

Ecosystem Oceanography of Seabird Hotspots: Environmental Determinants and Relationship with Antarctic Krill Within an Important Fishing Ground

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ABSTRACT

The discipline of ecosystem oceanography provides a framework for assessing the role of mesoscale physical processes on the formation and occurrence of biological hotspots. We used shipboard surveys over nine years to investigate environmental determinants of seabird hotspots near the Antarctic Peninsula, a region experiencing rapid climate change and an expanding krill fishery. We hypothesize that seabird hotspots are structured by mesoscale ocean conditions that reflect differences in prey distribution within oceanic and coastal waters. We used generalized additive models to quantify functional relationships of seabird hotspots with krill biomass, and a suite of remotely sensed environmental variables, such as

eddy kinetic energy. The spatial organization, changes in intensity, and distribution shifts of seabird hotspots indicate different environmental drivers within coastal and oceanic domains and reflect the seasonal variability of the ecosystem. Our results indicate at least eight mesoscale hotspot zones that represent ecologically important areas where significant krill and predator biomass may be concentrated. Our ecosystem assessment of seabird hotspots identified critical foraging habitat and provided reference points to benefit research on estimating their trophic impacts on Antarctic ecosystems and potential effects from the krill fishery. Our approach is generally applicable to other pelagic ecosystems that are structured by hydrographic fronts and eddies, and containing schooling forage species shared by multiple wide-ranging predators. Furthermore, identification of biological hotspots is useful for the designation of marine protected areas most critical to potentially endangered wildlife and fisheries resources.

Key words: albatross; conservation; ecosystem assessment; eddy kinetic energy; krill fishery; foraging ecology; marine protected area; mesoscale; petrel; spatial ecology; storm petrel.

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INTRODUCTION

The discipline of ecosystem oceanography focuses on relating populations of marine species and their interactions to environmental fluctuations to predict ecosystem responses to climate change and exploitation (Cury and others 2008). Pelagic ecosystems are vast, highly dynamic systems, and experimental design is often difficult or impossible, but this challenge is overcome through integration of large, multi-interdisciplinary abiotic and biotic datasets, combined with numerical modeling to assess ecosystem dynamics. In particular, ecosystem oceanography studies often examine the role of mesoscale ocean dynamics on biological processes, such as eddies (that is, circular movement of water), occurring on spatial scales ranging from 10 to 1000 km and temporally, from 10 to 30 days (Cury and others 2008), and their effect on the concentration of nutrients, primary production, and species distributions and interactions (Bakun 1996). The occurrence and spatial intensity of biological hotspots, areas of increased species abundance, diversity, and/or trophic transfer (Sydemann and others 2006), are thought to be linked to mesoscale ocean conditions, but functional relationships among biophysical conditions generating hotspots are not well known (Suryan and others 2012; Hazen and others 2013; Santora and others 2014). Through an integration of satellite remote sensing of ocean conditions, acoustic surveys for Antarctic krill (*Euphausia superba*; hereafter krill) biomass, and seabird foraging distributions, we investigate the mesoscale environmental drivers of seabird hotspots within the Northern Antarctic Peninsula (NAP) large marine ecosystem. This ecosystem is experiencing rapid climate change (Meredith and King 2005; Murphy and others 2013), increasing human presence (for example, tourism; Tin and others 2008), and an expanding commercial krill fishery (Nicol and others 2012). Moreover, there is growing concern that climate change and overexploitation of krill on regional scales may impact the resilience of this marine ecosystem (Trivelpiece and others 2011; Murphy and others 2013; Watters and others 2013), and integrated ecosystem assessments of biological hotspots will benefit ecosystem-based fishery management.

Living at the interface between sea and air, seabirds are excellent indicators of ocean climate variability, availability of epipelagic mid-trophic level food resources, and marine ecosystem dynamics and climate variability (Cairns 1988; Reid and others 2005; Cury and others 2011). Due to the

heterogeneity of marine ecosystems and patchiness of their prey, seabirds frequently form dense aggregations associated with hydrographic fronts and eddies because these features tend to concentrate prey (Hunt 1991; Bost and others 2009; Scales and others 2014). The spatial distribution of seabird hotspots (areas of consistently high local abundance) may provide information on the spatial structure and function of marine ecosystems, as well as location of critical foraging grounds, prey availability, and rates of local prey consumption (Piatt and others 2006; Lascelles and others 2012; Santora and Veit 2013). Seabirds are especially susceptible to fisheries interactions (for example, by-catch and entanglement; Weimerskirch and others 2000; Robertson and others 2014) and pollution (for example, oil spills), making identification of their hotspots a priority for their conservation in the Southern Ocean (Constable and others 2000; Hooker and others 2011; Harris and others 2015). Furthermore, commercial harvest of krill is concentrated near the Antarctic Peninsula and increased over time (Nicol and others 2012), warranting concern about depletion of krill within seabird hotspots.

