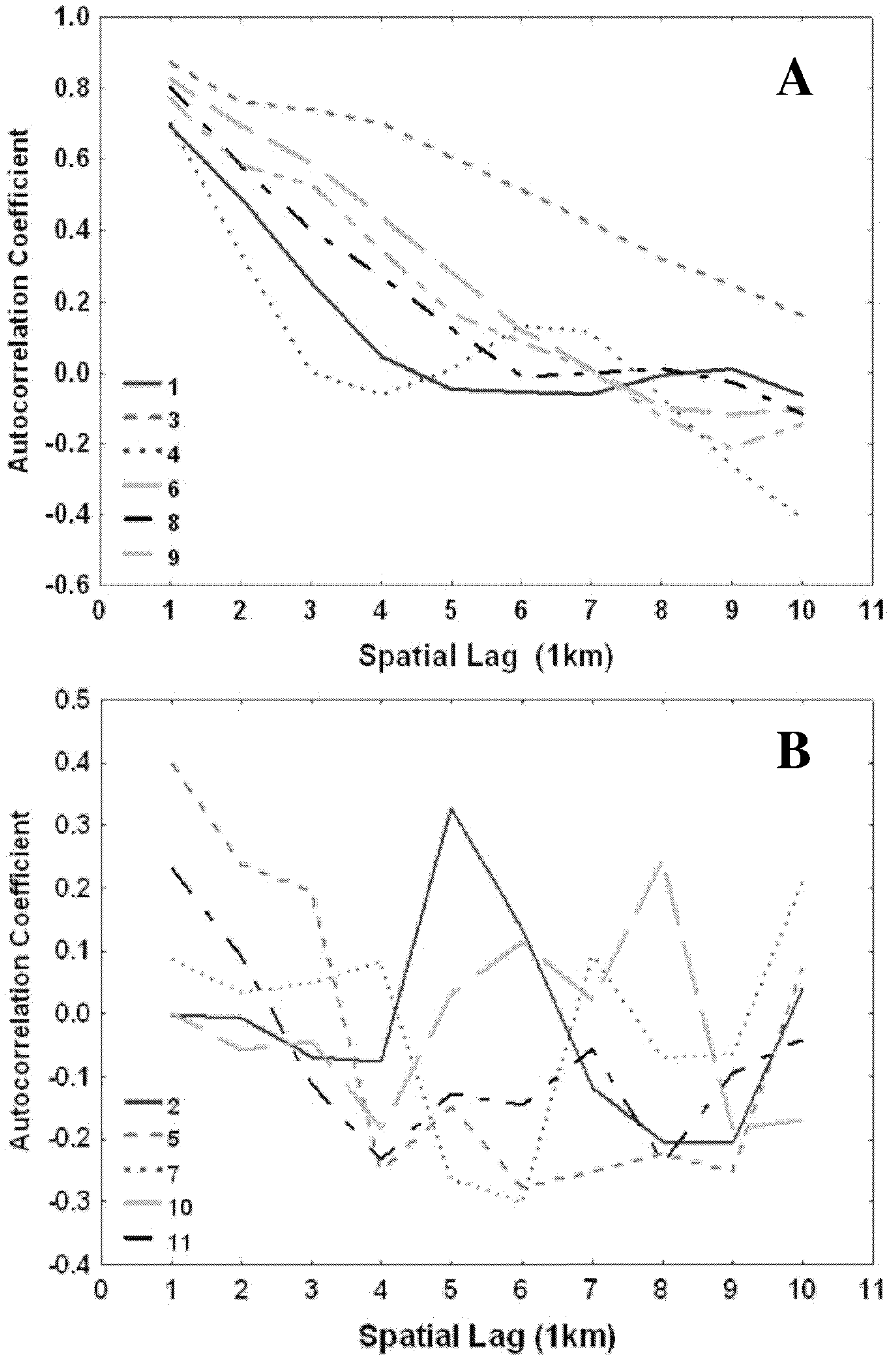

Figure 3.3: Spatial autocorrelation functions for acoustic krill transects classified as: (a) Uniform, and (b) Patchy distributions

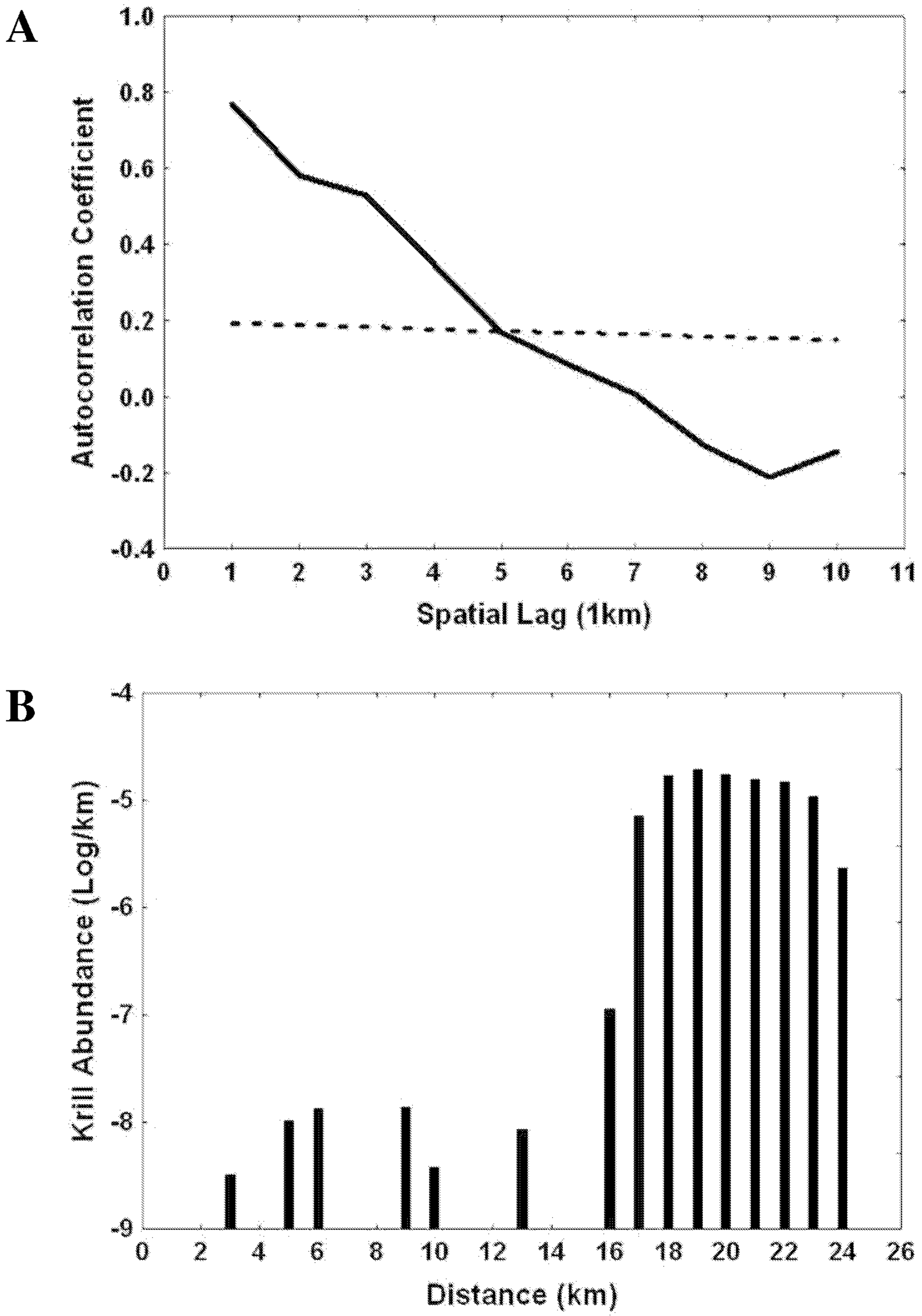

Figure 3.4a-b: Krill patchiness: (a) Autocorrelation of acoustically determined krill abundance on a transect deemed uniform (transect B) and (b) sequence of corresponding krill abundance. Here krill is autocorrelated out to lags of 5 km.

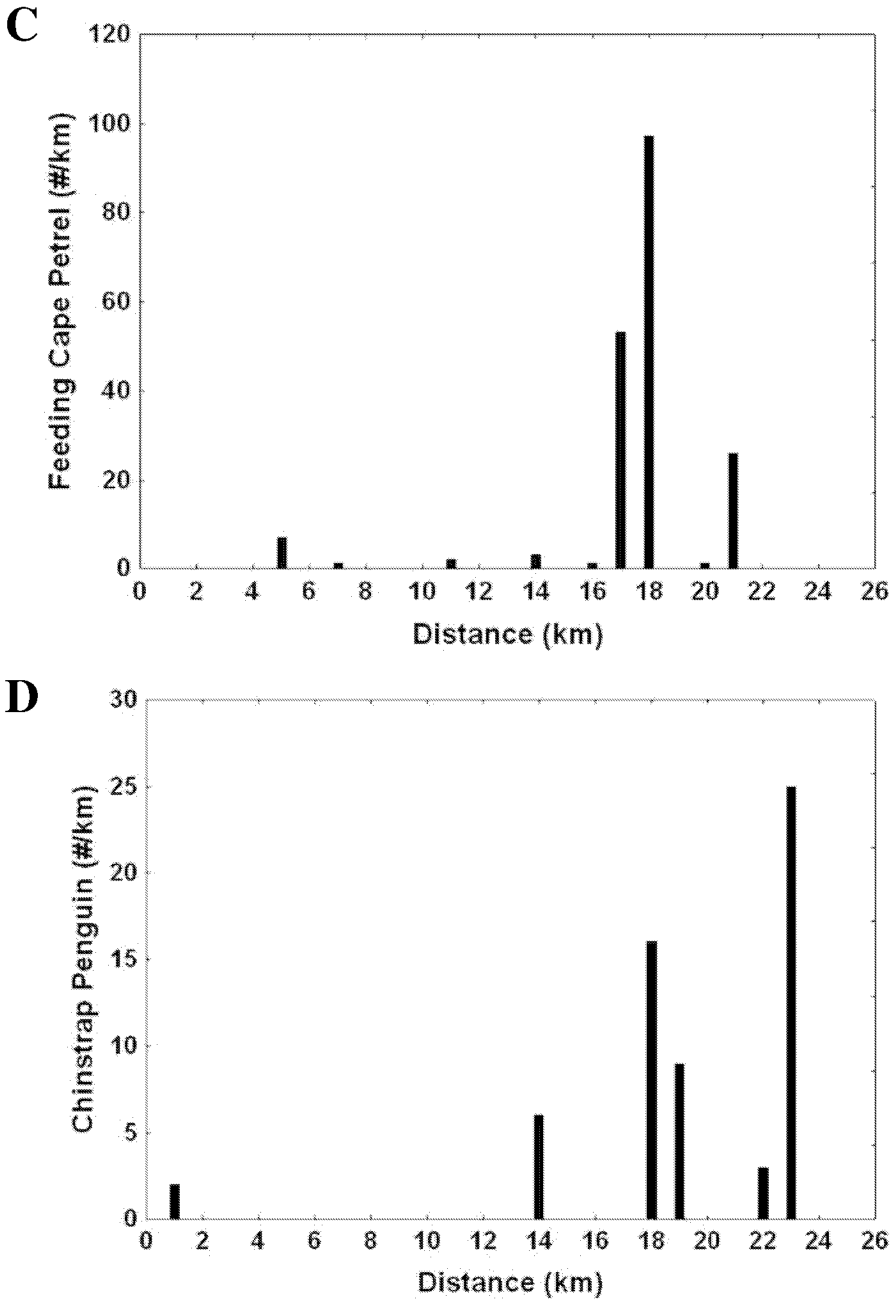

Figure 3.4c-d: Corresponding sequence of predator abundance: (a) Feeding Cape Petrels and (b) Chinstrap Penguins

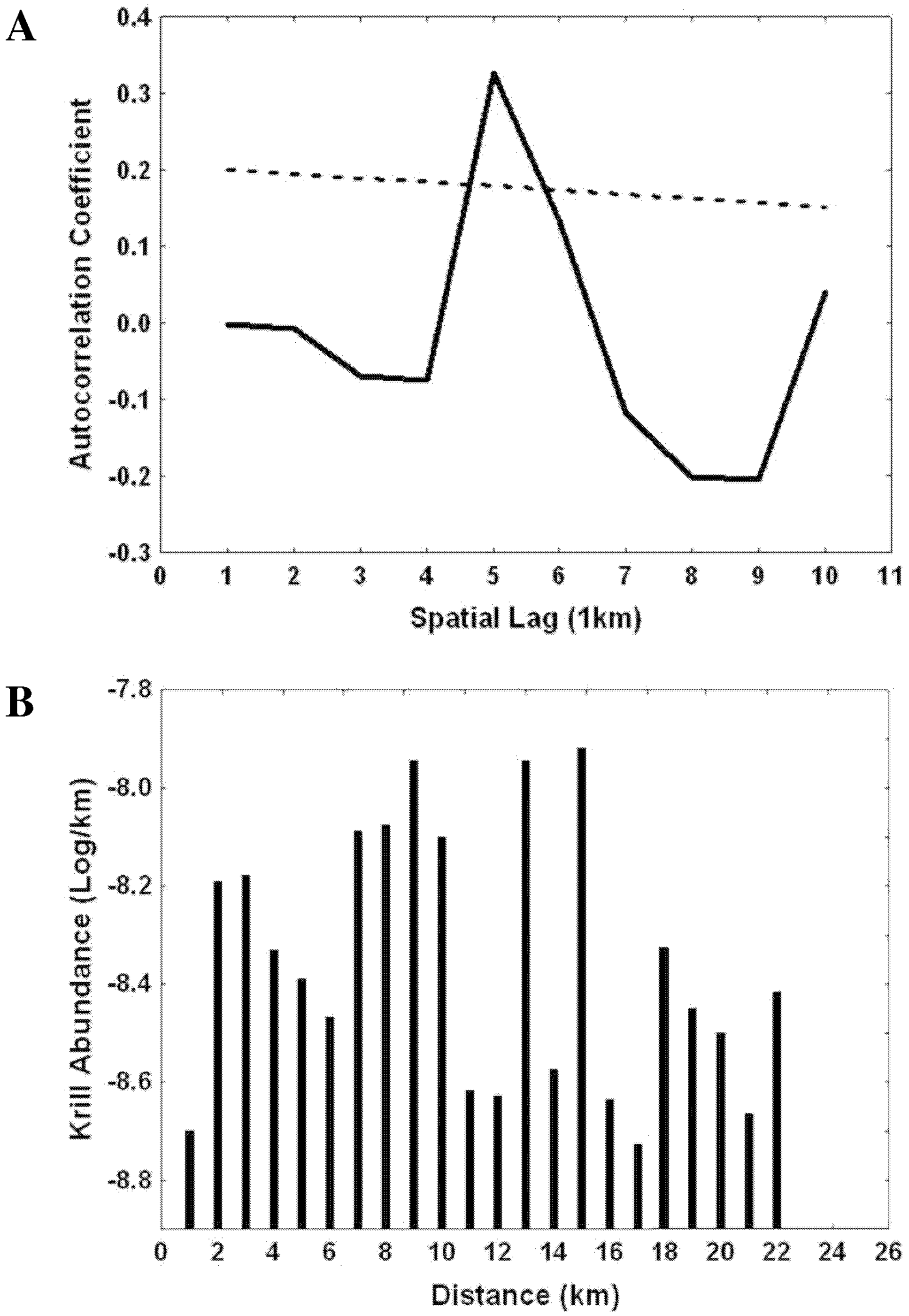

Figure 3.5a-b: Krill patchiness: (a) Autocorrelation of acoustically determined krill abundance on a transect deemed patchy (Transect F) and (b) Krill abundance along Transect F.

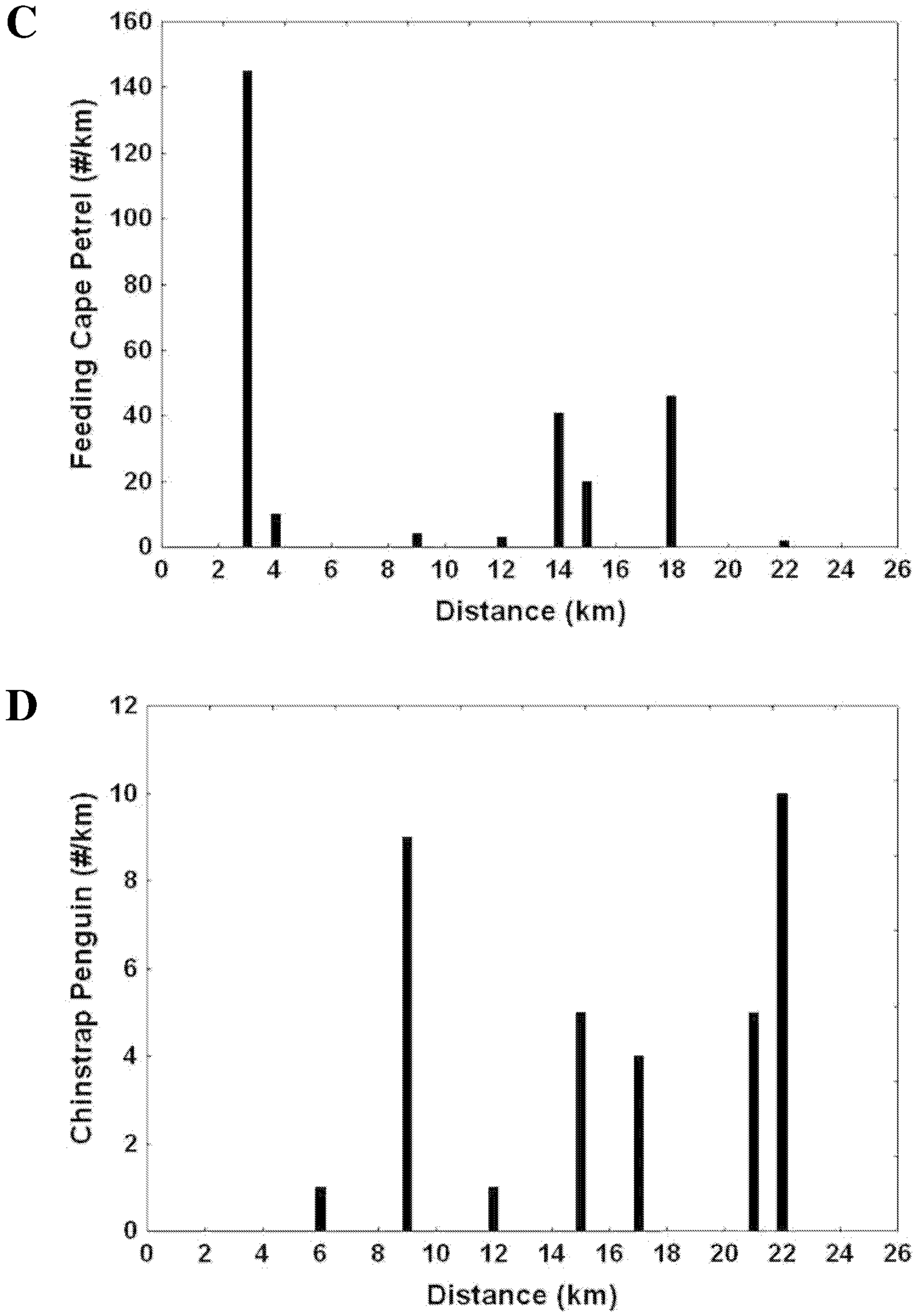

Figure 3.5c-d: (c) Feeding Cape Petrels and (d) Chinstrap Penguins on Transect F.

