Submesoscale distribution of Antarctic krill and its avian and pinniped predators before and after a near gale

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Abstract We conducted two ship-based surveys of the nearshore ecosystem north of Livingston Island, Antarctica during 2–10 February 2005. Between the two surveys, a low-pressure system (963 mbar) passed through the area providing the opportunity to measure ecosystem parameters before and after a near gale. A ship-based multiple-frequency acoustic-backscatter survey was used to assess the distribution and relative abundance of Antarctic krill (*Euphausia superba*). Net tows, hydrographic profiles, and meteorological data were collected to measure biological and physical processes that might affect the krill population. During the survey, the distribution and behavior of several krill predators [chinstrap penguins (*Pygoscelis antarctica*), cape petrels (*Daption capense*), and Antarctic fur seals (*Arctocephalus gazella*)] were measured from the vessel by visual observations. The survey encompassed an area of roughly 2,500 km^2, containing two submarine canyons with one to the west and one to the east of Cape Shirreff, which had different abundances of krill and predators. Several aspects of the nearshore ecosystem changed after the near gale including: hydrography of the upper 100 m of the water column, phytoplankton biomass, the abundance and distribution of krill, and the distribution of some krill predators. Differences in these parameters were also measured between the two canyons. These changes in the physical and biological environment during the survey period are quantified and show that the ecosystem exhibited significant changes over relatively short spatial (tens of kilometers) and time (tens of hours) scales.

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Introduction

The Scotia Sea is a highly productive area of the Southern Ocean where Antarctic krill (*Euphausia superba*) serves as a key prey species for many animals (Marr 1962; Siegel 2000; Croxall et al. 2002). Measuring the abundance and distribution of the krill population is important for ecological studies and the management of the commercial krill fishery (Agnew 1997; Jones and Ramm 2004). In conjunction with krill surveys, visual surveys can be used to study predator–prey relationships by measuring the abundance and distribution of important krill predators including penguins, petrels, other sea birds, fur seals, and other marine mammals (Santora et al. 2008; Veit 1999). If abundance measurements of krill and its predators are made over similar temporal and spatial scales then these observations can be used to examine the linkages between these different trophic levels.

Many of the avian and mammalian predators in these waters subsist almost entirely on krill, although fur seals may also forage for small fish (myctophids), squid, or other small nekton (Lynnes et al. 2002; Veit et al. 1993; Costa et al. 2000). Changes in the abundance or spatial distribution of krill, their preferred prey, may have significant impacts on their foraging and reproductive success. For

example, following a major reduction 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 South Shetland Islands fur seal population has been limited mostly to the colonies located on Livingston and Elephant Islands (Boveng et al. 1998) making the breeding success of these animals important to the overall population.

The distribution and abundance of krill varies over many different spatial and temporal scales (Everson and Murphy 1987; Watkins and Murray 1998; Hamner and Hamner 2000) and can be affected by both biological (top-down and bottom-up) and physical factors (Croll et al. 1998; Ainley et al. 1991). To better understand the dynamics of the krill ecosystem, it is important to know how ecologic, oceanographic, or meteorologic processes will affect the various components of the ecosystem. In particular, it is useful to understand how those parts of the ecosystem that have a direct impact on krill abundance and distribution, specifically the abundance and distribution of its prey and predators, are affected by a common meteorological disturbance such as a storm.

Both physical and biological factors (e.g., nutrient and phytoplankton availability, current velocity and direction) will determine the distribution of krill and its predators, but the relative importance of each factor may vary depending on the temporal or spatial scale at which the distributions are measured (Haury et al. 1978; Daly and Smith Jr 1993). Some physical factors, such as the extent of annual sea ice or sea surface temperature, can influence krill populations over very large (1,500 km) distances (Brierley et al. 1999). Krill predators have been shown to react to changes in the temporal or spatial distribution of krill (Boyd 1996; Reid et al. 1999) or the physical environment (Hunt Jr et al. 1992; Ainley et al. 1994). However, few studies have examined the effect of processes occurring over smaller spatial (tens of kilometers) and temporal (days) scales on krill and its predators.

To better understand the interactions between predator and prey species in this ecosystem, descriptive ecosystem parameters need to be measured over the temporal and spatial scales that are relevant to the most important ecosystem processes. Several studies have annually examined the interactions between zooplankton prey and predators (Croxall et al. 1999; Barlow et al. 2002; Croll et al. 2005), but few have examined this relationship on the time-scale of days. Croll et al. (1998) measured several ecosystem components: bathymetry, hydrography, zooplankton (euphausiids), and a key zooplankton predator (baleen whales) near the California coast over a 10-day period and found that whale foraging effort occurred in areas of high euphausiid abundance. Goebel et al. (2000) studied Antarctic fur seal foraging trips near Livingston Island over the course of several days to weeks and found dive behavior related to bathymetry as well as time of day. These studies examined predator–prey relationships

at small spatial and temporal scales, but they did not quantify how dynamic those relationships might be when the ecosystem is perturbed by physical forces.

Our study measures multiple ecosystem parameters over submesoscale time- (10 days) and space- (thousands of squared kilometers) scales which may affect predator foraging effort or success. We examine the various components of the Cape Shirreff nearshore (from land to the 1,000 m isobath) ecosystem before and after the occurrence of a short-term meteorological event (a near gale), and evaluate the changes that occurred. In particular, the responses of predators to the changes in the abundance and distribution of their prey is examined.

Materials and methods

Livingston Island (62.5°S, 61°W), one of the South Shetland Islands, is home to several Antarctic fur seal (*Arctocephalus gazella*) colonies and chinstrap penguin (*Pygoscelis antarctica*) rookeries. Many of these animals reside on the north side of the island, near Cape Shirreff (Fig. 1). As central-place foragers, these animals can maximize their energy uptake and that of their offspring by foraging in the waters surrounding Livingston Island. One of the more numerous petrels found in this region is the cape petrel (*Daption capense*). Little is known about the breeding locations of cape petrels, and it is impossible to determine their breeding status and origin using shipboard surveys. Given the timing of our survey, it is likely that the cape petrels we observed are resident to the South Shetland Island region. Nevertheless, our study provides a unique basis for comparing the response of three specialized predators in relation to krill availability.