Petrels, storm petrels, and albatrosses (Procellariid seabirds) are long-lived (for example, 20–70 years+) and highly mobile predators, capable of covering vast oceanic regions during foraging trips and post-breeding migrations (Schreiber and Burger 2001). They have diverse foraging strategies with broad diets and are surface feeders, consuming a variety of euphausiids, meso- and benthopelagic fishes, squids, and various microzooplankton (for example, copepods; Croxall and Prince 1980; Ainley and others 1992; Croxall and others 1997; Cherel and others 2002). Due to their collective biomass and demand for krill, procellariid seabirds may play a major role in the trophodynamics of Antarctic marine ecosystems, yet their consumption of krill is poorly quantified compared to penguins, seals, and whales (Croxall and others 1984, 1997; Trivelpiece and others 2011; Watters and others 2013). We used standardized shipboard surveys to investigate the ecosystem oceanography of hotspots for six seabird species. We chose two medium-sized fulmarine petrels [cape petrel (*Daption capense*), southern fulmar (*Fulmarus glacialisoides*)], two storm petrels [Wilson's storm petrel (*Oceanites oceanicus*), black-bellied storm petrel (*Fregatta tropica*)], and two albatrosses [black-browed albatross (*Thalassarche melanophrys*) and grey-headed albatross (*Thalassarche chrysostoma*)]. The fulmarine petrels and

storm petrels breed in the NAP region, while both albatrosses breed outside of the NAP on nearby islands north of the polar frontal zone (for example, Diego Ramirez Archipelago; Robertson and others 2007). All these species are primarily krill eaters, but they do take a variety of fish and zooplankton (Croxall and Prince 1980; Ainley and others 1992). These species represent a range of body sizes and flying and feeding strategies (Croxall and Prince 1980; Ainley and others 1992, 1994). The supplement Figure S. 1 contains additional natural history information (for example, feeding and breeding ecology) for the selected species.

Herein, we quantify the spatial organization and environmental determinants of seabird hotspots, and their relationship to krill biomass. We hypothesize that seabird species hotspots are spatially structured according to mesoscale ocean conditions that broadly reflect differences in physical drivers within oceanic and coastal waters. The reason for potential segregation of species hotspots within oceanic and coastal waters is unclear, but probably relate to ocean physics conducive to foraging (for example, frontal zones and eddies) and perhaps interactions with other predators (Ainley and others 1994; Reid and others 2004). Furthermore, we predict that changes in hotspot distribution and occurrence should reflect the seasonally variable NAP ecosystem and breeding biology of seabirds. Recent studies have shown that the relative abundance and spatial distributions of hotspots of some seals, whales, and dolphins shift between mid- and late-summer coinciding with changes in mesoscale ocean conditions (Santora 2013; Santora and others 2014); thus, we examine this possibility for flying seabirds to provide context about the ecosystems seasonal dynamics. We use a previously developed spatially explicit modeling framework (Santora and others 2014) involving a suite of abiotic and biotic variables to examine the how biological hotspots form within oceanic and coastal waters, and how seabirds may serve as indicators of the seasonal ecosystem dynamics.

METHODS

The U.S. Antarctic Marine Living Resources (AMLR) Program conducted annual ecosystem monitoring surveys in coastal and pelagic waters of the NAP during mid- and late-summer (January-March; Figure 1) from 1990 to 2011. Generally, the area was surveyed twice each summer, in early January and again beginning in mid-February through March (Reiss and others 2008; Santora and Veit 2013). A fixed grid of stations and transects was sampled to

assess the distribution and abundance of krill and top predators. The survey area was partitioned by the South Shetland Islands, with oceanic waters to the north and coastal waters to the south towards the Antarctic Peninsula. Circulation in the study area reflects inputs from the Antarctic Circumpolar Current (ACC), outflow from the Weddell Sea Gyre, and inflow from coastal upstream regions along the western Antarctic Peninsula that enter through western Bransfield Strait (Orsi and others 1995). Rugged bathymetry, including the insular shelf around islands, deep basins of Bransfield Strait, and the South Shetland Trench and Shackleton Fracture Zone ridge in Drake Passage, is a main driver of hydrographic variability in the region (Figure 1; Orsi and others 1995; Thompson and others 2009; Venables and others 2012). The southern ACC front (SACCF) is the southernmost deep-reaching front of the ACC, whereas the southern ACC Boundary