CHAPTER 4

Annual Spatial Variability of Krill Influences Seabird Foraging Behavior near Elephant Island, Antarctica

INTRODUCTION

In the western Antarctic Peninsula region, Antarctic Krill (*Euphausia superba,* hereafter krill) are the principle prey for a variety of birds (Croll and Tershy, 1998). Determining the causes for inter-annual variability of krill abundance is important because breeding success of many birds is associated with krill abundance (Murphy *et al.,* 1998; Croxall *et al.,* 1999; Boyd and Murray, 2001; Croxall *et al.,* 2002; Trathan *et al.,* 2003). In addition, commercial krill fisheries may impact krill predators by increasing competition (Croll and Tershy, 1998; Boyd and Murray, 2001; Trathan *et al.*, 2003; Reid *et al.,* 2004). Near the South Shetland Islands (Fig. 4.1), krill abundance is cyclical, declining with consecutive years of poor reproductive success and increasing following years of good recruitment (Hewitt *et al.,* 2003, 2004). Part of the response by birds to krill must reflect krill abundance, but there might be other aspects of krill biology that impact birds. We address the impact of krill patchiness.

In the Southern Ocean, at-sea surveys are regularly used to examine the distribution patterns of krill and predators (Obst, 1985; Hunt *et al.,* 1990; Veit *et al.,* 1993; Hewitt *et al.,* 2004; Reid *et al.,* 2004). Our survey (2004-2006) occurred in the Scotia Sea near Elephant Island (61°S, 62°W), an area of high krill biomass that attracts substantial numbers of seabirds (Hunt *et al.*, 1990; Hewitt and Demer, 1993; Agnew, 1997; Croll and Tershy, 1998; Santora *et al.,* 2005). Before 1990, the Elephant Island region was an active krill fishery (Everson and Goss, 1991; Jones and Ramm, 2004). Recent data suggest that krill biomass in the Southern Ocean has declined by an order of magnitude over the last ~50 years (Atkinson *et al.*, 2004). Near Elephant Island, krill biomass fluctuates with a period of roughly 8 years (Hewitt *et al.,* 2003) and successful reproduction and recruitment by krill is related to sea ice extent (Loeb *et al.,* 1997). That is, inter-annual variation in krill biomass has a pattern of alternating good and poor krill years characterized by high reproduction and recruitment success (Siegel and Loeb, 1995; Loeb *et al.,* 1997; Hewitt *et al.,* 2003). Although it is clear that biomass differs annually, it is also important to understand how spatial heterogeneity of krill varies annually because variation of krill patchiness may be useful for predicting where and why seabirds choose to forage.

Krill swarms are patchily distributed and measurement scale is important for interpreting spatial variability of krill patches (Macaulay *et al.*, 1984; Miller and Hampton, 1989; Hewitt and Demer, 1993; Powell and Okubo, 1994). Organisms that aggregate, such as krill, are sometimes distributed in a strikingly hierarchical fashion, where patches are nested within patches. Murphy *et al.,* 1988, suggested the following hierarchical patch structure for krill heterogeneity: (1) At fine scales, individuals are aggregated in swarms with a diameter of 1-100 m at time scales ranging from hours to days, (2) Swarms are aggregated into patches with a diameter of 1-100 km for a period of days to months, and (3) Patches are further aggregated into concentrations at a scale of 100's of kilometers for months. To our knowledge, there are no studies investigating changes in krill patch distribution on annual scales.

We define a patch as a surface area differing from its surroundings. In ecological terms it could be thought of as a region of the environment where the abundance of organisms or resources, is high (Roughgarden, 1977). Patches can be characterized by their size, shape, content, duration, structural complexity, and boundary characteristics (Wu and Loucks, 1995). The concept of patchiness, or habitat heterogeneity, is recognized as an important feature of ecological processes such as population dynamics, foraging behavior, and predator-prey interactions (Wiens, 1976; Southwood, 1977; Levin and Whitfield, 1994; Li and Reynolds, 1995). The implicit notion of patchiness is that discontinuities in environmental character states have biological significance and are important to the organism that is studied.

Spatial patchiness may be quantified in terms of patch composition (patch types and their relative abundance) and spatial configuration (patch size, shape, and contrast), (Wiens *et al.,* 1993; Wu and Loucks, 1995). Description of patchiness is accomplished by measuring the spatial variance in system attributes (Horne and Schneider, 1995; Li and Reynolds, 1995). Contrast and aggregation, two components of heterogeneity, constitutes "patchiness". Where aggregation refers the spatial distribution of patches, and contrast refers to the degree of difference between patches (Sutherland, 1983; Kotliar and Wiens, 1990). However, the term "patch" generally implies a discrete entity, which is seldom observed in nature. In the natural world, patches are distributed across a continuum and are best described as a hierarchical system (Wu and Loucks, 1995). Marine ecosystems are naturally patchy and environmental patterning, the non-uniform, spatial and temporal distribution of resources and abiotic conditions that influence species or species interactions is scale sensitive (Roughgarden, 1977, Addicot *et al.,* 1987; Hunt and Schneider, 1987; Levin and Whitfield, 1994; Irlandi *et al.,* 1995).

Seabirds may exploit patchily distributed prey by responding to habitat patches rather than individual prey types (Wiens, 1976; Duffy, 1986; Morris, 1987; Veit, 1999; Greene and Stamps, 2001). Given that krill patches are nested in a hierarchical fashion, foraging behavior (e.g. search pattern, foraging success) of krill-dependent predators should be influenced by krill patchiness (Boyd, 1996; Fauchald, 1999; Grunbaum, 1998; Alonzo *et al.,* 2003; Grünbaum and Veit, 2003). That is, seabirds may survey patch types in their environment, and select those in which foraging is most profitable. The profitability of a patch type could be thought of as a balance between energy budget and previous encounters with krill patches (i.e. area-restricted search), (Bernstein *et al.,* 1988; With *et al.,* 1999; Veit, 1999; Zollner and Lima, 1999). Once a patch or patch types are selected, a seabird may forage opportunistically within those patches, and repeatedly return to the regions where encounter rate with prey was highest; assuring profitably, and maximizing energy intake on a foraging trip.

Seabirds are long-lived organisms (Warham, 1990). Their breeding biology operates on long time scales, and they must forage over large expanses of ocean in search of prey. Breeding colonies of many seabirds are located within proximity to sufficient feeding locations. On Elephant Island, and its neighboring islets, there are large populations of krill-dependent seabirds, which forage for krill in the nearby waters (Croll and Tershy, 1998; Santora *et al.,* 2005). For example, penguins may have ~100 km foraging range around the islands, and subsist entirely on krill during the breeding season (December to March), (Agnew and Phegan, 1995). Changes in the spatial distribution of krill may have significant impacts on foraging and reproductive success of krill-dependent predators (Agnew and Phegan, 1995; Marin and Delgado, 2001). During the predator's breeding season, the adult animals depend on locating sufficient amounts of krill to support the energetic needs of themselves and their offspring. For example, following a major crash in krill availability around South Georgia, reproductive success of predator populations was poor in contrast to other years (Croxall *et al.,* 1999).

Seabirds track changes in prey distribution at several scales in order to balance energetic requirements and increase the likelihood of survival and successful reproduction (Fauchald, 1999; Davoren *et al.,* 2003). It has been postulated that an increase in prey patchiness should increase the foraging efficiency of seabirds, whereas a decrease in prey patchiness may force predators to switch to other prey items (Fauchald *et al.,* 2000). In the western Antarctic Peninsula region, krill is integral to the food web (Clarke *et al.*, 2007), and there are few if any prey species for krill-dependent birds to switch to. Obviously, fewer krill should decrease the likelihood of reproductive success by krill-dependent birds, but understanding why they do poorly should also be addressed by measuring changes in foraging behavior in relation to krill patchiness. If krill patches are scarce, predators likely spend more time searching for patches, and once they are found, predators should remain in those regions for longer time periods.

We present an analysis of Cape Petrel (*Daption capense*), Chinstrap Penguin (*Pygoscelis antarctica*), and krill distribution data near Elephant Island during January for threes consecutive years (2004-2006). There are two fundamental hypotheses concerning this research: (1) seabirds are locating and consuming krill, and concentrate their foraging effort where krill patches occur, and (2) foraging seabirds respond to changes in krill patchiness. We ask if variation in annual krill patchiness influences patch dimensions of predators. We use patchiness as a measure of spatial heterogeneity (Wiens, 1976; Powell and Okubo, 1994; Rose and Leggett, 1990). We also ask whether spatial association of krill and predators varies annually in relation to krill patchiness. For comparative purposes we investigate whether foraging behavior of petrels and penguins differ in regard to krill patchiness. Aerial petrels are highly mobile in contrast to penguins, which swim and dive in search of krill patches, whereas petrels are restricted to feeding at the surface. Differences in mobility, between petrels and penguins, may force them to respond to a particular structure of krill patchiness. Furthermore, in our study, we speak of "good" krill years when krill abundance is high and patchiness is low (i.e. krill is plentiful everywhere). We hypothesize that when abundance is low and patchiness of krill is high (i.e. fewer patches), foraging distributions of krill predator should be spatially associated with krill patches.

METHODS

Field Methods

We estimated krill (*Euphausiids spp.*) abundance using a combination of acoustics and nets, and conducted visual surveys of seabirds around Elephant Island (61°S, 62°W) during January of 2004, 2005 and 2006 as part of the Antarctic Marine Living Resources (AMLR) program. The area surveyed encompassed 43,865km^2 (18,866 mi^2), and consisted of seven north south transects, each 222 km (~120 nautical miles) long, (Hewitt and Demer, 1993), (Fig. 4.1). Hydrographic and biological sampling stations were occupied, along each transect, to characterize the oceanographic conditions, and to calibrate the acoustic estimates of krill. Ship speed during transect sampling was approximately18.52 kph (10 kn). We only analyzed daytime data because we could not sample birds at night.

Physical Oceanography

At each hydrographic station (n=48, Fig. 5.1), a Conductivity Temperature Depth (CTD) cast was made with a Seabird model 9-11 CTD to a depth of 750 m, or 10 m from the bottom at stations shallower than this. CTD casts were spaced approximately 20 nautical miles (37.04 km) apart.

Acoustic Sampling of Krill

Acoustic estimates of krill abundance were made with a multi-frequency echosounder (Simrad EK60) operating with 38, 70, 120, and 200 *kHz* transducers mounted on the hull 7 m below the surface. Pulses were transmitted every 2 seconds at 1 Kw for 1 ms. Positions were logged every 2 seconds. SonarData Echoview was used to aggregate acoustic data into one nautical mile (nmi) horizontal intervals. We use the nautical area scattering coefficient (NASC) as an index of krill and zooplankton abundance (log/nm), and we integrated NASC values over 10 m depth intervals (Hewitt and Demer, 1993; Madureira *et al.,* 1993; Hewitt *et al.,* 2004).

Net Sampling of Plankton

Krill and other zooplankton were captured with a 1.8 m^2 Isaacs-Kidd Midwater Trawl (IKMT) fitted with a 505 μm-mesh net. Filtered volume was measured using a GO model 2030 flow meter (General Oceanics, Inc.) mounted on the frame in front of the net. All tows were fished obliquely from a depth of 170 m or approximately 10 m above bottom to the surface. The net was a towed at approximately 2 knot and volumes of water sampled averaged 2300 m^3. Abundance of krill is expressed as numbers per 1000 m^3 water filtered. A representative set of krill from each net sample were measured for length and sexed.

Seabird distribution, behavior and abundance

One observer collected data on seabird abundance continuously during daylight hours. Counts of predators were made within an arc of 300 m directly ahead to one side of the ship while underway (Tasker *et al.,* 1984). Each record was assigned a time (to the nearest tenth of a second) and a spatial position from the ships global positioning system. The GPS was synchronized with the echosounder system. Individual birds, or flock of birds, were assigned a behavioral code. The behaviors were: flying, sitting on water, feeding, porpoising (penguins) and ship following (Veit, 1999). Ship-following birds were recorded when first encountered and ignored thereafter.

We focused on measuring the foraging distributions of Cape Petrels and Chinstrap Penguins. We chose these species because they breed during January on and near Elephant Island, and are the most abundant seabirds in the region (Santora *et al.*, 2005). Cape Petrels are medium sized petrels and are restricted to feeding in the upper few meters of the sea surface (Warham, 1990). They are highly gregarious and generally forage in dense flocks that are easily monitored for behavioral changes (Veit, 1999). For example, the frequency of their turning rates increases in proximity to krill swarms (Veit, 1999). That is, they likely restrict the amount of area they search when krill swarms are detected. Chinstrap Penguins are pursuit-diving predators, which are capable of diving to more than 50 m in search of krill, and usually forage primarily during daylight hours (Bengston *et al.,* 1993). Only sitting chinstrap penguins were analyzed for this study because they were more likely to be foraging as opposed to traveling.

Analytical Methods

We constructed contour maps of SST at 2 m CTD data to visualize the hydrographic conditions around Elephant Island each year (Ocean Data View, Schlitzer, 2004). These 2 m SST values were also pooled across years to examine if mean SST varied annually using a 1-way ANOVA. Acoustically determined krill and seabird abundance along each transect were binned into 1 nmi bins. The seabird variables were abundance (log ind.$\cdot$nmi^{-1}) of flying Cape Petrels and Chinstrap Penguins. Annual variability of mean abundance of seabirds and krill (estimated by net and acoustics) was tested using ANOVA, with a Bonferroni multiple comparisons test (Zar, 1999).

We calculated two statistics to quantify patchiness. First, we calculated all-directional spatial correlograms to examine patchiness of acoustically determined krill and seabird abundance (Rose and Leggett, 1990; Legendre and Legendre, 1998, Reid *et al.,* 2004). We compared plots of Moran's I versus distance for each year to examine patch size of krill and seabirds. Second, we calculated the Coefficient of Variation (CV) of abundance of krill and seabirds as an index of patchiness, and asked whether it differed among years.

To determine whether seabirds were spatially associated with krill patches, we used a geostatistical approach involving a spatially explicit regression model (Anselin *et al.,* 2006; GeoDaS Software) fitted with Maximum Likelihood estimation (Burnham and Anderson, 2002). A spatial weight variable (Euclidean distance measure) was determined for each nautical mile sample within each year. The regression model is:

$$\textit{eq.1:}\quad y = \rho\lambda + K\beta + \varepsilon$$

Where y is seabird abundance, K is krill abundance, β is a regression coefficient, and ε is an error term. The model (***eq.1***) has spatial lag components, where ρ is a spatial autoregressive coefficient, and λ is a lag term. The model takes into account whether or not the error terms across different spatial units are correlated as a function of geographic distance (i.e. spatial autocorrelation of residuals). We concluded that seabirds were spatially associated with krill patches in that year when krill distribution (**K**) was a significant predictor of seabird distribution,

Results

Hydrographic variability

Mean SST varied among years ($F_{2,138} = 63.3$, $P < 0.001$, Fig. 4.2) and 2006 was warmer than 2004 ($t = 10.27$, $P < 0.0001$) and 2005 ($t = 9.04$, $P < 0.001$). In each year, a surface temperature front was observed northwest of Elephant Island (along the shelf edge). In 2004 and 2005, the coolest water (SST <1.0°C) was found in the southeast part of the area, with the warmest waters near 60° S. In 2006, the surface waters around Elephant Island were much warmer than in either 2004 or 2005, and the only cool water was found on the southern and southeastern flank of the Elephant island insular shelf (Fig. 4.2).