A survey of krill and its predator populations north of Livingston Island was conducted from 2 to 10 February 2005 from the RV *Yuzhmorgeologiya*. Data from a multiple frequency echosounder were used to measure the distribution and abundance of krill, while simultaneous visual estimates of predator abundance and behavior were collected. Additionally, continuous meteorological observations and net tow and hydrographic stations were conducted throughout the survey. Spatial changes were examined within and between two submarine canyons which are similar in size, depth, area and separated by approximately 30 km. Temporal changes in the ecosystem are studied before and after the near gale (wind speed between 14 and 17 m s^{-1}) which occurred on 6 February 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 its avian and pinniped predators.

The survey consisted of ten transects, approximately 45 km long, 5 km apart, spanning the two submarine canyons
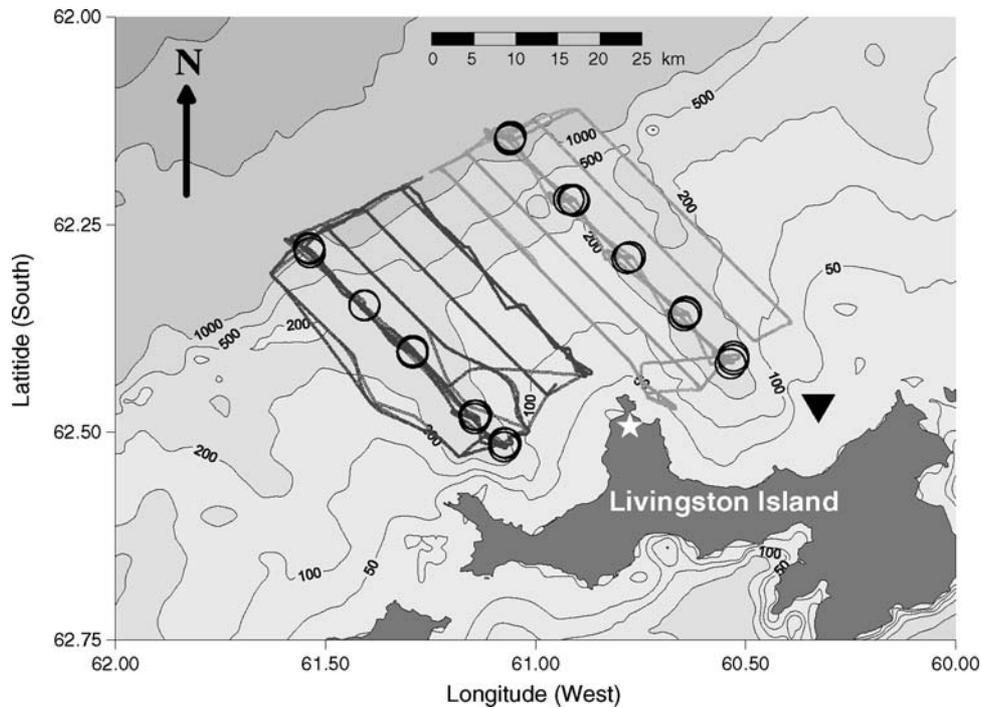
Fig. 1 Cruisetrack and station locations for the nearshore survey area north of Livingston Island, Antarctica. We define the nearshore as the area between land and the shelf break (roughly the 1,000 m isobath). *Circles* represent station locations where hydrographic profiles and net tow data were collected. *Lines* represent the cruise track of RV *Yuzhmorgeologiya* (*dark gray*: western canyon, *light gray*: eastern

canyon). Bathymetric contours are shown as *thin lines*. The *white star* marks the location of Cape Shirreff. The *black triangle* marks the location of Desolation Island. The amount of cruisetrack covered during each section of the survey was: west canyon, before near gale (258 km); west canyon, after near gale (221 km); east canyon, before near gale (380 km); and east canyon, after near gale (344 km)

which flank Cape Shirreff (Fig. 1). The survey was approximately bounded by the 1,000 m isobath offshore and the 50 m isobath inshore covering a total area of approximately 2,500 km². The ship covered the entire survey grid starting at the westernmost transect and working eastward three times (2–4 February, 5–7 February, 8–10 February); however, the second pass through the grid was interrupted by the near gale. Two of the transect legs had five stations, which were only sampled at night, and included a CTD hydrographic profile and net tow sample (Fig. 1). In total, the ten station sites yielded 29 CTD casts and 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 geographic position were recorded and averaged over 1-min intervals from a meteorological station (WeatherPak 2000, Coastal Environmental Systems Inc., Seattle, WA, USA) and GPS receiver.

Hydrographic and net tow sampling

At each station, a SeaBird 911 CTD rosette was lowered to the shallower of 750 m depth or 10 m above the bottom. In addition to conductivity, temperature, and density profiles,

water samples were collected at several depths (surface, 5, 10, 15, 20, 30, 40, 50, 75, 100, 200 m, and at the maximum depth of the cast) 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 and Riemann 1978). Integrated chlorophyll and phaeopigment concentrations were calculated from samples from 100 m depth (or the bottom of the cast if shallower) to the surface. After each CTD cast, a 2 m² 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) to calculate sampled volume. Zooplankton samples were identified to the species level and enumerated on-board the ship. Sub-samples were analyzed from large catches. Adult krill were measured for length and sexed. All animals (except adult krill and small fish which were used for other studies) were then preserved in a 10% buffered formalin solution.

Acoustic survey of krill

Krill distribution in the ocean is patchy (Miller and Hampton 1989; Hamner and Hamner 2000; Siegel et al. 2004). To

sample a krill population 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 over net sampling (e.g., improved vertical and horizontal resolution, ability to rapidly survey large areas), they provide an indirect measure of the krill population and must be validated, typically by the use of net or video techniques (Wiebe et al. 2004; Lawson et al. 2004; Demer and Conti 2005).

The nearshore Livingston Island ecosystem is well-suited for acoustic sampling methods. First, there are relatively few cohabitant species at this high latitude. That is, there are only a few species that contribute appreciably to the total acoustic scattering measured in the water column. This fact permits the acoustically-significant species found in the water column to be discriminated from each other by the use of multiple acoustic frequencies (Watkins and Brierley 2002). Consequently, acoustic sampling methods have been used routinely in nearby waters for many years to assess and manage krill stocks (Hewitt and Demer 2000).