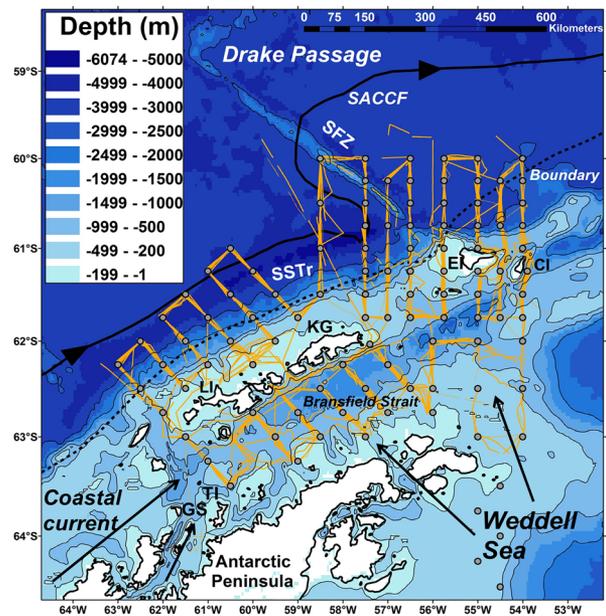


Figure 1. Study area and shipboard trackline coverage (yellow) during 14 U.S. Antarctic Marine Living Resources (AMLR) surveys, January–March, 2003–2011. The AMLR sampling grid is fixed, and transects are highly replicated. Sampling stations where net hauls were conducted are marked as gray circles. The average location of the (black line) southern Antarctic Circumpolar Current Front (SACCF) and the southern ACC boundary (dashed black line) is averaged positions derived from Orsi and others (1995). Arrows indicate generalized direction of water circulation within the ACC, coastal current, and Weddell Sea. CI Clarence Island, EI Elephant Island, GS Gerlache Strait, KG King George Island, LI Livingston Island, SSTR South Shetland Trench, SFZ the Shackleton Fracture Zone.

(Boundary) defines the southernmost limit of ACC-derived waters (Orsi and others 1995). Additionally, the southern ACC front and boundary is located north of the archipelago and is an important hydrographic feature that may concentrate primary production, krill, and top predators (Tynan 1998; Kahru and others 2007; Atkinson and others 2008). The southern Bransfield Strait and Gerlache Strait regions are also an important confluence region that supports persistently high diversity of top predators (Santora and Veit 2013). The El Niño–Southern Oscillation (ENSO) influences the hydrographic variability (for example, extent of ACC water poleward) and is related to demography and distribution of krill and other zooplankton populations in the NAP ecosystem (Loeb and Santora 2015). Please see the supplement for additional information on surface water circulation in the NAP region (Figure S. 1).

Seabird Surveys

Visual surveys of seabirds were conducted on 14 shipboard surveys during 2003–2011 (Figure 1). The extensive shipboard trackline covered open water, bays, inlets, and passages between islands (Figure 1). Nine surveys were conducted in mid-summer (Leg 1; early January to early February) and 5 were in late-summer (Leg 2; mid-February to mid-March; Santora 2013). Strip transect methods were used to estimate seabird abundance, and counts were made within a 90° arc out to 300 m on the side of the trackline with the best visibility (Santora and Veit 2013). Ship speed during transits between sampling stations (Figure 1) was generally 10 knots (18.6 km h⁻¹), and observers used hand-held binoculars to scan from a height of 13 m above sea level. Each sighting was assigned a time and spatial position, and entered into a computer that was synchronized with the ship's navigational and acoustic system. Seabird behaviors, including flying, sitting on the water and feeding were assigned to each sighting; following birds were recorded when first observed and ignored thereafter. Sea surface state (Beaufort scale) and visibility were continuously monitored, and sampling effort during unfavorable conditions (for example, heavy fog) was excluded prior to analysis.

Acoustic Krill Surveys

AMLR acoustic surveys and krill biomass (g⁻²) estimation techniques are described by Reiss and others (2008), and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMR) acoustic working group, SG-ASAM

(2010). Details on the use of acoustically derived estimates of krill biomass to assess the spatial distribution and environmental determinants of krill hotspots in the NAP are described in Santora and others (2012). Acoustic data were collected during each cruise using three acoustic frequencies (200, 120, and 38 kHz), providing a continuous record of acoustic targets attributed to krill (Reiss and others 2008). Briefly, krill biomass was estimated and mapped using hydroacoustics along north–south tracklines (Figure 1) during daylight hours and was vertically integrated from the depth of the transducer (7 m) to 250 m and partitioned into 1 nmi horizontal segments ($n = 9905$ and 4327 nmi during mid- and late-summer surveys). Spatial mean biomass for each grid cell was calculated for mid- and late-summer surveys (Santora and others 2014).