Krill abundance and distribution

Euphausia superba and *Thysannoessa macrura* were the two numerically dominant krill species caught in nets (Fig. 4.3). Although *E. superba* exhibited similar mean abundances of ~60 per $1000m^{-3}$ in 2004 and 2005 and ~25 individuals per $1000m^{-3}$ in 2006, their variances were large owing to patchiness and net inefficiencies (Fig. 4.3). Krill larvae varied annually ($F_{2,139} = 7.02$, $P = 0.001$), where mean abundance in 2006 was greater than in 2005 ($t = 3.22$, $P = 0.005$) or 2004 ($t = 3.25$, $P = 0.004$). *T. macrura*, were most abundant in 2005 with mean abundances that year in excess of 350 individuals per $1000m^{-3}$. Annual abundance of *T. macrura* varied significantly ($F_{2, 139} = 5.26$, $P = 0.001$), whereas *E. superba* did not ($F_{2, 139} = 1.59$, $P = 0.21$). *T. macrura* was significantly more abundant in 2005 than in 2004 ($t = 3.53$, $P = 0.002$) or 2006 ($t = 2.88$, $P = 0.014$).

Acoustic estimates and patchiness indices of plankton

Acoustic estimates of krill varied significantly (Figs. 4.3, 4.4) among years ($F_{2.1622} = 185.3$. $p < 0.0001$, and was approximately two orders of magnitude less in 2006 than in 2004 ($t = 14.66$, $P<0.0001$) or 2005 ($t = 18.46$, $P<0.0001$). Acoustic estimates of krill were higher in cooler (< 2 °C) areas of the Elephant Island area. This was most evident in 2006, when krill were present exclusively in the eastern and southeastern flanks of the Elephant Island insular shelf (Fig. 4.4). In 2004 and 2005, the krill patches were concentrated around the periphery of the Elephant Island insular shelf region (Fig. 4.4).

Acoustically determined krill abundance was patchy in all years (Figs. 4.4, 4.5). Patchiness of krill, measured using CV, was negatively correlated with abundance ($r = -0.93$, $P = 0.25$, Fig. 4.6), indicating that when krill is less abundant, patches are fewer. Patch size of krill, using Moran's I, indicated that patch size of krill was similar at large spatial scales (<50 nmi) among years (Fig. 4.5). However, correlation of patch size at small scales (1-10 nmi), varied among years (Fig. 4.5). For example, in 2006 krill was comparatively weakly autocorrelated (Lag 1 correlation ~0.2), indicating that when krill is significantly less abundant, patchiness increases (Fig. 4.5).

Seabird abundance and patchiness

Abundance of Cape Petrels varied among years ($F_{2, 260}$ =162.70, P<0.0001), and decreased over the study period (r = -0.21, P<0.0001), (Figs. 4.3, 4.4). Abundance of cape petrels was greater in 2005 than in 2004 (t =4.95, P<0.0001) and 2006 (t =18.01, P<0.0001). Chinstrap Penguin abundance also varied over the three years of the study ($F_{2, 1621}$ = 18.9, P < 0.0001, Figs. 4.3, 4.4), and also declined over the study period (r = -0.15, P <0.0001). Chinstrap Penguins were clustered in the vicinity of Elephant and Clarence Islands during each year, which is probably related to good foraging locations within proximity to breeding colonies.

Patch size of Cape Petrels, measured using Moran's I, was larger during 2005, with patches ~35 nmi in size (Fig. 4.5). During 2006, patch size was less than 15 nmi (Fig. 5). Patchiness of cape petrels, measured using CV, was negatively correlated with abundance (Fig. 4.6).

Patch size of Chinstrap Penguins, measured using Moran's I, was similar among years (Fig. 4.5). However, patchiness of penguins, measured using CV, was negatively correlated with abundance (Fig. 4.6), suggesting that when penguins are less abundant, they are more likely found in fewer locations.

Association of seabirds with krill abundance and patchiness

Correlation of foraging birds and krill varies with krill patchiness (Figs. 4.7, 4.8). Spatial association between seabirds and krill patches differed markedly among years

(Table 4.1-4.2). In 2006, when krill was scarce, but patchiness of krill was highest, cape petrels and krill were closely associated (Table 4.1-4.2). In 2005, when krill was abundant and patchiness was lowest, cape petrels were also closely associated with krill (Table 4.1). Cape petrels were not spatially linked to krill in 2004 when krill abundance was high, but patchiness was low. By comparison, chinstrap penguins were associated with krill when abundance of krill was high, and patchiness was low (2004 and 2005), (Tables 4.1-4.2).

Discussion

Krill abundance and distribution differed among years, and influenced the apparent foraging distributions of cape petrels and chinstrap penguins in the vicinity of Elephant Island, Antarctica. The inverse relationship between abundance and patchiness of krill suggests that when krill is less abundant, there are potentially fewer patches available to foraging birds. When krill abundance decreased by ~2 orders of magnitude between 2005 and 2006, our index of krill patchiness nearly doubled. Not only were there fewer krill, but also there were fewer patches available to predators.

Response by seabirds to krill patchiness

Our principal finding that patchiness of krill was inversely related to krill abundance. This finding enabled us to assess the response of foraging seabirds in relation to low, medium, and high krill patchiness. We asked whether spatial association of seabirds and krill, depended on krill patchiness. Our results yielded insight on how variations in size and arrangement of krill patches might impact foraging success of predators.

We demonstrated that foraging distributions of cape petrels and chinstrap penguins, two of the most abundant seabirds in the Antarctic Peninsula region, exhibited responses to krill patchiness. When krill abundance decreased by 2 orders of magnitude between 2005 and 2006, abundance of cape petrels decreased and correlation between bird and krill patches was higher. Interestingly, the probability of spatial association between cape petrels and krill was greater when patchiness of krill was either high or low, but not at intermediate levels. During 2005, when patchiness of krill was lowest, cape petrels were spatially associated with krill. On the other hand, in 2006, when krill was comparatively scarce, and patchiness was highest, cape petrels were also associated with krill patches. Penguins were associated with krill patches when krill abundance was high and patchiness was low (2004).

Abundance of foraging chinstrap penguins decreased during the study, which coincided, with the decrease in krill abundance, and increase in patchiness of krill. Previously, Croll *et al.*, (2006) showed that annual variability in krill abundance is correlated with reproductive performance (e.g. breeding population size and breeding success), but not foraging effort by chinstrap penguins. Furthermore, they suggested that penguins reduce reproductive success rather then increase foraging effort in response to decreases in krill abundance. We emphasize that foraging effort by krill-dependent seabirds should be evaluated in relation to abundance and patchiness of krill. By contrast, our study of foraging distribution of chinstrap penguins was conducted over the entire Elephant Island region, while theirs was focused on 5-8 penguins per year that bred at one colony. Interestingly, they found that breeding population size of penguins was correlated with krill abundance. We found that abundance and patchiness of foraging penguins throughout the Elephant Island area was correlated with krill distribution. They found that foraging effort of (5-8 penguins per year) did not vary according to krill abundance. Our study reinforces their findings that population size of chinstrap penguins is likely regulated by krill abundance, but we emphasize that krill patchiness adds additional insight on changes in penguin foraging distribution. The problem is that we need to combine information of individual foraging effort, and breeding population size, while simultaneously tracking changes in foraging distribution of penguins at the population level (i.e. thousands).

Krill patchiness affects foraging behavior

Foraging behavior is an ecological process that should be evaluated with consideration of an organism's activity during a particular time period (Wiens, 1976). Petrels and penguins breeding near Elephant Island during January are provisioning resources for chick rearing. In our study, we evaluated the response of foraging petrels and penguins to krill patchiness. There are two fundamental assumptions concerning the foraging behavior of seabirds in this study: (1) seabirds are locating and consuming krill, and concentrate their foraging effort where krill patches occur, and (2) foraging seabirds respond to changes in krill patchiness.

There are two foraging strategies that seabirds can use to locate krill patches: area-restricted search and local enhancement (Kareiva, 1990; Buckley, 1996, 1998). Seabirds practice “area-restricted search” by concentrating foraging effort for some time in the location of their last successful prey capture (Veit, 1999; Pinaud and Weimerskirch, 2007). Moreover, if foraging success (i.e. prey capture) is related to prey patchiness, than the amount of time spent searching within a location should, in part, depend on abundance and patchiness of prey in that location. In relation to our study, high spatial correlation between birds and krill might result in higher foraging success than low correlation.

Since Cape petrels cannot dive greater than a few meters, they probably choose foraging locations where krill are close to the surface. Unfortunately, we were unable to monitor krill patches near the surface. Krill can be closer to the surface during the evening and early morning (Hewitt and Demer, 1993), and petrels may aggregate in locations where they had previous success feeding the night before (Hunt, 1990). Each year, we observed aggregations of cape petrels sitting on the water numbering in the hundreds. These birds were not observed to feed. We speculate they may congregate because they found krill patches that were closer to the surface during the previous evening. Congregations could serve as “information centers” whereby birds may learn where others had success in locating prey (Pöysä, 1992; Silverman *et al.*, 2004).

There is a growing body of evidence suggesting that local enhancement is important part of foraging strategies used by seabirds to locate patchy prey (Harrison *et* *al.*, 1991; Silverman and Veit, 2001; Silverman *et al.*, 2004). For example, Grunbaum and Veit (2003) found that density dependence of albatrosses might affect the outcome of foraging success of albatrosses foraging for krill. In relation to our study, this may also be true. By comparison, in 2006, when krill patches were scarce, we recorded relatively fewer penguins and petrels, indicating that there were fewer predators searching for krill near Elephant Island. Therefore, if krill patches are scarce, seabirds may spend more time searching for predators.

Implications

Foraging distributions of seabirds are linked to krill distribution. It is reasonable to suppose that factors influencing krill distribution ought to alter seabird behavior as well. Our study has implications for two aspects for the ecology of krill and seabirds near Elephant Island: (1) climate variability, and (2) commercial krill harvesting.

Near the Antarctic Peninsula, air temperature has risen dramatically in the last ~50 years, and is related to winter sea ice extent (Smith et al., 1996; Moline *et al.*, 2004; Clarke *et al.*, 2007; Murphy *et al.*, 2007). Near South Georgia, the occurrence of krill has been linked to "warm" and "cold" (based on air temperature) periods associated with changes in sea-ice extent in the Scotia Sea (Murphy *et al.*, 1998; Trathan *et al.*, 1998; Murphy *et al.*, 2007). We found an interesting result regarding annual changes in sea surface temperature (SST °C at 2m). During this study, SST's exceeding ~3.5 °C, were found throughout the Elephant Island region during 2006, whereas in 2004 and 2005, when krill abundance was two orders of magnitude greater, SST was cooler (~1.2 °C).

This anomalous temperature pattern may be related to the low abundance and restricted distribution of krill in 2006 (Moline *et al.,* 2004, Clarke *et al.,* 2007). A likely explanation for the warm SST in 2006 was the poleward movement of the southern Antarctic Circumpolar Current front (sACCf) that occurred (Tynan, 1998; Constable *et al.*, 2003). Future investigations of krill distribution and foraging behavior by seabirds near Elephant Island ought to explore the importance of the sACCf in relation to climate variability.

Successful management and conservation of resources requires that we describe spatial pattern and predict how organisms respond to it (Cairns, 1992; Mangel, 1994, Furness and Camphusen, 1997). Therefore, it is important to understand how krill-dependent predators forage for krill and how they may respond to variable conditions of krill patchiness. Krill is important resource for birds, and is also a resource targeted by commercial fisheries (May *et al.*, 1979; Everson and Goss, 1991; Croxall, 1992; Mangel, 1994; Marin and Delgado, 2001).

Land-based krill predators breeding on the South Shetland Islands consume ~0.83 million tons of krill during the reproductive season (Croll and Tershy, 1998). The krill fishery that operated near the South Shetland Islands and Elephant Island during the 1980's and 90's targeted krill patches that was within <100 km of penguin and petrel colonies during their breeding periods (Agnew and Phegan, 1995; Marin and Delgado, 2001). Potential impacts on krill-dependent predators through commercial harvesting of krill should be addressed by incorporating the foraging demand of predators (Mangel, 1994; Mangel and Switzer, 1998; Marin and Delgado, 2001). Based on our study, we urge that future modeling work must emphasize the impact of krill patchiness in relation to predator foraging demand. For example, negative effects such as competition, through the depletion of patches by fishing vessels utilized by predators, may cause predator populations to suffer (Cairns, 1992; Alonzo *et al.*, 2003, Reid et al., 2005). This may be especially true if fisheries target krill patches in proximity to major breeding colonies. Therefore, we should consider the effects of krill harvesting on predators, not only in terms of abundance and biomass, but also considering dynamics involving patch depletion.

ACKNOWLEDGEMENTS:

We would like to thank the United States Antarctic Marine Living Resources program for facilitating fieldwork during this survey. We greatly appreciate the assistance of the captain and crew of the RV *Yuzhmorgeologiya.* A. J. Bernick, M. P. Force, and D. J. Futuyma assisted in data collection of predators. We would like to thank R. Hewitt, and A. Cossio for maintaining and processing acoustic data during 2004 through 2006. Seabird data collection was made possible due to NSF-OPP grant (OPP-9983751) to R.R. Veit.

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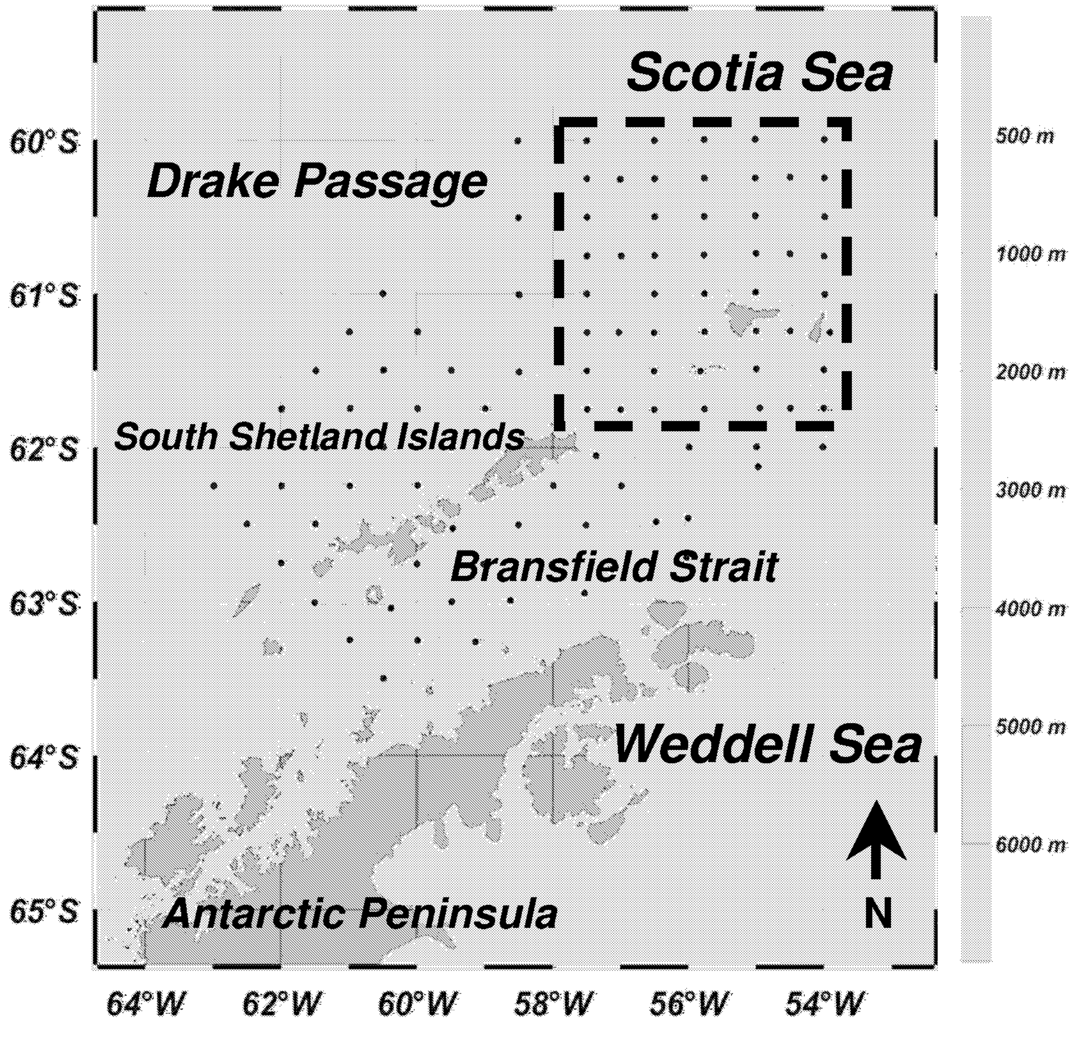
Table 4.1: Results for test of spatial association of seabirds and krill. Spatial association between seabirds and krill occurred when **K** (krill abundance and distribution) was found as a significant predictor of seabird spatial distribution. Maximum Likelihood estimates of significant parameters for spatial regression model: Coefficient is the maximum likelihood estimate, SE is standard error of the coefficient, *z* is the maximum likelihood test value, and P is probability of rejecting null hypothesis given the test value. λ is spatial lag term; --- indicates no parameter found. R^2 is coefficient of determination.

	Variable			**R^2 Coefficient ± SE** ***z, P***		
YEAR	**2004**	**2005**	**2006**	**2004**	**2005**	**2006**
Cape Petrel				0.08	0.3	0.24
	λ	λ	λ	0.25±0.04 6.2, <0.001	0.44±0.04 10.8, <0.001	0.4±0.04 9.6, <0.001
	—	**K**	**K**	—	0.1±0.03 3.4, <0.001	0.04±0.02 2.0, 0.04
Chinstrap Penguin				0.47	0.37	0.12
	λ	—	—	0.33±0.04 8.7, <0.001	—	—
	K	**K**	—	0.05±0.02 3.1, 0.002	0.05±0.02 2.5, 0.01	—

Table 4.2: Summary of results for annual association of seabirds and krill.

TEST	RESULT BY YEAR		
	2004	2005	2006
Krill Patchiness	Medium	Low	High
Krill Abundance	High	High	Low
Spatial Association of Cape Petrels and Krill	NO	YES	YES
Spatial Association of Chinstrap Penguins and Krill	YES	YES	NO

Figure 4.1: Western Antarctic Peninsula region and the location of the Elephant Island study area (dashed line), and nearby South Shetland Islands. Black dots indicate position of Conductivity-Temperature-Depth (CTD) and net sampling stations. Bathymetry (m) is indicated by color bar on right.