The acoustic system used in this study was a multiple frequency (38, 70, 120, and 200 kHz) echosounder (SIMRAD EK 60) with hull-mounted transducers (Simrad ES38B, ES70-7C, ES120-7 and ES200-7C, respectively). The echosounder was calibrated in early January in Admirality Bay, King George Island using a standard target (38.1 mm diameter sphere made from tungsten carbide with 6% cobalt binder material). Volume backscattering strength data at each frequency were averaged over 1 m vertical depth bins. Pulses (all 1 kW power and 1 ms duration) were synchronously transmitted every 2 s. Typical vessel speed during the survey was 5 m s^{-1} although sea-state and weather sometimes resulted in slower speeds. Only acoustic survey data collected during the day were analyzed in this study to minimize errors resulting from diel vertical migration of krill (Marr 1962; Everson and Murphy 1987; Demer and Hewitt 1995).

The acoustic data were processed using a multiple frequency target identification technique (Watkins and Brierley 2002). Differences (as stated in Hewitt et al. 2003) in volume backscattering strength measured at different frequencies were used to identify the backscattering from krill. Volume backscattering from krill was integrated (Nautical Area Scattering Coefficients, s_A, with units of $\text{m}^2 \text{ m}^{-2}$) in 10 m vertical depth bins from the shallower of 110 m or 5 m above the bottom to 10 m below the surface over 1 km cruisetrack segments. The 10-m binned data were used for statistical analyses and were summed vertically to provide a total s_A value for each cruisetrack segment to be used for spatial (horizontal) analysis. It is unlikely that these surveys missed swarms of krill in deeper waters as 90% of krill biomass in the Scotia Sea is found in the upper 100 m of the

water column (Demer 2004). However, like all ship-based acoustic surveys of krill that use hull-mounted transducers, these data may underestimate the abundance of krill if some reside in the unsampled water very near the surface (i.e., the upper 10 m).

The s_A were converted to estimates of krill biomass using the length-distribution of krill caught in nets and a theoretical acoustic scattering model (Demer and Conti 2005). The SDWBA model (Demer and Conti 2005) was used to predict the amount of acoustic backscatter from a single krill of a particular length (L = 15–60 mm in 1 mm increments). These scattering contributions were then weighted by the probability density function of the lengths of the krill caught in the net tows during the survey to produce a value that represents the amount of backscatter an "average" krill would produce (similar to the method used by Lawson et al. 2006). The s_A were then converted to krill biomass using this weighted-scattering contribution and the relationship between L and biomass (Hewitt et al. 2003).

Predator distribution, behavior and abundance

Two observers used binoculars continuously during daylight hours to collect data on seabird and pinniped abundances and distributions. Counts of predators were made within an arc of 300 m directly ahead and to one side of the ship while underway (Tasker et al. 1984; Veit et al. 1993). Sea-state was measured on the Beaufort scale. Before and after the near gale, the sea-state was nearly Beaufort 0 which allowed effective observations of fur seals and penguins. Each record was indexed in time (to the nearest tenth of a second) and space (geographic position). Individual animals, or flock of birds, were assigned a behavioral classification: flying, sitting on water, feeding, porpoising (penguins and fur seals), or ship following (Veit 1999). Ship-following birds were recorded when first encountered and ignored thereafter. Predator observations were binned into 1 km sections and aligned with acoustic estimates of krill biomass.

We focus on describing the foraging distributions of two conspicuous Antarctic seabirds and one pinniped species which breeds locally in the South Shetland Islands. All three animals feed extensively on krill. Cape petrels (*Daption capense*) are medium sized petrels, highly gregarious, and feed primarily within the upper few meters of the sea surface. They generally forage in flocks and their behavior is thus easily monitored (Veit 1999). For cape petrels, we make the distinction between birds that were observed flying or searching, from those that are feeding. These two types of observations were analyzed separately as well. Chinstrap penguins (*Pygoscelis antarctica*) 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 able to dive to several hundred meters but spend most of their foraging effort at shallower depths (<100 m) (Croxall et al. 1985). When fur seals were observed to be stationary (i.e., resting at the surface), they were considered to be non-transiting. 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

To study the spatial and temporal dynamics of the near-shore Antarctic ecosystem, the study area was divided spatially into western and eastern canyons, and temporally before (2–5 February 2005) and after (7–10 February 2005) the near gale. The western canyon contains the five western-most survey transects, and the eastern canyon is composed of the five eastern-most survey transects (Fig. 1). All four categories (western area before gale, eastern area before gale, western area after gale, and eastern area after gale) contain roughly similar amounts of trackline (258, 380, 221, and 344 km, respectively) and survey effort. There was more effort in the eastern canyon due to more accommodating bathymetry and the fact that some western tracklines were shortened due to inclement weather.

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 near gale. We did so by examining changes in various parameters describing the hydrographic conditions and the phytoplankton, zooplankton, and krill predator populations. Parameters examined included: depth of the surface mixed layer as evidence of the strength of surface mixing processes; temperature, dissolved oxygen, and σ_θ (seawater density calculated with in situ salinity, potential temperature, and pressure = 0, $-1{,}000$ kg m^{-3}) at 100 m depth to indicate changes in sub-surface hydrography; depth of the 27.5 σ_θ isopycnal as a measure of vertical movement of water masses; and phytoplankton biomass [vertically integrated chlorophyll-*a* (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 near gale. We used a factorial ANOVA to determine whether the predator encounter rate (# km^{-1}) and acoustically-determined krill biomass (g m^{-2}) differed between the east and west canyons before and after the near gale.

Canyon locations and the near gale event were treated as fixed factors, and multiple comparison tests were done using Bonferroni post-hoc tests (Zar 1999). Temporal correlations between krill and predator abundance were calculated both before and after the near gale.