Satellite Remote Sensing of Environmental Conditions

Satellite data were used to construct spatial climatologies of eddy kinetic energy (EKE), sea surface temperature (SST), and Chlorophyll-*a* (Chl-*a*) that correspond with survey coverage (Santora and others 2014). Ecologically, SST and EKE generally link seabird observations to ocean processes that are favorable for physical habitat and conducive for aggregating their prey, whereas Chl-*a* is considered an index of surface primary productivity. Regionally, the spatial distribution of SST relates to differences between ACC and coastal waters, and EKE provides a measure of the relative intensity of ocean circulation and turbulence. EKE data were derived from calculations on the merged sea-level anomaly product created by Archiving, Validation, and Interpretation of Satellite Oceanographic (AVISO), specifically, the global, delayed-time and updated map of sea-level anomaly (MSLA). EKE (cm² s⁻²; 0.25° resolution) was calculated by $EKE = 1/2 * (u'^2 + v'^2)$, where u' and v' are the geostrophic velocity anomalies defined as the difference of the observed currents with the annual mean currents. The EKE climatology was calculated by extracting the MSLA (7-day interval) and calculating u' and v' using centered finite difference of the MSLA (Sudre and others 2013). Monthly means (January and February) of EKE were calculated for each year, 2003–2011, and the final climatology is the average of the nine annual means for each month. SST data (obtained from NOAA Coastwatch; <http://coastwatch.pfeg.noaa.gov/erddap>) were derived from a daily global blended sea surface temperature