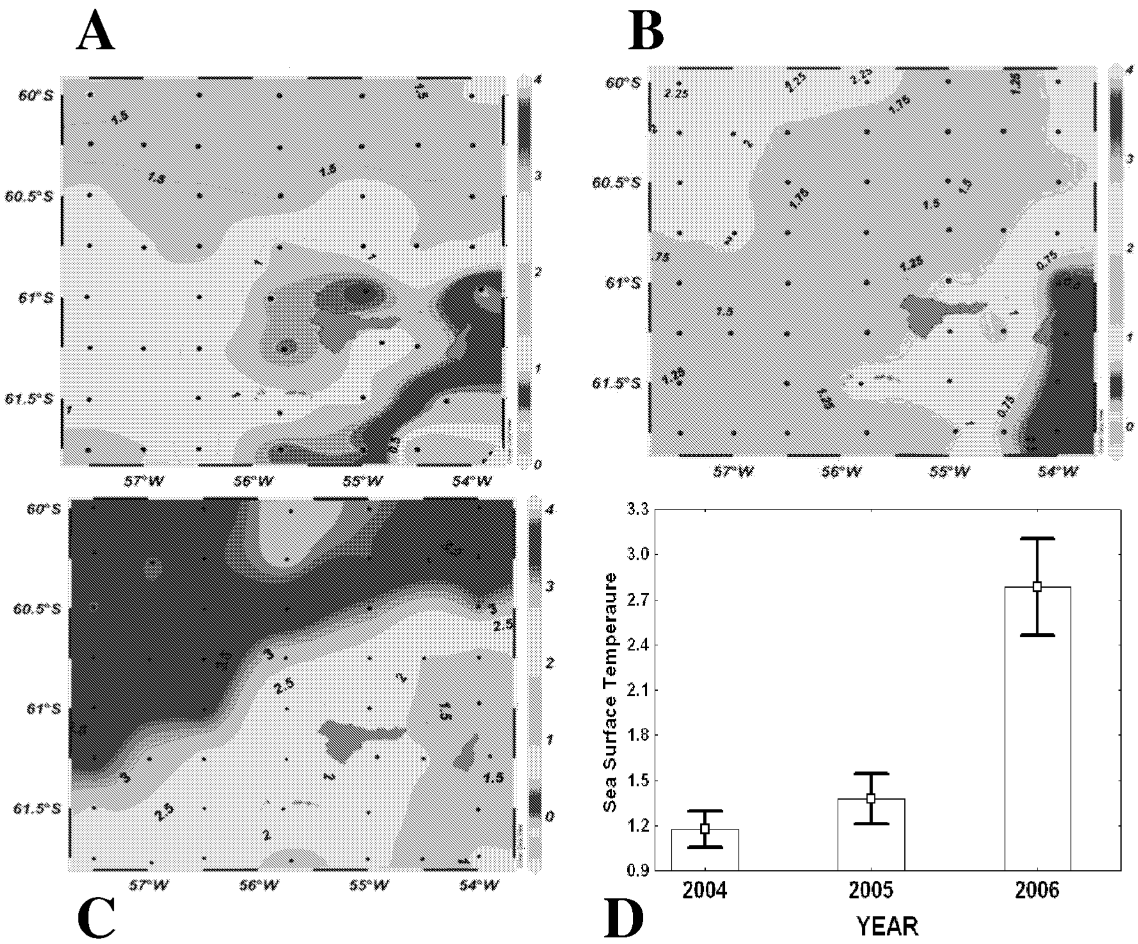


Figure 4.2: Inter-annual variability of SST (°C at 2 m) near Elephant Island: (a) 2004, (b) 2005, and (c) 2006. Dots indicate position of CTD station (separated by approximately 20 nautical miles; (d) Comparison of mean annual SST.

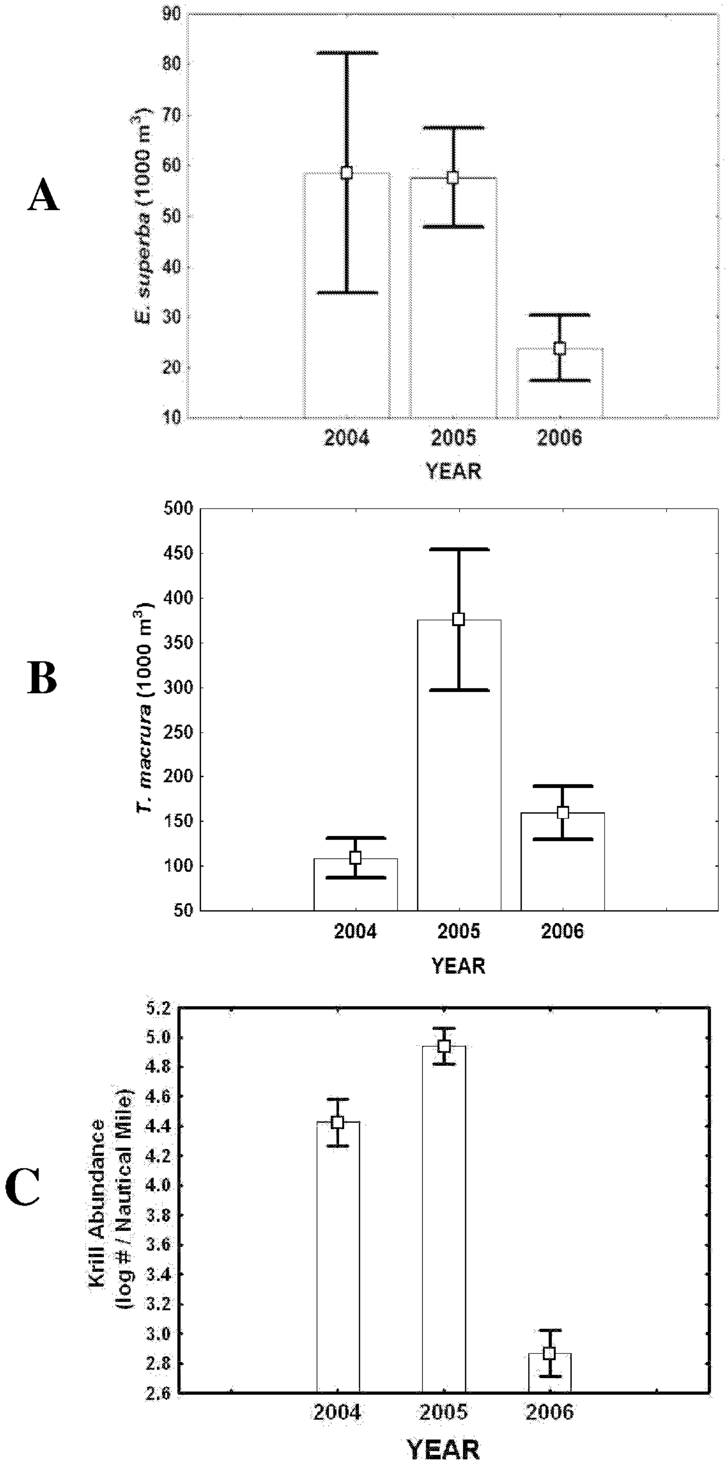


Figure 4.3: Abundance (Mean±SE) of: (a) *E. superba*, (b) *T. macrura*, (c) Acoustically estimated krill (NASC)

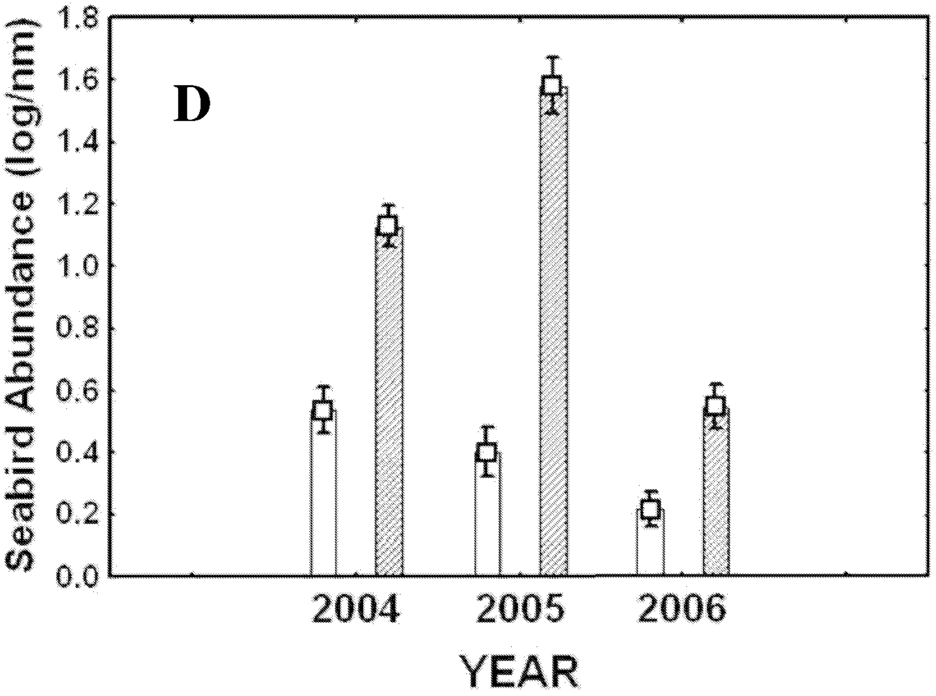


Figure 4.3d: Abundance of Cape Petrels (shaded bars) and Chinstrap Penguins (open bars).

Figure 4a-c: Distribution of krill (NASC): (a) 2004, (b) 2005, and (c) 2006

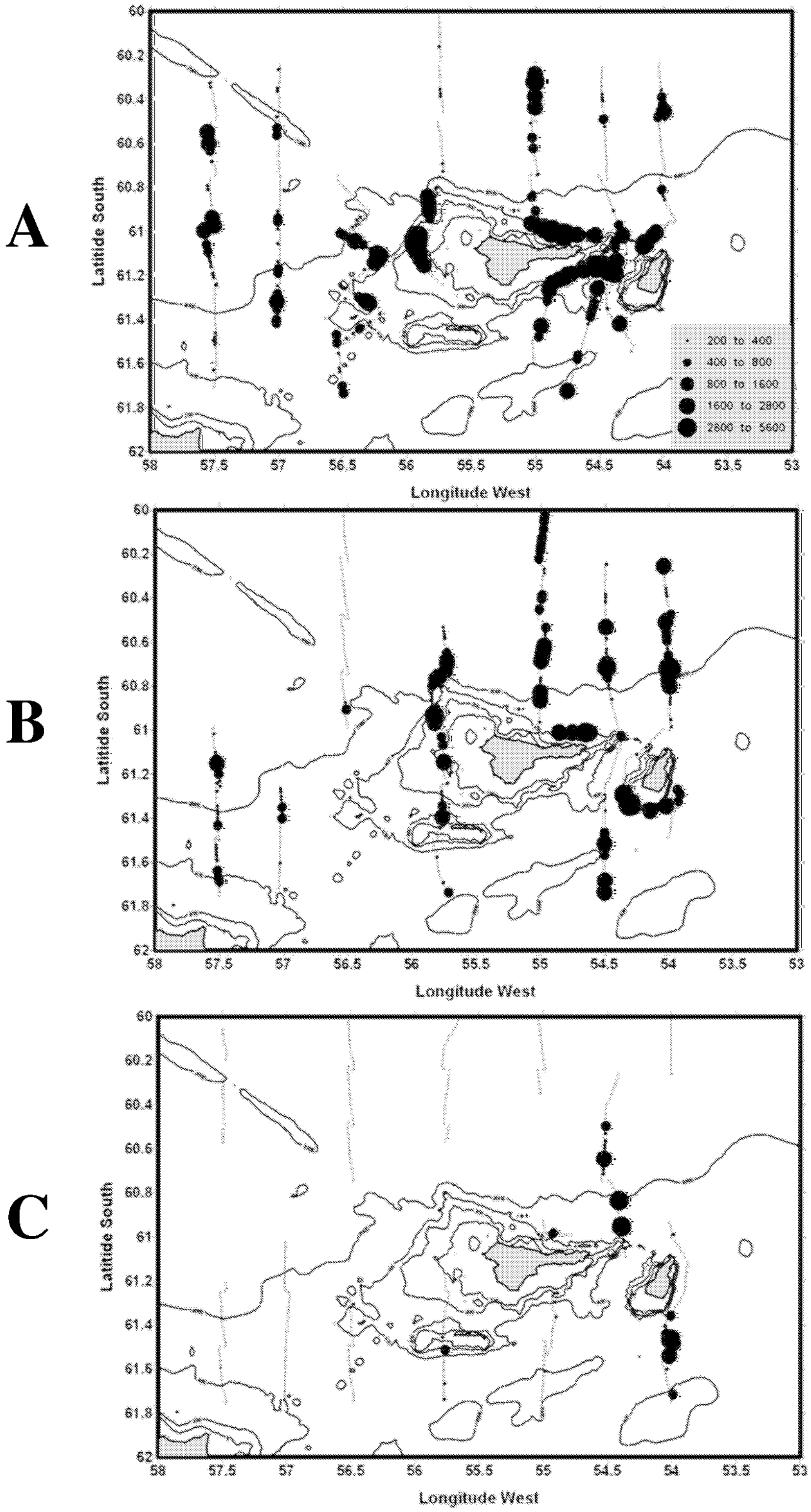


Figure 4.4d-f: Distribution of Flying Cape Petrels, (d) 2004, (e) 2005 and (f) 2006.

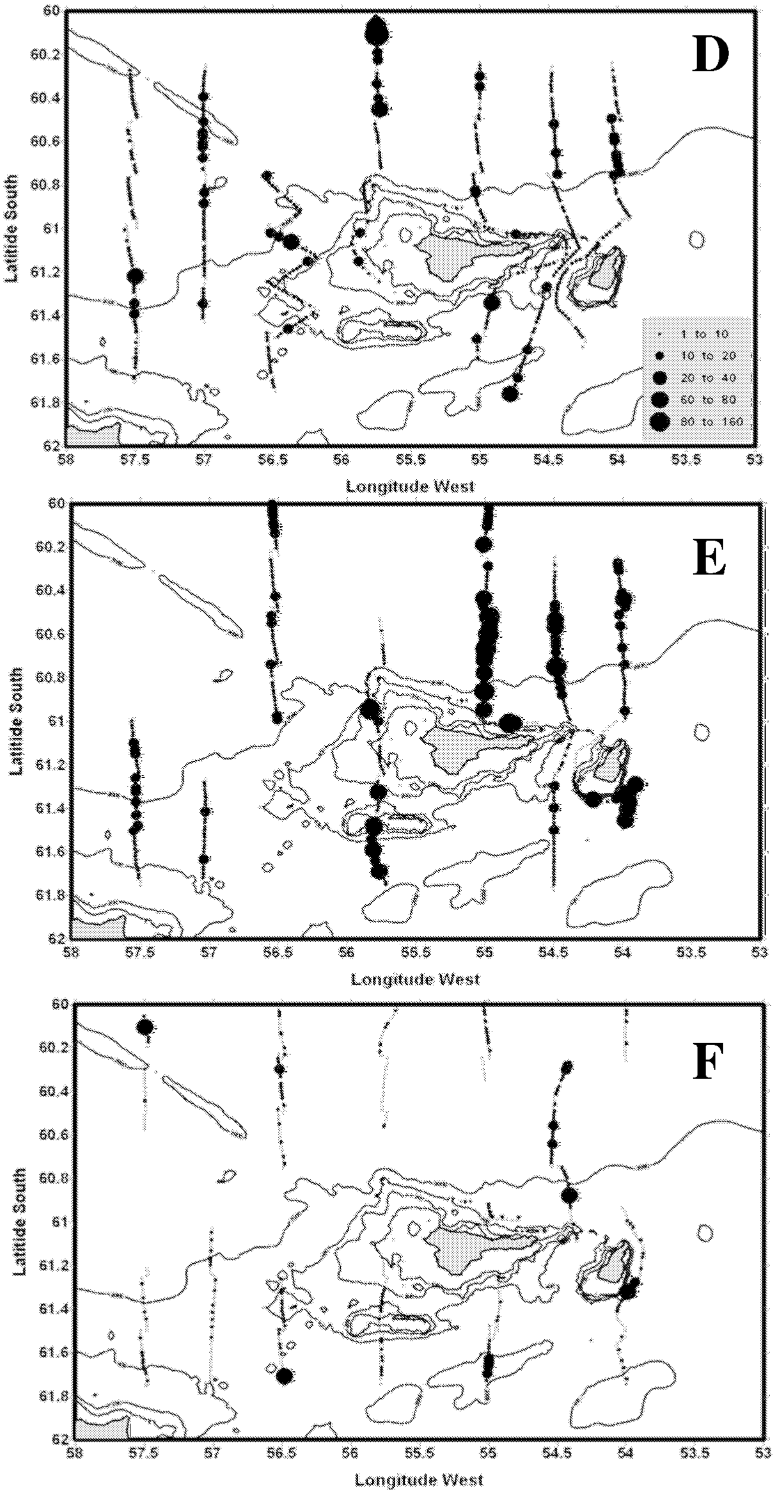
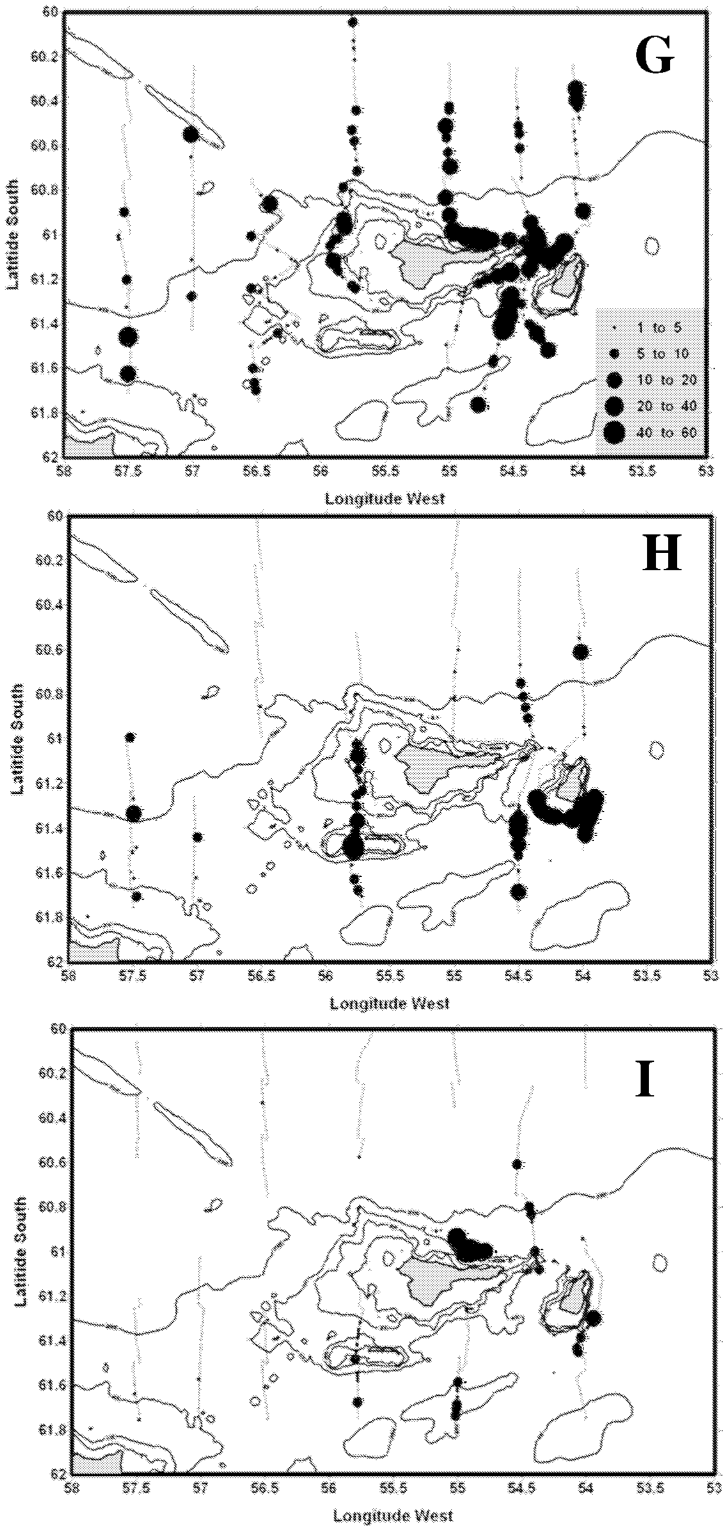