Results

Environmental conditions and phytoplankton biomass

A strong low-pressure system (minimum barometric pressure = 963 mbar) entered the survey area on 6 February 2005, which caused most ship-based sampling to halt until the sea-state improved. Wind speeds (averaged over 1 min) during the near gale (World Meteorological Organization classification) were consistently greater than 14 m s^{-1} for approximately 8 h. Wind speeds varied between 2 and 14 m s^{-1} both before and after the near gale, but were not as consistently strong as during the near gale. Throughout the survey (including the near gale) the wind was blowing from the southwest. The water column in both canyons experienced dramatic changes after the near gale (Tables 1, 2), with both canyons showing a similar hydrographic response. Solar insolation was similar before and after the near gale with each period containing two cloudy and two sunny days. Peak PAR values were similar (within 10%) before and after the near gale for both sunny and cloudy days.

The deepening of the surface mixed layer in both canyons after the near gale was not statistically significant ($P = 0.15$; Tables 1, 2). However, other hydrographic parameters were found to be significantly different either spatially or temporally during the study. The depth of the $\sigma_\theta = 27.5$ kg m^{-3} isopycnal deepened by roughly 50% after the near gale had passed. Several hydrographic variables (temperature, dissolved oxygen and σ_θ) measured at 100 m depth changed after the near gale becoming warmer, more oxygen rich, and lighter, respectively (Tables 1, 2). These changes are consistent with a change in the depth of the surface mixed layer. Both chl-*a* and phaeopigment values increased between 30 and 50% in both canyons after the near gale (Tables 1, 2).

Spatial and temporal distribution patterns of Antarctic krill

Net samples conducted in both canyons before and after the near gale suggest that the composition of the zooplankton community did not vary spatially or temporally during the study period. The dominant taxa for all sampling periods in terms of biomass was krill (*E. superba*), although smaller euphausiids (*Thysanoessa macrura* and *Euphausia frigida*) were also present. Other zooplankton caught in abundance

Table 1 Comparison of hydrographic and phytoplankton biomass parameters of the western and eastern canyons near Cape Shirreff both before and after the near gale

Period relative to near gale	West canyon		East canyon	
	Before ($n = 9$)	After ($n = 5$)	Before ($n = 10$)	After ($n = 5$)
Mixed layer depth (m)	30.3 ± 9.8	42.0 ± 39.9	22.0 ± 11.6	46.7 ± 22.1
Temperature at 100 m (°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

Mean and standard deviations ($\pm$) are provided for the data as well as the number of samples (n). Several of these parameters exhibit a high degree of variability which may be due to the differences in bathymetry (roughly 750 m offshore to 100 m inshore) between the stations along each transect

Table 2 Factorial ANOVA for physical characteristics and phytoplankton biomass

Significant values ($P < 0.05$) are shown in bold

[a] Degrees of freedom = 3, 25

Variable	Effect[a]					
	Canyon		Near gale		Canyon × Near gale	
	F	P	F	P	F	P
Mixed layer depth (m)	2.21	0.15	0.03	0.87	2.21	0.15
Temp at 100 m (°C)	6.05	**0.02**	1.34	0.26	9.31	**0.005**
Dissolved O_2 at 100 m (ml l^{-1})	1.71	0.20	0.03	0.87	3.57	0.07
σ_θ at 100 m (kg m^{-3})	2.66	0.12	0.31	0.58	3.90	0.06
Integrated chl-a (mg m^{-2})	5.24	**0.03**	10.71	**0.003**	0.27	0.61
Integrated phaeo (mg m^{-2})	14.22	**0.001**	30.10	**1.6E-5**	1.55	0.23

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 Scotia Sea (Ward et al. 2004). The mean and standard deviation of adult *E. superba* lengths were 47 and 4 mm, respectively. Unlike previous studies, which showed large heterogeneity in krill lengths within a swarm or between nearby swarms (Watkins et al. 1986, 1990), the length-distributions of krill caught in the nets were similar for all samples.

The distribution of acoustically-measured krill biomass shows that the western canyon had between 20 and 30% more biomass than the eastern canyon both before and after the near gale (Fig. 2; Table 3; $P = 0.003$). The total krill biomass in each canyon decreased by roughly half after the near gale. In addition to this change in abundance, the distribution of krill also changed both horizontally and vertically. Before the near gale, large amounts of krill were found throughout both canyons; after the near gale, krill were less abundant and only found along the canyon edges (Fig. 2; Table 3). The vertical distribution of krill also changed after the near gale in both canyons (Fig. 3; Table 3), with fewer krill being found at deeper depths.

Predator distribution and behavior

The distributions 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 1,000 m isobath at the mouths of each canyon (Fig. 4). There was a significant difference in the abundances of flying cape petrels between the canyons before and after the near gale ($P = 0.02$; Tables 4, 5; Fig. 4). 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. 4); and afterward feeding aggregations were entirely restricted to the western canyon ($P < 0.0001$; Tables 4, 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. 5). However, chinstrap penguins were significantly more abundant in the eastern canyon after the near gale (Tables 4, 5). We found dense aggregations of penguins in proximity to Desolation Island (location marked with a triangle in Fig. 1), which may have been foraging in locations not sampled
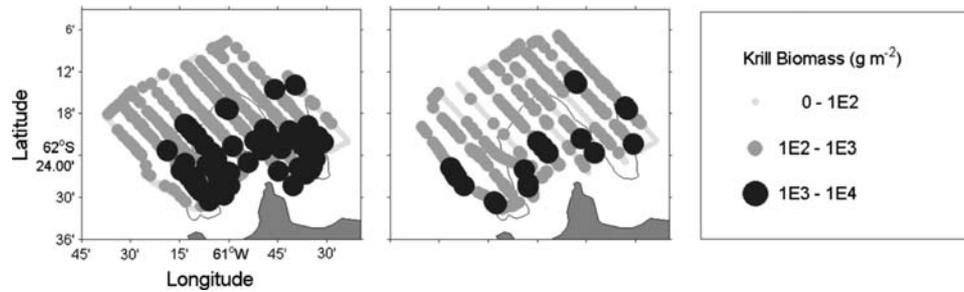
Fig. 2 *Euphausia superba.* Krill biomass before (*left*) and after (*right*) the near gale. Integrated volume backscattering coefficients were apportioned to krill using a multiple frequency target identification method, and then converted to biomass using the length-distribution of animals caught in net tows and a theoretical target strength model. The

thin black line marks the 200 m isobath where aggregations of krill were persistent. Krill biomass was 50% less abundant after the near gale. During both periods, the western canyon had more biomass than the eastern canyon