Figure 4.4g-i: Distribution of Chinstrap Penguins (g) 2004, (h) 2005 and (i) 2006.



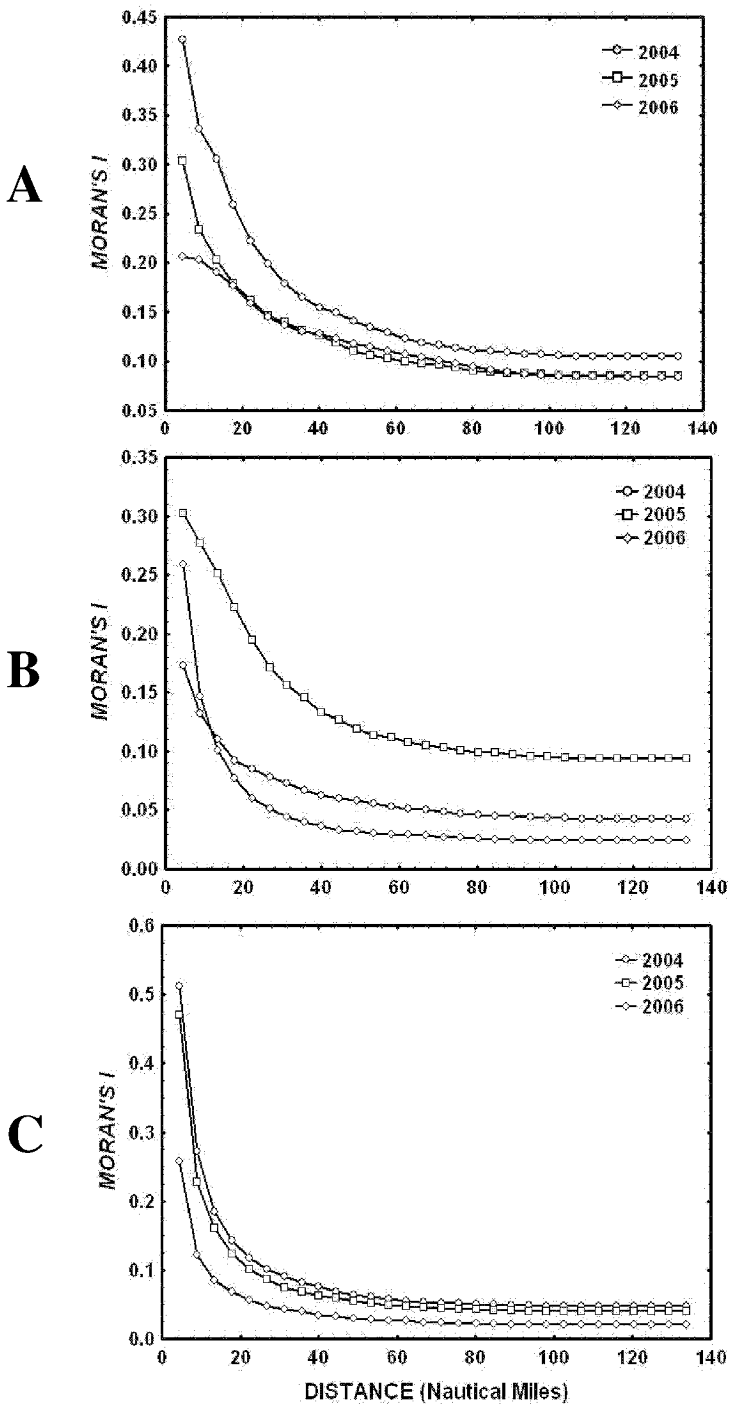


Figure 4.5: Spatial autocorrelation functions (*Moran's I*) of (a) krill, (b) *Flying* Cape Petrels, and (c) Chinstrap Penguins.

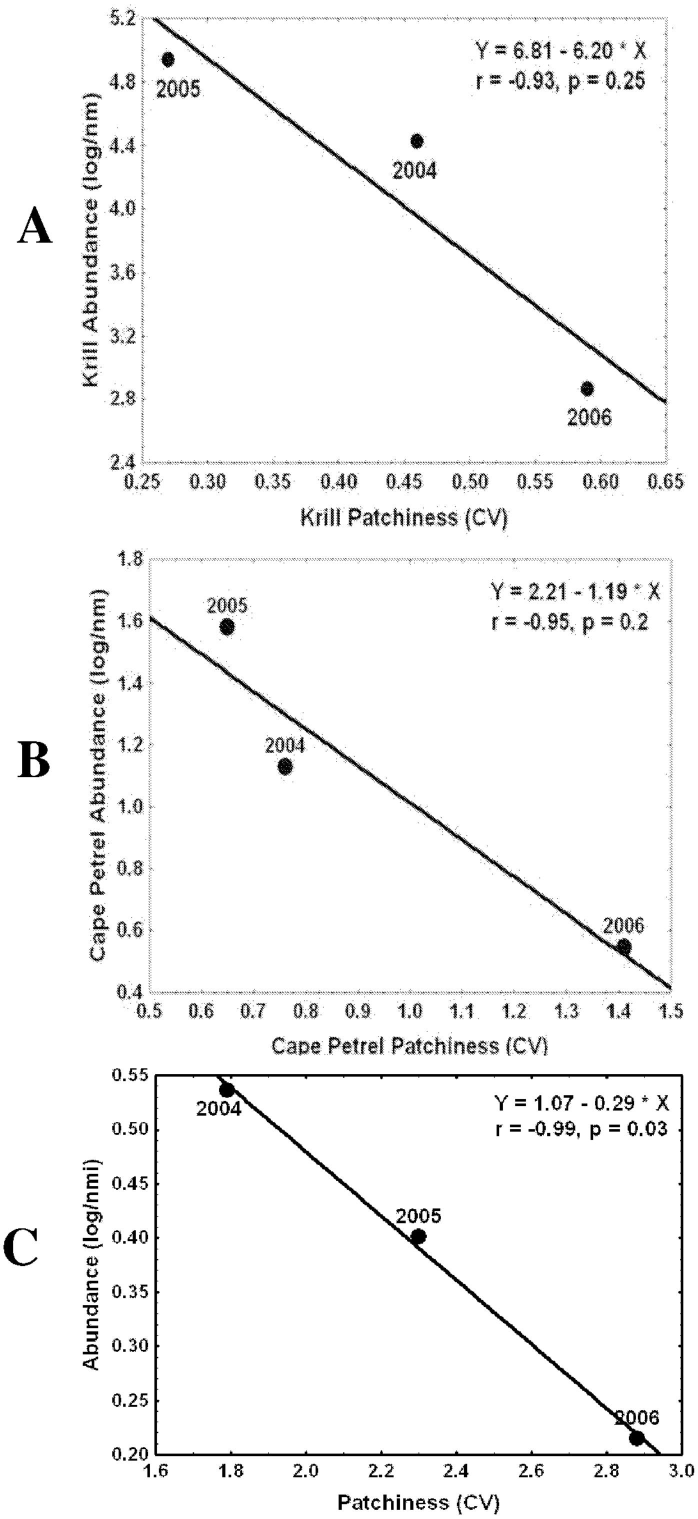


Figure 4.6: Relationship between abundance and patchiness (CV) of: (a) krill, (b) *Flying* Cape Petrels, and (c) Chinstrap Penguins.

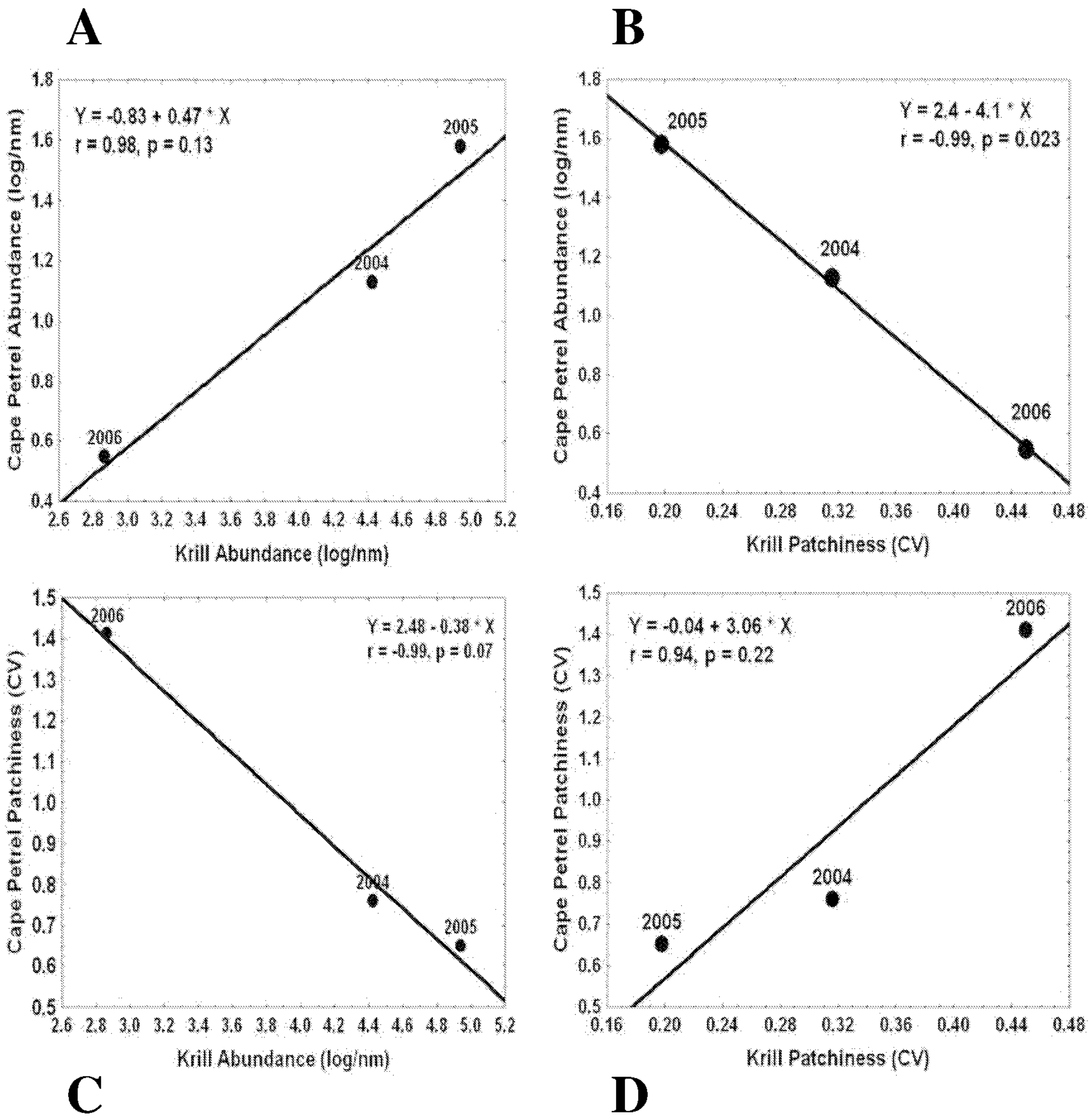


Figure 4.7: Relationship between abundance of Cape Petrels and (a) abundance and (b) patchiness of krill; (c-d) Relationship between patchiness of Cape Petrels and (c) abundance and (d) patchiness of krill.

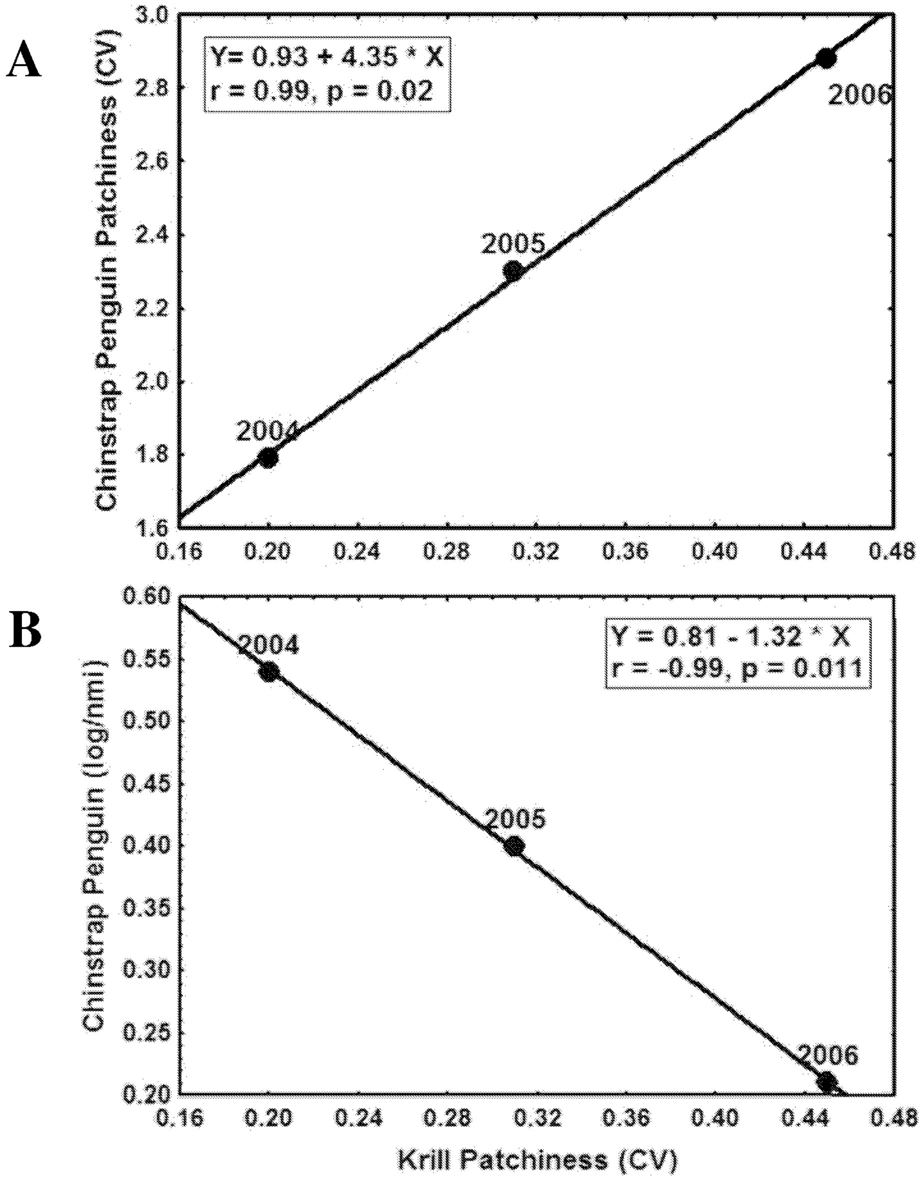


Figure 4.8: Relationship between krill patchiness and (a) abundance and (b) patchiness of Chinstrap Penguins

CHAPTER 5

Effect of a near gale on the distribution of Antarctic krill and its avian and pinniped predators

INTRODUCTION

We examine the role that a short-term meteorological event had on various components of the Antarctic nearshore ecosystem. Spatial changes are examined based on the differences between two submarine canyons that are similar in size, depth, and area. We studied temporal changes in the ecosystem before and after the storm that occurred on 6 Feb 2005. Aspects of the ecosystem included in this analysis are the physical properties of the water column, phytoplankton biomass, and the distribution and abundance of krill and avian and pinniped predators. Hydrographic properties (temperature, salinity, dissolved oxygen and density) of the water column were measured, as well as the depth of the mixed layer, as an indicator of environmental change due to the gale. It is likely that both physical and biological factors play a role in determining the distribution of krill and its predators, although it may depend on the scale as to which factor is more important (Murphy *et al.* 1998, Daly and Smith Jr 1993). We examine how small changes in both spatial distance (on the order of kms) and time (on the order of days) can influence on the components of a marine ecosystem. In particular, the response of predators to the change in the abundance and distribution of their prey is examined. To better understand the dynamics of this ecosystem, it is necessary to have an understanding of the impact a simple perturbation (a gale) can have on multiple components of the nearshore Antarctic krill ecosystem.