Table 3 Factorial ANOVA for assessing the effects of environmental parameters on krill biomass

Krill distribution		
Effect	*F*	*P*
Depth[a]	81.82	**<0.00001**
Canyon[b]	8.95	**0.003**
Near gale[b]	53.61	**<0.00001**
Depth × Canyon[a]	5.90	**<0.00001**
Depth × Near gale[a]	9.31	**<0.00001**
Canyon × Near gale[b]	0.08	0.77
Depth × Canyon × Near gale[a]	0.53	0.84

Parameters considered were depth (10 m vertical bins; vertical spatial dimension), canyon (horizontal spatial dimension), and near gale (temporal dimension). Significant values ($P < 0.05$) are shown in bold

[a] Degrees of freedom = 8, 10758

[b] Degrees of freedom = 1, 10758

during the survey and merely passing through the survey area to or from colonies on Desolation Island. During sampling after the near gale, we detected an aggregation of foraging penguins in the west canyon along the 200 m isobath where cape petrels were also observed intensively feeding (Fig. 4). Distribution patterns of foraging fur seals were more concentrated in the western canyon and large aggregations (12–15 animals) were detected along the 1,000 m isobath (Tables 4, 5; Fig. 6). 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 time-series correlation between krill and its predators showed that the different animals had different connections to the changes in krill abundance (Fig. 7). 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 linearly associated with krill biomass before the near gale ($r = 0.03$; $P = 0.40$);
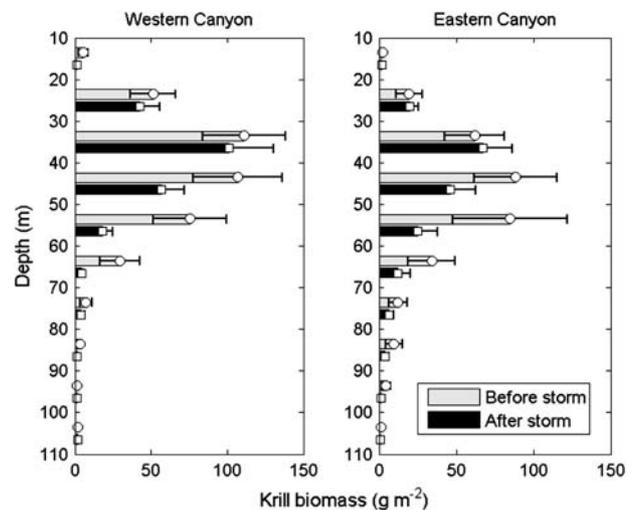
Fig. 3 *Euphausia superba.* Vertical distribution of mean krill biomass in each canyon for 10 m layers before (*circles, gray*) and after (*squares, black*) the near gale with bars indicating standard error. The majority of the krill were located between 30 and 60 m deep. Surface krill aggregations (to a depth of 10 m) were not sampled as the echosounder transducers were located on the hull of the vessel at a depth of approximately 5 m. After the near gale, the largest decreases in krill biomass occurred between 40 and 60 m

but after, when krill biomass decreased by nearly half, they were correlated with krill ($r = 0.24$; $P < 0.001$). Chinstrap penguins were linearly 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

Many physical and biological characteristics of the nearshore environment varied temporally and spatially during this study. Changes to the water column structure were

Fig. 4 *Daption capense.*
Distribution of flying (*left*) and
feeding (*right*) cape petrels
before (*top*) and after (*bottom*)
the near gale. The majority of
persistent aggregations of flying
petrels occurred in offshore
areas between the 200 and 1000 m
isobaths in both canyons. Aggre-
gations of feeding petrels prior
to the near gale were predomi-
nant throughout the eastern can-
yon from offshore to nearshore.
After the near gale, feeding
aggregations were significantly
reduced and concentrated along
the edge of the western canyon
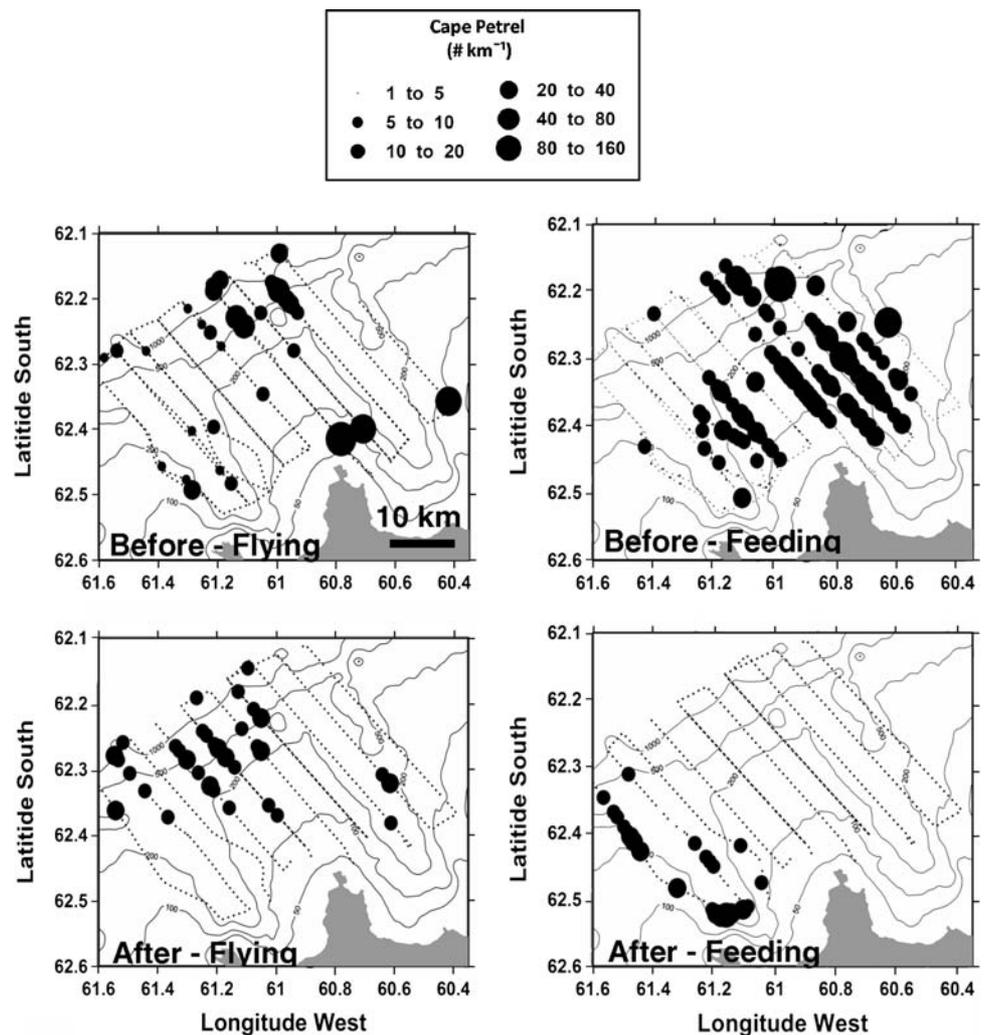
Table 4 Mean and standard error for krill biomass and predator abundance during the survey for both regions

Predator-prey estimates				
Period relative to near gale	West canyon		East canyon	
	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

evident to at least a depth of 100 m and included the waters below the surface mixed layer. These hydrographic changes may be the result of advection of surface water offshore by wind-driven currents and replacement of these waters by deeper water or by mixing surface and sub-surface water masses. Several hydrographic factors (mixed layer depth, dissolved oxygen and potential density anomaly at 100 m) did not show significant differences due to spatial (canyon) or temporal (near gale) factors. One reason for this may be

the normal variability in these parameters as measurement locations within each canyon were separated by tens of kilometers and had differences in bottom depth of several hundred meters.

Chl-*a* and phaeopigment concentrations increased after the near gale in both canyons, while measurements of PAR for the two canyons were similar during both survey peri- ods. This suggests that light levels were not a primary fac- tor influencing the change in phytoplankton biomass. There

Table 5 Factorial ANOVA for assessing the effects of environmental parameters on predator distribution

Parameters considered were changes in space (canyon) and time (before or after the near gale). Significant values (*P* < 0.05) are shown in bold

[a] Degrees of freedom = 1, 1199

Variable	Effect[a]					
	Canyon		Near gale		Canyon × Near gale	
	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	**<0.0001**	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**
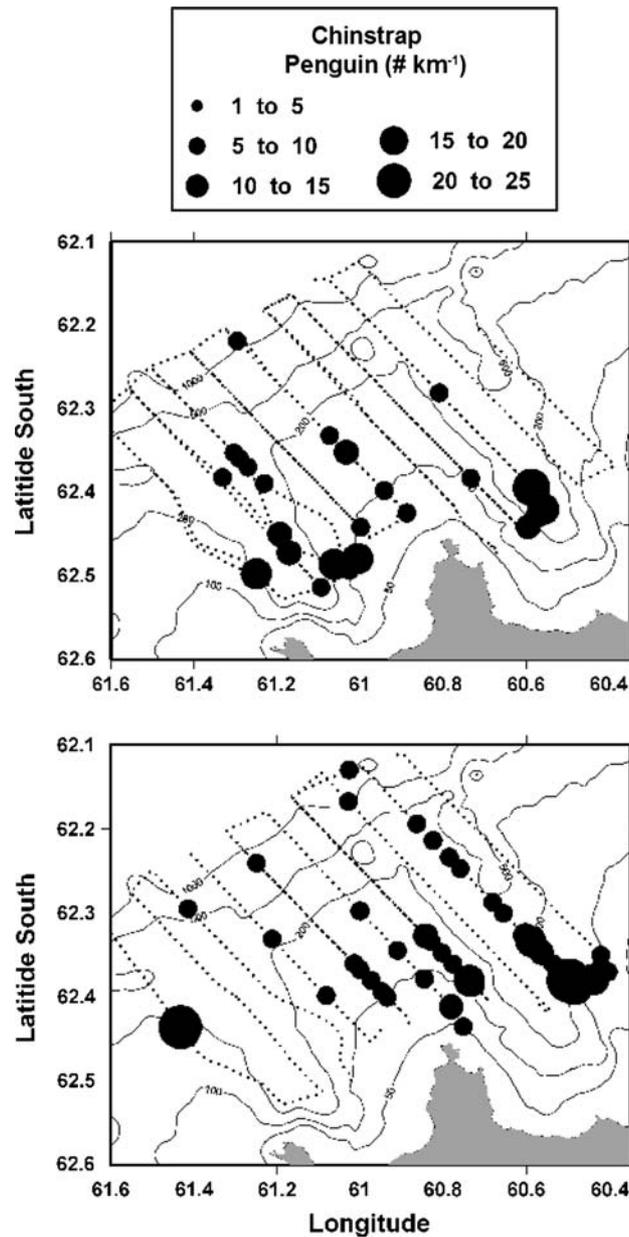
Fig. 5 *Pygoscelis antarctica*. Distribution of sitting chinstrap penguins before (*top*) and after (*bottom*) the near gale. The majority of chinstrap penguin aggregations were located close to shore, near colonies on Cape Shirreff and Desolation Island (62°28′S, 60°20′W, not shown in figure)
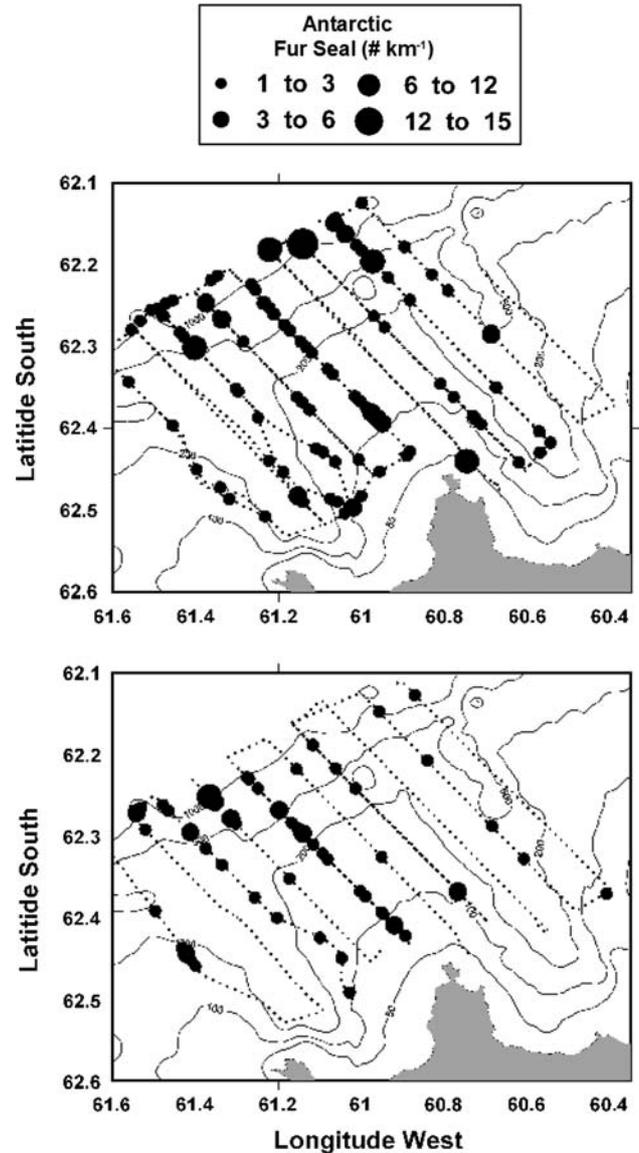
Fig. 6 *Arctocephalus gazella*. Distribution of Antarctic fur seals before (*top*) and after (*bottom*) the near gale. The largest aggregations were found offshore along the 1,000 m isobath. Both before and after the near gale, fur seals preferred the western canyon