The Scotia Sea ecosystem is a highly productive area of the Southern ocean with Antarctic krill being a key prey species for many of the higher trophic-level animals

(Marr 1962, Siegel 2000, Croxall *et al.* 2002, Atkinson *et al.* 2004). Livingston Island (62.5° S, 61° W), one of the South Shetland Islands, is home to Antarctic fur seal (*Arctocephalus gazella*) and chinstrap penguin (*Pygoscelis antarctica*) colonies. Several colonies and rookeries for these animals are on the north side of the island, near Cape Sherriff (Fig. 6.1). These animals support the energy needs of themselves and their offspring by foraging for food in the surrounding waters of Livingston Island. One of the more conspicuous and numerous petrels found in this region is the Cape Petrel (*Daption capense*). All three predators subsist almost entirely on Antarctic krill, although fur seals may also forage for small fish (myctophids), squid, or other small nekton (Costa et al. 1989, Veit et al. 1993, Lynnes et al. 2002).

Changes in the spatial distribution of their preferred prey (krill) may have significant impacts on their foraging and reproductive success. During the predator's breeding season, the adult animals depend on locating sufficient amounts of krill to support the energetic needs of themselves and their offspring. For example, following a major crash in krill availability around South Georgia, reproductive success of predator populations was poor in contrast to other years (Croxall et al. 2002). The recovery of the fur seal population in the South Shetland Islands has been mostly limited to the colonies located on Livingston and Elephant Islands (Boveng et al. 1998), making the breeding success of the animals at Livingston Island important to the overall population. Many studies have examined the interaction between prey and predators on an annual basis (Croxall et al. 1999); but few, if any, have examined this relationship on the timescale of days. There is little known about the response of predator foraging behavior to fine-scale changes in the prey distribution field.

METHODS

We surveyed krill and predator populations north of Livingston Island during 1 – 10 February 2005 from the RV *Yuzhmorgeologiya*. The vessel used a multiple frequency acoustic echosounder to measure the distribution and abundance of krill, during which simultaneous visual estimates of predator abundance and behavior were collected. Additionally, continuous meteorological observations and net tow and hydrographic stations were made throughout the survey.

The survey consisted of 10 transects, approximately 45 km long, 5 km apart, and spanning the two submarine canyons which flank Cape Shirreff (Fig. 6.1). The survey range was approximately bounded by the 1000 m isobath offshore and the 50 m isobath inshore with a total survey area of approximately 2500 km^2. The ship surveyed each transect three times during this study. Two of the transect legs had five stations where a CTD hydrographic profile and net tow sample were taken during the survey (Fig. 6.1). In total, the 10 station sites resulted in 40 CTD casts and 38 net tows as some operations were canceled due to sea state and weather conditions. Meteorological conditions (Photosynthetically Active Radiation (PAR), air temperature, wind speed and direction corrected for ship velocity and heading, and barometric pressure) and GPS position were recorded and averaged over 1 min intervals from a WeatherPak 2000 (Coastal Environmental Systems Inc., Seattle, WA, USA) meteorological station.

Hydrographic and net tow sampling

At each station, a SeaBird 911 CTD rosette was lowered to 750 m or to 10 m above the bottom. In addition to conductivity, temperature, and density profiles, water samples were also collected at several depths and used to measure phytoplankton biomass. Chlorophyll and phaeopigment concentrations were measured from filtered water samples that were extracted with absolute methanol and analyzed using standard fluorometric methods (Holm-Hansen et al. 1965; Holm-Hansen & Riemann 1978). After each CTD cast, a 2 m^2 Isaacs-Kidd Midwater Trawl (IKMT) was obliquely towed to 170 m (or 20 m above the bottom in waters shallower than 170 m). The IKMT had a net mesh size of 505 μm and a flow meter (General Oceanics) attached to calculate sampled volume. Zooplankton samples were immediately identified (to the species level) and enumerated on board the ship after collection. For tows collecting large amounts of biomass, a sub-sample was analyzed. Adult krill in the net sample were measured for length and sexed. All animals (except adult krill and small fish which were used for other studies) were preserved in a 10% buffered formalin solution after the sample was processed.

Acoustic survey of krill

In order to sample a distribution that is spatially and temporally variable, conventional net sampling methods are often combined with acoustic surveys (Hewitt and Demer 1993, Hewitt and Demer 2000). While acoustic survey techniques provide many advantages (improved vertical and horizontal resolution, ability to rapidly survey large areas) over net sampling, they provide an indirect measure of the krill population and must be validated, typically by the use of net or video techniques (Lawson *et al.* 2004, Demer and Conti 2005).

The nearshore Livingston Island ecosystem is well-suited for acoustic sampling methods as (1) these methods have been used in nearby waters for many years to assess and manage krill stocks (Hewitt and Demer 2000); (2) the acoustically-significant species found in the water column can generally be discriminated from one another by the use of multiple acoustic frequencies (Watkins and Brierley 2003); and (3) there are relatively few (compared to other areas of the world) acoustically-significant species; that is, species that contribute a measurable amount to the total acoustic scattering measured in the water column.

The acoustic system used was a multiple frequency (38, 70, 120, and 200 kHz) hull-mounted echosounder (SIMRAD EK 60). The echosounder was calibrated in early January in Admirality Bay, King George Island using a standard target (38.1 mm diameter tungsten carbide sphere). Acoustic data were collected in 1 m vertical depth bins with a synchronized ping every 2 s. Typical survey speed during the cruise was 5 m s^{-1} although sea state and weather sometimes resulted in slower speeds. The acoustic data were processed using a multiple frequency discrimination technique (Watkins & Brierley 2003, Hewitt et al. 2003) that uses the difference in volume backscattering strength at the different frequencies to identify scattering as being from krill. Scattering from krill was integrated into Nautical Area Scattering Coefficients (NASC) from the shallower of 110 m or 5 m above the bottom to 10 m below the surface over 1 km cruisetrack segments. These values of NASC were then converted to estimates of krill biomass using the length-frequency distribution of krill caught in nets and a theoretical acoustic scattering model (Hewitt *et al.* 2003; Demer and Conti 2005).

Predator distribution, behavior and abundance

Two observers collected data on seabird and pinniped abundance and distribution during each cruise using binoculars continuously during daylight hours. Counts of predators were made within an arc of 300 m directly ahead to one side of the ship while underway (Tasker *et al.* 1984, Veit *et al.* 1993). Each record was assigned a time (to the nearest tenth of a second) and a spatial position from the ship's global positioning system, which was synchronized with the echosounder system. Individual animals, or flocks of birds, were assigned a behavioral code. The behaviors were: flying, sitting on water, feeding, porpoising (penguins and fur seals) and ship following (Veit 1999). Ship-following birds were recorded when first encountered and ignored thereafter.

We focus on describing the foraging distributions of two conspicuous Antarctic seabirds and one pinniped species which breed locally in the South Shetland Islands, and are known to feed extensively on krill. Cape Petrels (*Daption capense*) are medium sized petrels, which are highly gregarious and feed primarily by surface seizing in the upper few meters of the sea surface. They generally forage in flocks that are easily monitored for behavior characteristics (Veit 1999). For Cape Petrels, we make the distinction between birds that were observed flying or searching from those that are feeding. Chinstrap Penguins (*Pygoscelis antarctica*) are pursuit-diving predators, which are capable of diving to more than 50 m in search of prey (Bengtson et al. 1993). Only sitting Chinstrap Penguins were analyzed for this study because they were more likely to be foraging as opposed to traveling. Antarctic fur seals (*Arctocephalus gazella*) are also pursuit-diving predators, however they are able to dive to deeper depths (Croxall et al. 1985). Only observations of non-transiting fur seals were analyzed in this study. While all three predators rely on krill for energy, their feeding strategies and abilities differ which may result in different responses to changes in the abundance and distribution of their main food resource.

Analytical Methods

In order to study the spatial and temporal dynamics of the nearshore Antarctic ecosystem, the study area was divided spatially into western and eastern canyons, and temporally before and after the gale. The before survey occurred from 1-5 February 2005 and the after survey from 7-10 February 2005. The western canyon contains the five western-most survey transects, and the eastern canyon is composed of the five eastern-most survey transects (Fig. 6.1). All four categories contain similar amount of trackline and survey effort, although there was an additional day of survey effort before the storm.

Our primary objective was to determine whether the distribution and abundance of krill and foraging predators differed with respect to canyon location (east or west) and before and after the storm. In addition, the hydrography of the water column was also examined to see if there were changes either between canyons or as a result of the storm that altered the physical environment of the krill. Parameters examined included: depth of the surface mixed layer as evidence of strength of surface mixing processes; depth of the 27.5 σ_θ isopycnal as a measure of vertical movement of water masses; and temperature, dissolved oxygen, and σ_θ at 100 m depth to indicate changes in sub-surface hydrography. We measured phytoplankton biomass (vertically integrated chl-a and phaeopigment concentrations) to determine if the food available to the krill differed either spatially or temporally.

We constructed distribution maps of predators and acoustically determined krill abundance before and after the storm. We used a factorial ANOVA to determine whether the abundance of predators (# km^{-1}) and acoustically determined krill biomass (g m^{-2}) differed between east and west canyons before and after the storm. Canyon location and storm event were treated as fixed factors, and multiple comparison tests were done using Bonferroni post-hoc tests (Zar 1999).

RESULTS

Environmental Conditions

A strong low-pressure system (minimum barometric pressure 963 mbar) entered the survey area on 6 February 2005, which caused most shipboard-based sampling to halt until sea state improved. Wind speeds (averaged over 1 minute) during the near gale were consistently greater than 14 m s^{-1} for approximately 8 hours. Wind speeds varied between 2 and 14 m s^{-1} both before and after the storm, but were not as consistently strong as during the storm. The water column in both canyons experienced dramatic changes after the storm (Tables 6.1 and 6.2), with both canyons showing a similar hydrographic response.

The deepening of the surface mixed layer in both canyons after the storm was not statistically significant ($p = 0.15$, Tables 6.1 and 6.2). However, other differences in hydrographic data were found to be significant either between the two canyons or before and after the gale. The depth of the $\sigma_\theta = 27.5$ kg m^{-3} isopycnal deepened by roughly 50% after the storm had passed. Several hydrographic variables (temperature, dissolved oxygen and σ_θ) measured at 100 m depth changed after the gale becoming, respectively, warmer, more oxygen rich, and lighter (Tables 6.1 and 6.2). These data suggest that the effects of the storm were evident at least to a depth of 100 m and that the waters below the surface mixed layer were affected by the storm event. These hydrographic changes may be the result of advection of surface water offshore and replacement of these waters by deeper water or by mixing surface and sub-surface water masses.

Phytoplankton biomass

Measurements of integrated (from 100 m or the bottom to the surface) chlorophyll a and phaeopigment increased between 30 and 50% in both canyons after the gale (Tables 6.1 and 6.2). Interestingly, the changes observed in chlorophyll a and phaeopigment concentration were not observed in the PAR values for the two canyons before and after the gale which supports the hypothesis that nutrient, and not light, availability is a limiting factor in primary productivity (Holm-Hansen et al. 2004). The passage of the storm may have provided additional nutrients (either from land runoff or mixing of deep water) to the upper water column or decreased stratification, which could lead to increases in phytoplankton biomass although these changes would not occur immediately after the storm. Another potential explanation is that phytoplankton biomass was advected into the nearshore region by the storm which would result in immediate changes to the chlorophyll a and phaeopigment measurements.

Spatial and temporal distribution patterns of Antarctic krill

Net samples conducted in both canyons before and after the storm suggest that the composition of the zooplankton community did not vary spatially or temporally during the study period. The dominant taxa in terms of biomass for all sampling periods was krill (*E. superba*), although smaller euphausiids *(Thysanoessa macrura* and *Euphausia frigida)* were also present. Other zooplankton caught by net tows included: copepods (*Metridia gerlachei, Calanus acutus, Calanus propinquus*, *Rhincalanus gigas* and *Pareucheata spp.)* and salps (*Salpa thompsoni*). The zooplankton sampled with the net were similar to those in a larger-scale study of the Scotian Sea (Ward et al. 2004). Adult *E. superba* lengths were nearly 5 cm. The length-frequency distribution of krill caught in the net was the same for all samples.

The distribution of krill biomass shows that the western canyon had more biomass (20%) than the eastern canyon both before and after the storm (Fig. 6.2, Table 6.4, p = 0.003). The total krill biomass in each canyon decreased by roughly half after the storm. In addition to this change in abundance, the distribution of scattering also changed both horizontally and vertically. Before the storm, large amounts of krill were found throughout both canyons; after the storm, krill were less abundant and only found along the canyon edges (Fig. 6.2, Table 6.4). The distribution of krill vertically in the water column also changed after the storm in both canyons (Fig. 6.3, Table 6.4), with fewer krill being found at deeper depths.

Predator distribution and behavior

The distribution of predators changed markedly after the near gale. Before and after the near gale, persistent aggregations of flying Cape Petrels were encountered along the outer 1000 m isobath at the mouths of each canyon (Fig. 6.4-6.5). There was a significant difference in flying Cape Petrel abundance between the canyons before and after the near gale (p = 0.02, Tables 6.3 and 6.5, Fig. 6.4-6.5). Before the near gale, the eastern canyon had more observations of flying cape petrels, but after the near gale the abundance of flying Cape Petrels was greater in the western canyon. The distribution of feeding Cape Petrels prior to the near gale was predominantly located throughout the eastern canyon (Fig. 6.4-6.5), and afterwards feeding aggregations were entirely restricted to the western canyon ($p < 0.0001$, Tables 6.3 and 6.5).

Chinstrap Penguin aggregations were located close to major penguin colonies (e.g. Cape Sherriff and Desolation Island), both before and after the near gale (Fig. 6.6). However, Chinstrap Penguins were significantly more abundant in the eastern canyon after the near gale (Tables 6.3 and 6.5). Foraging fur seals were more concentrated in the western canyon and large aggregations (12 to 15 animals) were detected along the 1000 m isobath (Tables 6.3 and 6.5, Fig. 6.7). There was no detectable difference in fur seal foraging distribution, except that they were significantly less abundant in the eastern canyon after the near gale.

The temporal correlation between krill and its predators showed that the different animals responded differently to changes in krill abundance (Fig. 6.8). Flying Cape Petrels were not correlated with krill biomass before ($r = -0.02$, $P = 0.62$) or after ($r = -0.09$, $P = 0.03$) the near gale. Feeding Cape Petrels were not associated with krill biomass before the near gale ($r = 0.03$, $P = 0.40$); but after, when krill biomass decreased by nearly half, they were correlated with krill ($r = 0.24$, $P<0.001$). Chinstrap Penguins were associated with krill biomass both before ($r = 0.12$, $P = 0.001$) and after ($r = 0.12$, $P = 0.02$) the near gale. Fur seals were not correlated with krill biomass before ($r = -0.008$, $P = 0.82$), or after ($r = 0.07$, $P = 0.09$) the near gale.

DISCUSSION

The storm altered both physical and biological characteristics of the nearshore environment. The water column in both canyons became warmer, more oxygenated and more mixed. Measures of phytoplankton biomass increased after the storm, while krill biomass declined by roughly 50%. Krill were more likely to be found in the western canyon before and after the storm. Feeding aggregations of Cape Petrels were linked to changes in krill distribution, but distributions of foraging Chinstrap Penguins and fur seals were not. Somewhat independent of the storm, fur seals showed a strong preference for foraging at the 1000 m isobath near the mouth of the western canyon whereas Chinstrap Penguins foraged closer to shore and at the heads of the canyons.

While some of these observations may be of stable features of the region (e.g. the western canyon containing more krill biomass than the eastern canyon), other parts of the ecosystem were rapidly altered when a near gale passed through the area. Even in the austral summer, these low-pressure systems and associated winds are regular occurrences (Turner et al. 1998). Furthermore, changes in the measured variables were also observed between the two canyons suggesting that geographic factors may play a role in determining how the ecosystem responds to such an event.

Nearly every component of the Antarctic nearshore ecosystem (water column properties, phytoplankton, zooplankton, seabirds and fur seals) showed a response to the storm event which lasted less than a full day. The storm may have altered the physical environment by mixing the water column and bringing deep water nearer to the surface. Upwelling of Upper Circumpolar Deep Water (UCDW) has been linked to increased productivity in other areas in the Southern Ocean (Prézelin et al. 2000, Lawson et al. 2004). Several of our CTD casts measured UCDW, as determined by hydrographic properties (potential temperature and salinity) (Klinck et al. 2004). However it must be noted that the casts that encountered UCDW water were all at the furthest offshore (deepest) stations. Other casts did not detect UCDW, which could be explained by the fact that as the water progresses up the submarine canyons it mixes with surface and near-surface water and loses its characteristic properties.