are several possible processes that could lead to the observed increase in phytoplankton biomass. If nutrient, and not light, availability is a limiting factor in primary
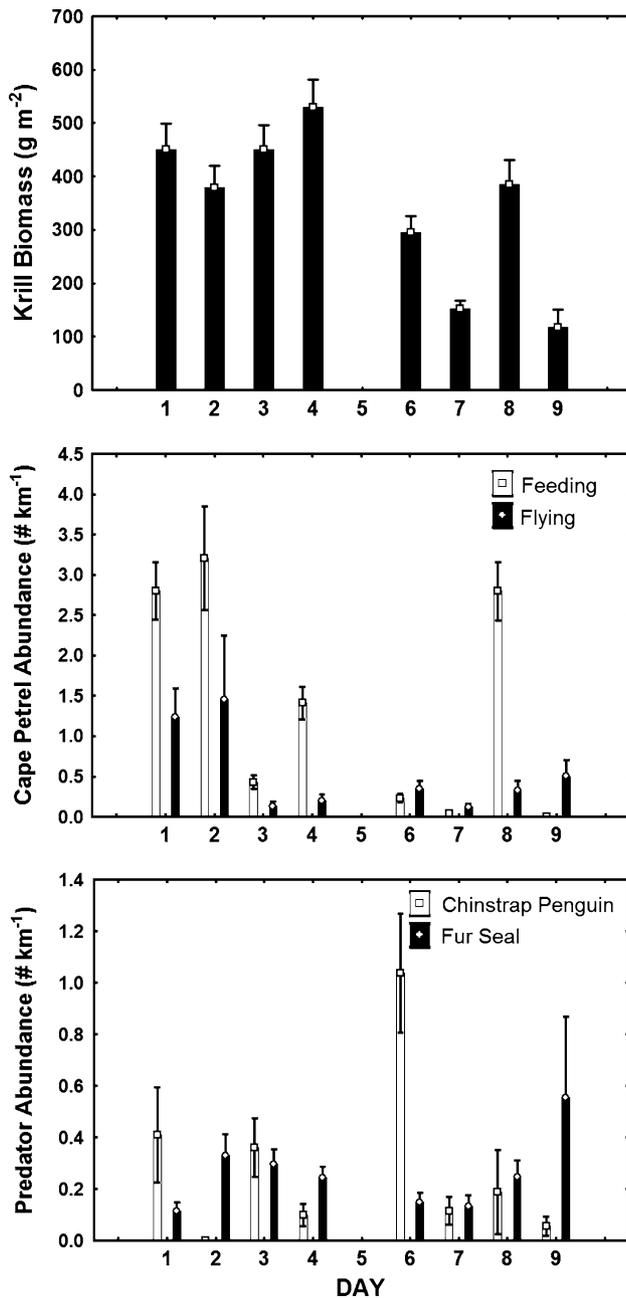
Fig. 7 *Euphausia superba*, *Daption capense*, *Pygoscelis antarctica*, and *Arctocephalus gazella*. Time sequence of daily mean abundance and standard error of krill biomass (*upper panel*); feeding (*white*) and flying (*black*) cape petrels (*middle panel*); and chinstrap penguins (*white*) and Antarctic fur seals (*black, lower panel*). The gale occurred on day 5 and interrupted sampling. The *horizontal axis* corresponds to days of the survey from 2–10 February

advected into the nearshore region. However, without measurements from the surrounding areas before and after the near gale, the likelihood of this explanation is unknown.

While phytoplankton biomass increased after the storm, krill biomass decreased by roughly half over the same time period in both canyons. 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 h), but some patterns were constant such as higher abundances of krill in the western canyon before and after the near gale. Changes in the physical environment may occur immediately during and after the passage of a near gale, but it is not known how long it may take the other parts of the ecosystem to respond to the altered environment. If currents driven by the near gale advect animals into or away from a region, changes in abundance and distribution would occur immediately. However, longer times would be required for the lower trophic levels (primarily phytoplankton and mesozooplankton) of the ecosystem to respond to changes in their environment such as increased nutrient concentration or prey availability. 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 resulting in increases in egg production on time scales greater than 12 h (Bochdansky and Bollens 2004).