The variability of the krill ecosystem is high within the spatial and temporal scales measured in this study (10^2 – 10^3 km^2, 10-10^2 hr). Thus, ecosystem surveys that visit a site or station only once or multiple times separated by weeks or more may be biased as a result of recently or presently occurring mesoscale phenomena such as the passing of a low pressure system, as in this study. However, for some situations where perturbation frequency is such that several events occur during the sampling period, the biases associated with these events may balance out over the survey period. While changes in the physical environment may occur immediately during and after the passage of a storm, it is not known how long it may take the other parts of the ecosystem to respond to the changed environment. If currents driven by the storm advect animals, changes would occur immediately; however longer times would be required for other trophic levels of the ecosystem to respond. Primary production could respond within hours to days (Hitchcock et al. 1987, Tenore et al. 1995), and copepods have been found to integrate changes in food availability on time scales greater than 12 hours (Bochdansky & Bollens 2004). The zooplankton community on the other hand has been observed to respond to physical changes in the environment over time scales closer to a week (Cowles et al. 1987, Tenore et al. 1995). In this study, changes in the distribution of krill (and its predators) occurred quickly after the passage of the storm suggesting that krill were not responding to changes in food availability but rather migrated or were advected out of the survey area.

This study shows how a near gale can alter multiple components of an Antarctic nearshore ecosystem. Krill distribution on large scales (e.g. Scotia Sea, hundreds of days) is the result of physical processes controlling the recruitment and transport of animals (Hofmann *et al.* 1998) or hydrographic properties (Trathan *et al.* 2003), but physical processes also play an important role on much smaller scales, as was observed in this study. The changes in the krill distribution likely have significant implications for predator foraging success. Different foraging strategies may allow animals to respond more quickly or be less affected by changes in the horizontal and vertical distribution of krill. Cape Petrels were the most affected by changes in krill biomass distribution. Persistent feeding aggregations were repeatedly detected in the eastern canyon prior to the storm event, and no feeding aggregations were found there in the post storm survey, with all feeding aggregations being located in the western canyon where krill biomass was greater. Therefore, foraging aerial predators adapted their foraging effort to track the changes in their principal prey within the course of a few days.

On the other hand, Chinstrap Penguins and fur seals, displayed little variation in their foraging distribution patterns with respect to the storm event. We found dense aggregations of penguins detected in proximity to Desolation Island (located at the southeastern edge of the 100 m isobath in the eastern canyon), which may have been foraging in locations not sampled during the survey and merely passing through the survey area to or from colonies on Desolation Island. Interestingly, during the post-storm sampling, we detected an aggregation of foraging penguins in the west canyon along the 200 m isobath where cape petrels were observed intensively feeding (Fig. 6.5). These predators may have been using similar krill resources after the storm. Because penguins are pursuit-diving predators, they are more capable of acquiring prey deeper in the water column than the Cape Petrels, and therefore may not be as restricted to foraging locations associated with surface krill swarms. Chinstrap Penguins and fur seals showed persistent foraging preferences for regions of the nearshore environment, which may not change over the course of the breeding season, as long as krill abundance in these areas is adequate and consistent. This difference may be related to their abilities to forage upon krill swarms deeper in the water column. This study collected observations of foraging behavior of multiple krill predators during their breeding season. We focused on changes in predator foraging distribution at the population level. Future effort should be made to contrast the variability of individual and population level foraging distribution patterns with respect to krill distributions.

Acknowledgements. The Captain and crew of the RV *Yuzhmorgeologiya*' provided excellent assistance in completing this survey. We greatly appreciate the assistance of D. J. Futuyma in collection of predator observations. Acoustic echosounder data were collected and processed by A. Cossio and C. Reiss. Zooplankton net tow data were collected and processed by K. Dietrich, R. Driscoll, D. Lombard, P. Kappes, T. Reddy, and S. Wilson who were led by V. Loeb. D. Needham and M. van den Berg collected the hydrographic data. C. D. Hewes provided the phytoplankton biomass measurements. Support for this project was jointly provided by the Office of Polar Programs at the National Science Foundation (grants # OPP-0338196 and OPP-0633939 to J.D.W. and D.A.D.) and NOAA's Antarctic Marine Living Resources program led by R. Holt. J.A.S. was supported by National Science Foundation grant OPP-9983751 awarded to R.R. Veit.

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Table 5.1. Comparison of hydrographic and phytoplankton biomass parameters of the western and eastern canyons near Cape Sherriff both before and after the gale. Mean and standard deviations are provided for the data as well as the number of samples.

	West Canyon		**East Canyon**	
Time period relative to gale	**Before (n = 9)**	**After (n = 5)**	**Before (n = 10)**	**After (n = 5)**
Mixed layer depth	30.3 ± 9.8	42.0 ± 39.9	22.0 ± 11.6	46.7 ± 22.1
Temperature at 100 m (^{o}C)	0.84 ± 0.28	1.20 ± 0.14	0.40 ± 0.34	1.11 ± 0.18
Dissolved O_2 at 100 m (ml l^{-1})	6.65 ± 0.17	6.85 ± 0.08	6.45 ± 0.31	6.84 ± 0.12
σ_θ at 100 m (kg m^{-3})	27.36 ± 0.05	27.30 ± 0.04	27.41 ± 0.07	27.28 ± 0.09
Integrated chl-a (mg m^{-2})	129.0 ± 42.0	166.0 ± 28.7	98.8 ± 31.7	149.0 ± 28.3
Integrated phaeo (mg m^{-2})	18.9 ± 5.39	30.2 ± 4.61	15.6 ± 3.27	22.8 ± 2.9

Table 5.2. Factorial ANOVA for physical characteristics and phytoplankton biomass.

Variable	EFFECT[1]					
	CANYON		STORM		CANYON * STORM	
	F	P	F	P	F	P
Mixed layer depth	2.21	0.15	0.03	0.87	2.21	0.15
Temp at 100 m	6.05	**0.02**	1.34	0.26	9.31	**0.005**
Dissolved O_2 at 100 m	1.71	0.20	0.03	0.87	3.57	0.07
σ_θ at 100 m	2.66	0.12	0.31	0.58	3.90	0.06
Integrated chl-a	5.24	**0.03**	10.71	**0.003**	0.27	0.61
Integrated phaeo	14.22	**0.001**	30.10	**1.6E-5**	1.55	0.23

1. Degrees of Freedom = 3, 25.

Table 5.3. Descriptive statistics for krill biomass and predator abundance during the survey.

Underway Predator-Prey Estimates				
	West Canyon		East Canyon	
Time Period	**Before**	**After**	**Before**	**After**
Krill biomass (g m^{-2})	407.16±30.7	246.68±24.4	339.76±27.7	185.72±17.6
Cape petrel 'Flying' (# km^{-1})	0.17±0.05	0.38±0.09	1.37±0.53	0.17±0.06
Cape petrel 'Feeding' (# km^{-1})	0.93±0.12	1.55±0.22	3.05±0.44	0.10±0.03
Chinstrap penguin (# km^{-1})	0.23±0.06	0.17±0.09	0.15±0.07	0.71±0.16
Antarctic fur seal (# km^{-1})	0.31±0.03	0.36±0.07	0.24±0.05	0.06±0.02

Table 5.4. Factorial ANOVA for assessing the effect on krill biomass of vertical position in the water column (depth), canyon, and storm.

Test: Krill Distribution		
EFFECT	F	P
Depth[1]	81.82	**<0.00001**
Canyon[2]	8.95	**0.003**
Storm[2]	53.61	**<0.00001**
Depth * Canyon[1]	5.90	**<0.00001**
Depth * Storm[1]	9.31	**<0.00001**
Canyon * Storm[2]	0.08	0.77
Depth * Canyon * Storm[1]	0.53	0.84

[1] Degrees of Freedom = 8, 10758

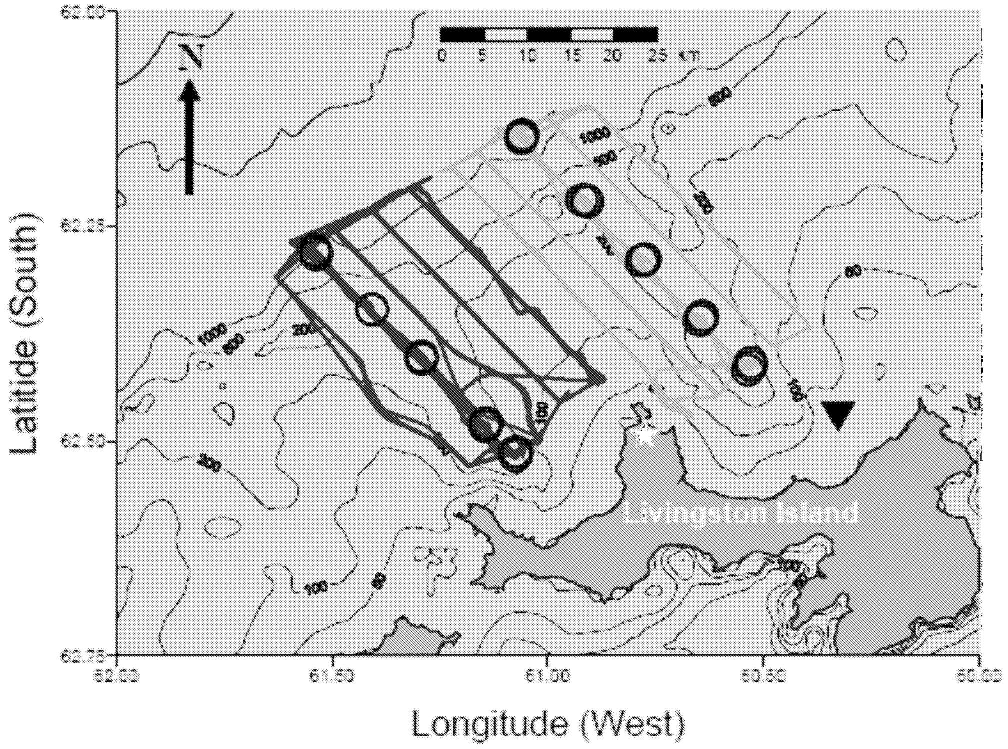
[2] Degrees of Freedom = 1, 10758

Table 5.5: Factorial ANOVA for krill biomass and predator distribution.

Variable	**EFFECT**[1]					
	CANYON		**STORM**		**CANYON * STORM**	
	F	**P**	**F**	**P**	**F**	**P**
Cape petrel 'Flying' (# km^{-1})	2.38	0.12	2.49	0.11	4.91	**0.02**
Cape petrel 'Feeding' (# km^{-1})	1.41	0.23	16.93	**<0.001**	40.31	**<0.0001**
Chinstrap penguin (# km^{-1})	4.98	**0.02**	5.47	**0.02**	8.61	**0.003**
Antarctic fur seal (# km^{-1})	10.70	**0.001**	0.92	0.34	8.08	**0.004**

[1] Degrees of Freedom = 1,1199; there were 1200 km sampled.

Figure 5.1: Survey and station locations for the survey area north of Livingston Island, Antarctica. Circles represent station locations where hydrographic profiles and net tow data were collected. Lines represent the cruise track of RV Yuzhmorgeologiya (dark grey: western canyon, light grey: eastern canyon). Bathymetric contours are shown as thin lines. The white star marks the location of Cape Shirreff. The amount of cruisetrack covered during each section of the survey was: west canyon, before storm (258 km); west canyon, after storm (221 km); east canyon, before storm (380 km); and east canyon, after storm (344 km).



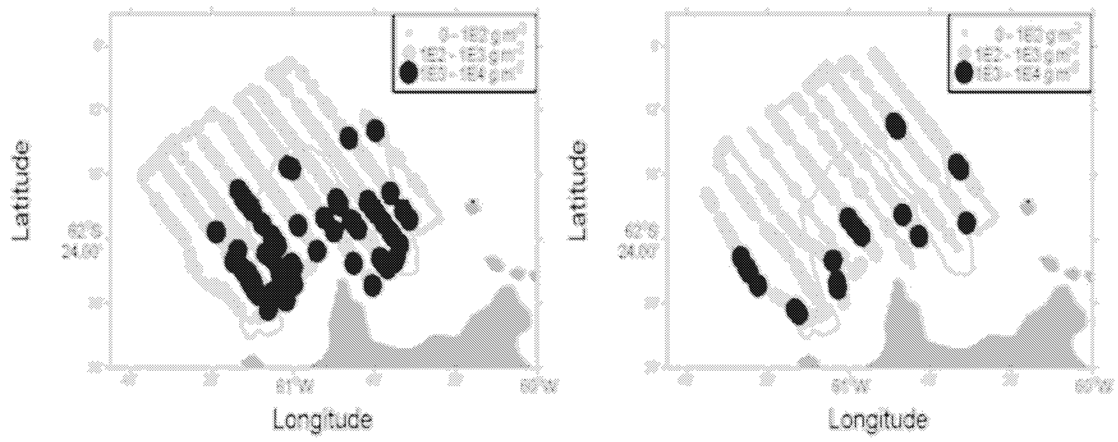


Figure 5.2: *Euphausia superba.* Integrated krill biomass before (left) and after (right) the storm. Krill biomass was calculated from integrated acoustic backscatter measurements using a multiple frequency discrimination method and then converted to biomass using the lengths from animals caught in net tows and a theoretical acoustic scattering model. The thin black line marks the 200 m isobath where aggregations of krill were persistent. Krill biomass was more abundant prior to the storm with post-storm total biomass being 50% of pre-storm levels. The western canyon during both pre- and post-storm periods had more biomass than the eastern canyons.

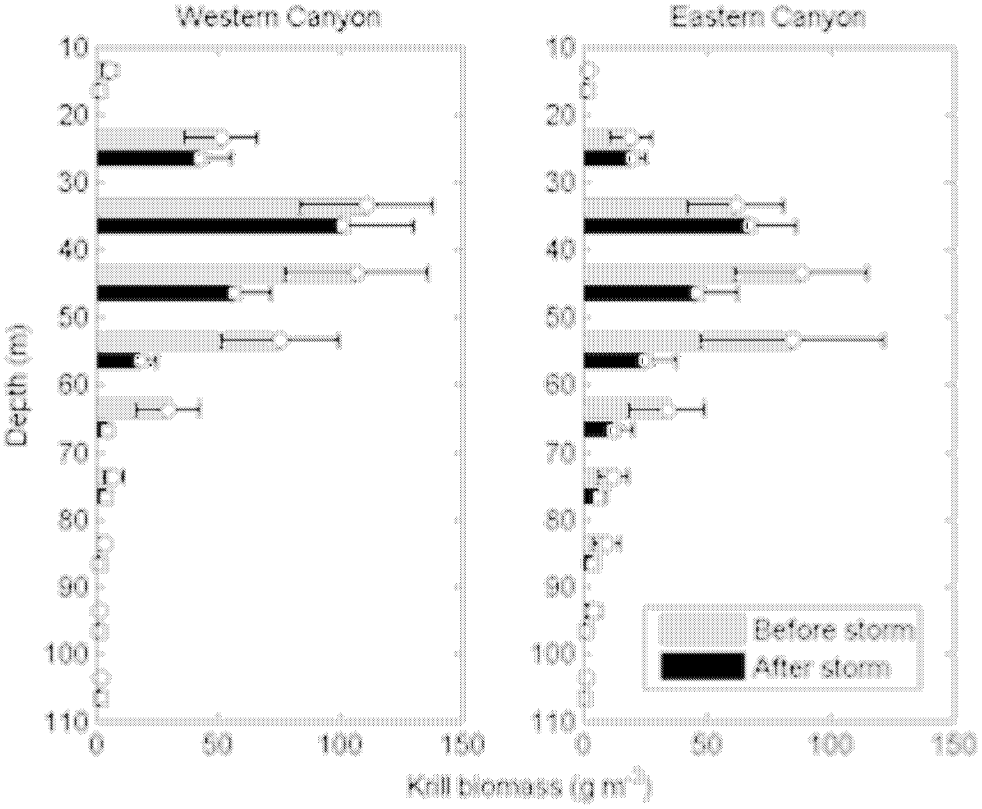


Figure 5.3: *Euphausia superba.* Vertical distribution in each canyon of mean krill biomass for 10 m layers before (circles, grey) and after (squares, black) the storm event with bars indicating standard error. The majority of the krill were located between 30 and 60 m deep. Surface krill aggregations (to a depth of 10 m) were not sampled as the acoustic echosounder was located on the hull of the vessel at a depth of approximately 7 m. After the storm, the largest decreases in krill biomass occurred between 40 and 60 m.