While individual animals can respond fairly rapidly to changes in their environment, mesozooplankton communities have been observed to respond to physical changes in their 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 near gale suggesting that krill were not responding to changes in food availability, but rather migrated or were advected out of the survey area. An acoustic survey in a nearby area (King George Island) has shown that offshore krill swarms can be advected by surface currents on temporal and spatial scales similar to this study (tens of kilometers, 1–10 days; Everson and Murphy 1987).

A simple estimate of how far a zooplankton passively drifting with the surface currents would travel during the near gale was made to determine if advection of krill out of the nearshore region was possible. Assuming that wind speeds were 15 m s^{-1} for a duration of 8 h and that surface currents are approximately 5% of wind velocity, a passive drifter would be advected roughly 20 km downwind. This simplified analysis suggests that advection of krill out of the survey area is a plausible explanation as the wind was primarily blowing from the southwest to the northeast during the near gale. However this estimate is only valid for surface currents which would diminish with depth, thus krill not at the surface would be advected a smaller distance. If surface waters were advected away from Livingston Island, this might cause upwelling in the nearshore

productivity (Holm-Hansen et al. 2004), then the passage of the near gale 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 increased phytoplankton biomass. The rapid change could also be explained by phytoplankton biomass being

which could explain some of the hydrographic changes that we observed.

The changes in krill distribution that were observed in this study may affect the foraging success of cape petrels. Feeding aggregations of cape petrels decreased or disappeared from areas where krill abundance decreased, but distributions of fur seals and foraging chinstrap penguins did not. Cape petrel abundance correlated most strongly with krill biomass distribution among observed predators (Figs. 2, 4, 7). Persistent cape petrel feeding aggregations were repeatedly detected in the eastern canyon prior to the near gale, but after the near gale all feeding aggregations were located in the western canyon where krill biomass was greater. This shift in feeding intensity mirrored the overall shift in krill biomass from the eastern to western canyon after the near gale. The cape petrels that remained to forage in the survey area were able to continue to locate krill patches even after the marked decrease in krill availability. Thus when prey abundance was reduced the spatial distribution of feeding cape petrels and krill biomass were significantly correlated.

The response of cape petrels to changes in krill distribution may be a functional response to krill availability (Piatt and Metheven 1992), that is, there is likely a threshold level of krill biomass that influences the profitability and consumption rate of foraging petrels. If krill were advected from the survey region, then it is likely that cape petrels also moved out of the area in search of surface krill patches (Veit 1999) through either visual (surface swarms were sighted occasionally during the survey) or olfactory (Nevitt et al. 2004) cues. The foraging distribution of cape petrels has been linked to changes in krill abundance and patchiness on annual scales (Santora et al. 2008) and at finer scales ranging from 1 min to 1 h (Veit et al. 2008), so it seems likely that cape petrels are indicators of changes in krill distribution in surface waters.

Cape petrel foraging effort and fitness may have been particularly affected (more than other krill predators) by the gale itself as they remain above the surface of the water exposed to the wind while foraging and have limited energy-storage capacity due to their small body size. These factors cause cape petrels to forage and feed more frequently than other predators and may explain why only cape petrel distribution was correlated with krill abundance. The correlation between feeding cape petrels and acoustic estimates of krill abundance is especially interesting since the petrels feed on surface swarms of krill which may be under-sampled or missed entirely by acoustic observations using hull-mounted echosounders (typically located at a depth of several meters). This suggests the possibility that acoustic estimates of sub-surface krill swarms are indicative of surface swarms or those feeding cape petrels may be a useful biological indicator of surface krill swarms which hull-mounted echosounders do not sample.

The foraging effort and ability of all three predators varies with predator size in several ways including longer foraging trips both in distance and duration, deeper diving ability, and greater energy-storage capacity. Any of these factors may explain the variations in the responses of the three predator species to the changes in the krill distribution. Chinstrap penguins and fur seals displayed little variation in their foraging distribution patterns with respect to the near gale (Fig. 7). However, throughout the survey, chinstrap penguin abundance was correlated with krill biomass while fur seal abundance was not. Relative to cape petrels, penguins and fur seals may not be as dependent on finding prey over small time-scales due to their longer foraging-trip length and energy-storage capacity and may not need to alter their foraging effort or locations in response to short-term changes in krill distribution. Gale-produced winds would have a larger effect on the transiting ability of cape petrels than wind-driven currents would have on the transiting ability of chinstrap penguins and fur seals. Penguins and fur seals are also capable of acquiring prey deeper in the water column than the cape petrels, so their prey may be less susceptible to being advected out of the ecosystem by residing at depths where wind-driven currents may be less. There may also be resource partitioning occurring vertically as well as horizontally in this ecosystem, evidenced by the different foraging capabilities of the predators.

Throughout the survey, chinstrap penguins and fur seals showed persistent preferences for particular foraging areas. Fur seals were observed at the 1,000 m isobath near the mouth of the western canyon whereas chinstrap penguins were routinely found closer to shore and at the heads of the canyons. The areas of high fur seal abundance agree with data from satellite-tagged female fur seals rearing pups at Cape Shirreff, Livingston Island (Goebel et al. 2000) and may be a preferred foraging area.

The contrasting "responses" of these predators to the change in krill biomass after the near gale may be due to their differing abilities of prey detection or exploitation, mobility, or immediate energy demands. Petrels have the ability to search a much larger horizontal area than penguins or seals in a given period. The time-scale of our post-gale observations seems to have been long enough to observe petrels relocating to areas of higher prey density. Since penguin and seal distributions largely did not change during the survey, we suggest they are less responsive to changes in krill biomass occurring in space and time at the submesoscale.

While some of our observations of the ecosystem (e.g., the western canyon containing more krill biomass than the eastern canyon) were static during our study period; other measurements show the dynamic response of the ecosystem when a submesoscale meteorological event (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). Therefore, surveys that visit a site or station only once or multiple times separated by weeks or more may be biased as a result of recent or presently occurring meteorological events. This issue may not be as important for larger spatial or temporal surveys where multiple events may occur during the survey and the changes in the ecosystem may be averaged over the course of the study. Future ecosystem studies may need to sample over multiple temporal and spatial scales that are specifically relevant to key ecosystem components to adequately capture the functional response of the ecosystem to perturbations.

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