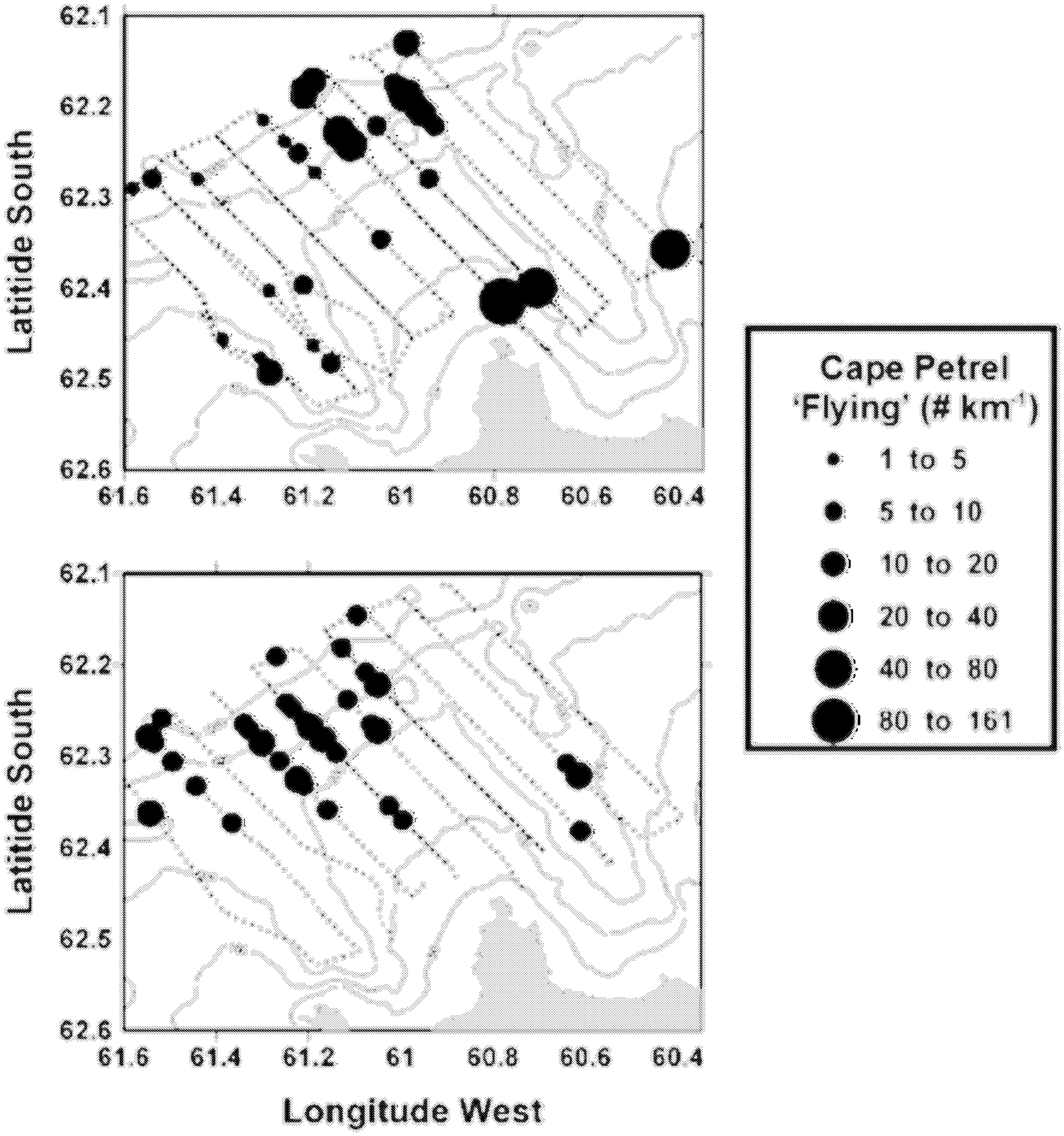


Figure 5.4: *Daption capense.* Distribution of flying cape petrels before (top) and after (bottom) the storm event. The majority of persistent aggregations occurred in offshore areas between the 200 and 1000 m isobaths in both canyons.

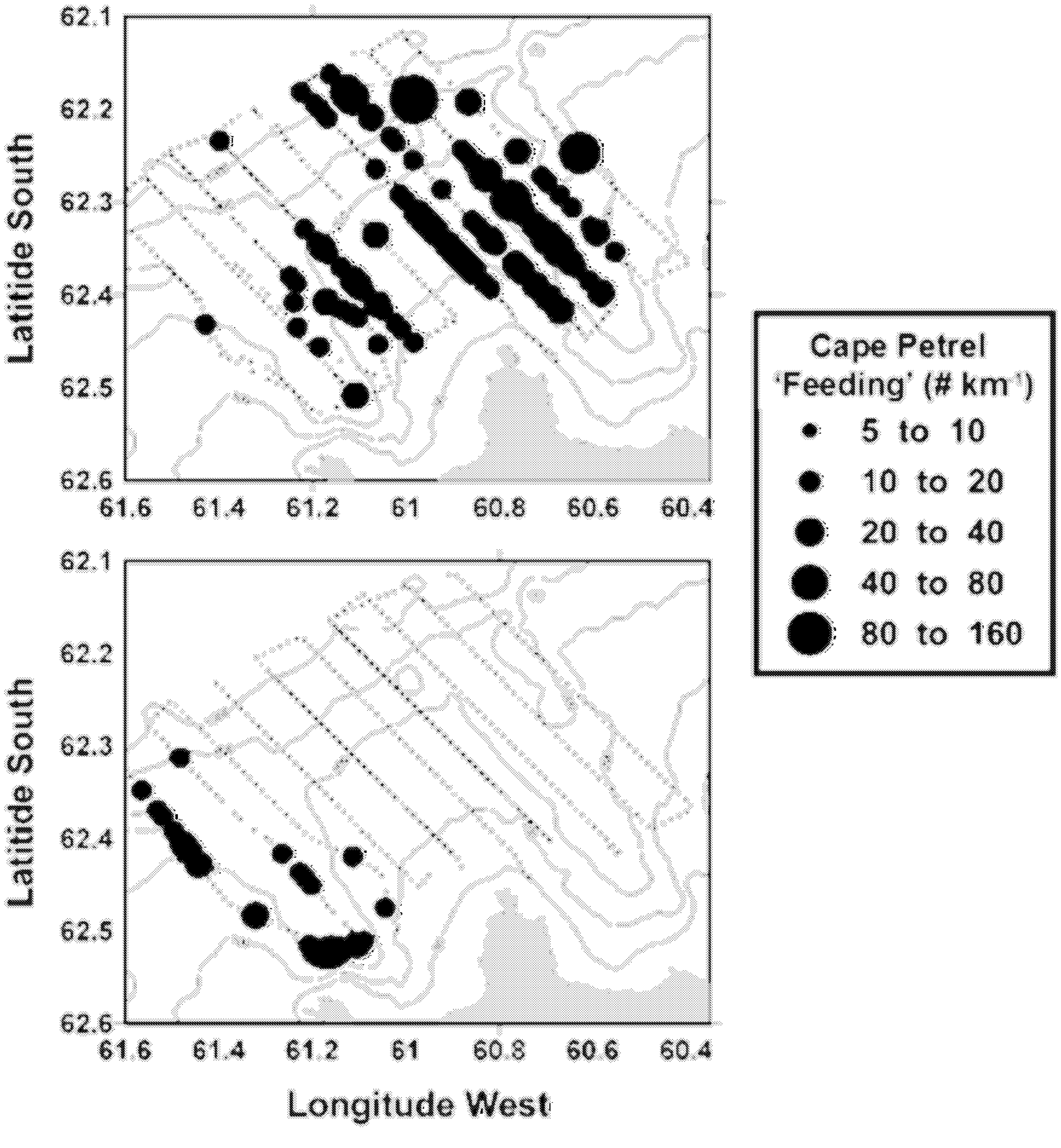


Figure 5.5: *Daption capense*. Distribution of feeding cape petrels before (top) and after (bottom) the storm event. Aggregations prior to the storm were predominant throughout the eastern canyon from offshore to nearshore. After the storm, feeding aggregations were significantly reduced and concentrated along the edge of the western canyon.

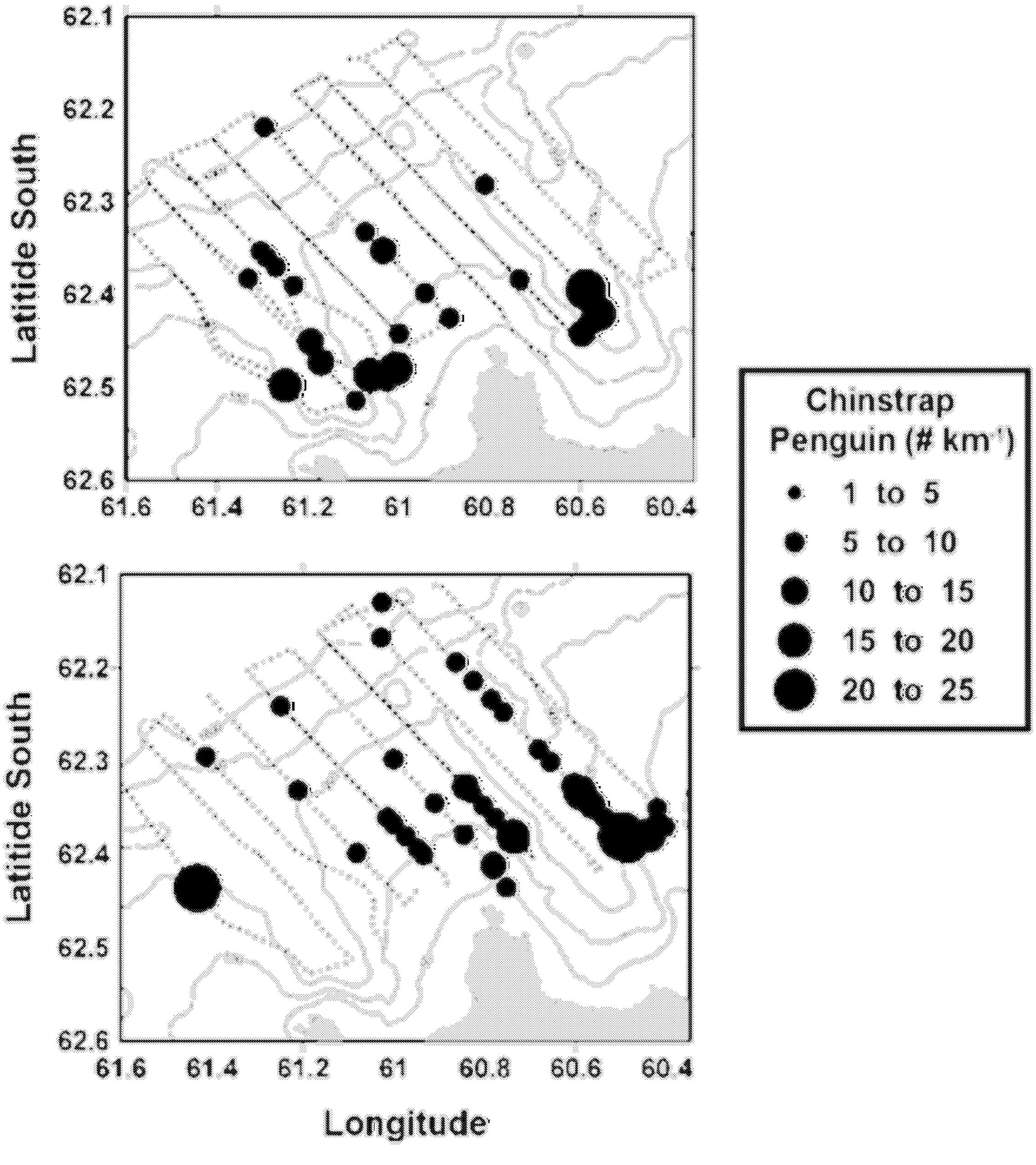


Figure 5.6: *Pygoscelis antarctica.* Distribution of sitting chinstrap penguins before (top) and after (bottom) the storm event. The majority of chinstrap penguin aggregations were located close to shore, near colonies on Cape Shirreff and Desolation Island.

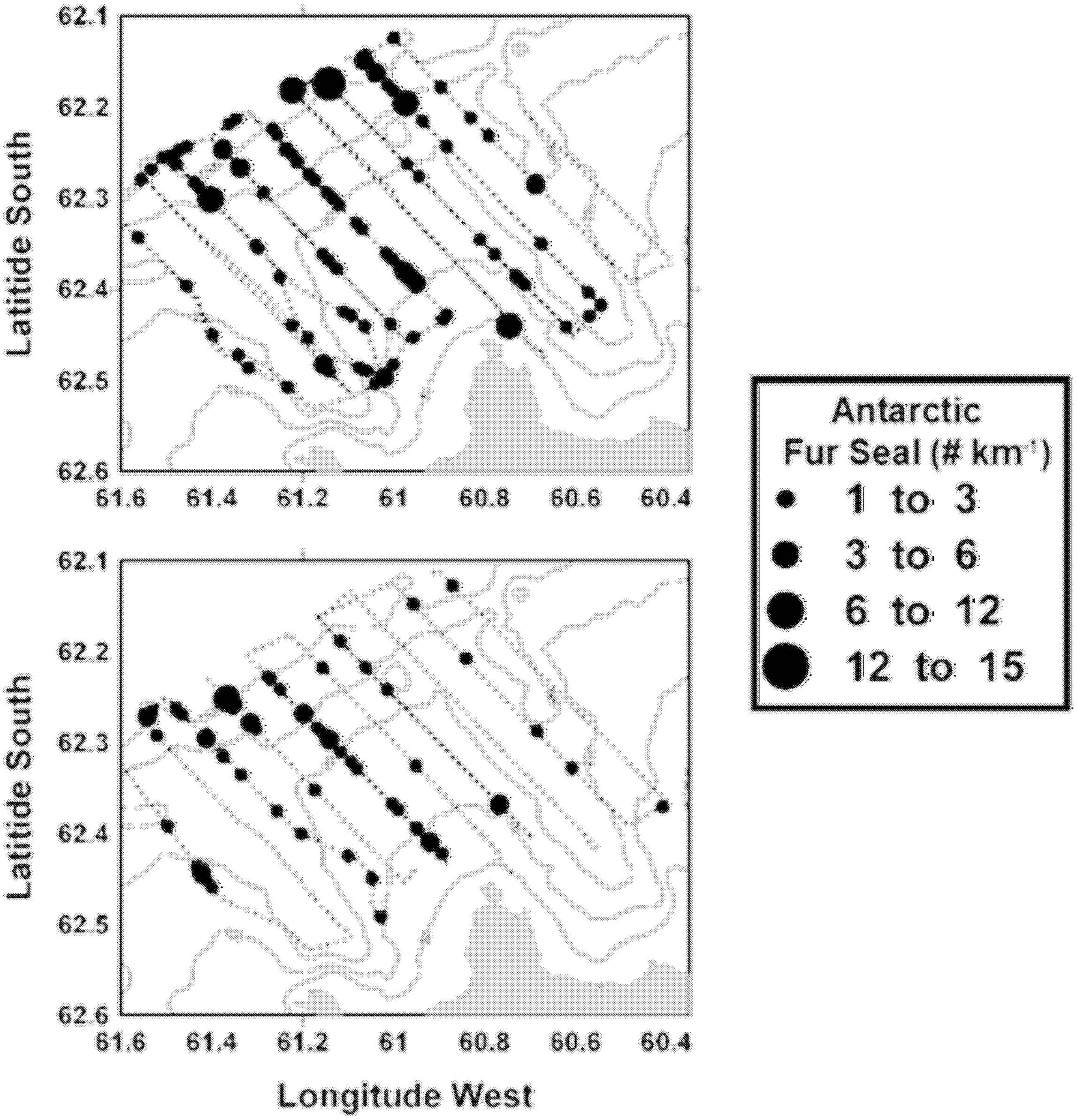


Figure 5.7: *Arctocephalus gazella*. Distribution of Antarctic fur seals before (top) and after (bottom) the storm event. The largest aggregations were found offshore along the 1000 m isobath. Both before and after the storm, fur seals preferred the western canyon.

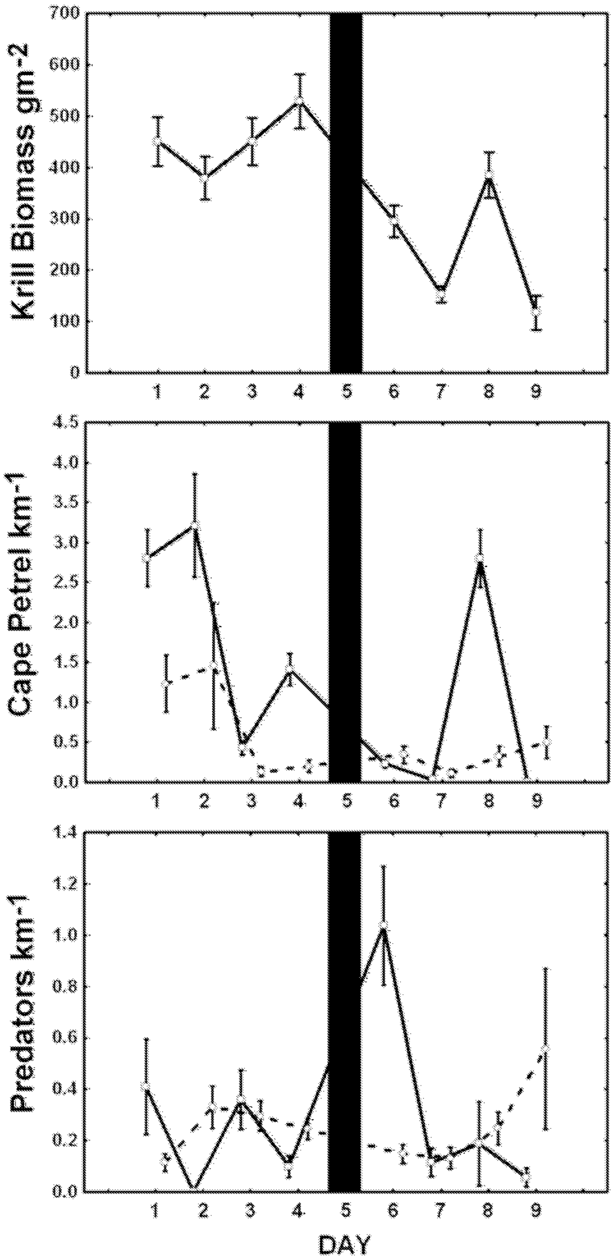


Figure 5.8: Time sequence of daily mean abundance and standard error of (a) krill biomass, (b) feeding (solid line) and flying (dashed line) cape petrels, and (c) chinstrap penguins (solid line) and Antarctic fur seals (dashed line). The gale occurred on day 5 (black bar) and all shipboard operations ceased for 24 hours. The horizontal axis corresponds to days of the survey from 2 to 10 February.

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