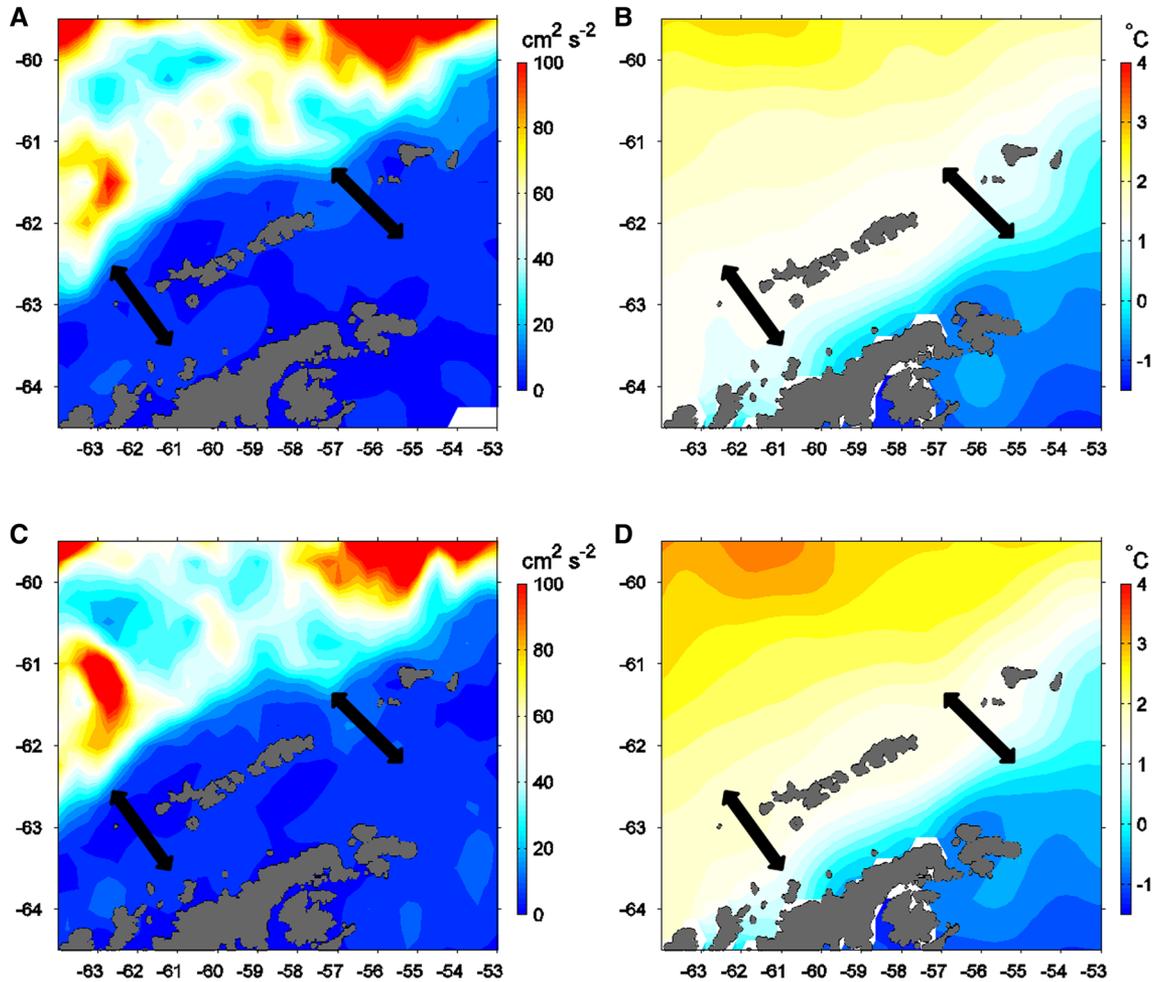


Figure 2. Climatological spatial conditions of satellite-derived hydrographic conditions (spatial mean of January–February during 2003–2011): **A–C** January and February eddy kinetic energy (EKE), **B–D** January and February sea surface temperature (SST). *Black arrows* indicate probable latitudinal shifts in Antarctic Circumpolar Current and Weddell Sea water sources (Loeb and Santora 2015).

analysis (GRHSST Level 4 AVHRR). The daily SST product was used to construct monthly means and then spatially averaged to produce climatologies for 2003–2011. Chl-*a* concentration data (Level 3; mg m^{-3} ; 0.08° resolution) are derived from SeaWiFS (<http://oceancolor.gsfc.nasa.gov/SeaWiFS>) to index surface phytoplankton concentrations and calculated monthly means and spatially averaged climatologies for 2003–2011. For subsequent geospatial modeling of seabird hotspots, EKE, SST, and Chl-*a* were spatially averaged and linked to the survey grid. For example, the spatial climatology of EKE and SST indicates broad-scale gradients that reflect differences in oceanic and coastal boundaries and strong seasonal mesoscale variability of hydrographic conditions (Figure 2; Santora and others 2014).

Analysis

A review of the geo-statistical analysis of AMLR data, including survey effort, standardization of relative abundance of top predators, and estimating Individuals-Per-Unit-Effort (IPUE), is provided by Santora and Veit (2013). Briefly, survey effort (number of hours sampled per cell and survey) was binned into 54 cells, each 0.5° latitude \times 1.0° longitude in dimension ($\sim 2860 \text{ km}^2$). For seabird surveys, a total of 546 cells and 1684 hours were sampled over the 14 surveys for a mean \pm SD of $38 \pm 11 \text{ cells survey}^{-1}$ and $3 \pm 0.3 \text{ h cell}^{-1} \text{ survey}^{-1}$, respectively. We established a spatial climatology (that is, long-term spatial mean) of standardized relative abundances of each seabird species within the grid cells (Santora and Veit 2013). The distance

(km) from the centroid of each grid cell to the nearest point on land (islands and continent) and other covariates (krill biomass, EKE, SST, and Chl-*a*) were spatially linked to the grid. Distance to land was included as a covariate to provide context for the fulmarine and storm petrel species that breed near the NAP (Croll and Tershy 1998) and because CCAMLR modeling studies used distance to organize boundaries of fishing grounds in ecosystem models (Watters and others 2013).

Previous analyses (Santora 2013; Santora and others 2014) suggest marked intra-seasonal differences in the abundance and distribution of several top predator species near the NAP. To examine this, we calculated standardized anomalies (subtract long-term mean and divide by standard deviation) of seabird abundance to assess the presence/absence of inter-annual trends and differences between mid- and late-summer surveys. We developed an index of hotspot intensity where seabird abundance grid cells were categorized according to their deviation from the mean (Santora and others 2010; Santora and Veit 2013). Medium-intensity hotspots were defined as those cells where the standardized abundance was greater than 1 standard deviation from its mean (yellow). High-intensity hotspots were defined as those cells where the mean abundance was greater than 2 standard deviations from its mean (red). See Suryan and others (2012) for additional detail on detecting and mapping seabird hotspots.

To examine our hypothesis, we investigated the relationships between environmental conditions, krill biomass, and the distributions of seabird hotspots from a climatological perspective (long-term spatial mean). We used generalized additive models (GAMs) to investigate variability in the locations of seabird hotspots relative to EKE, SST, Chl-*a*, distance to land, and krill biomass. Prior to modeling relationships, all variables were screened using Pearson correlation, and no strong correlations were found (that is, $r > 0.7$), permitting their use in GAMs. We used two GAMs to investigate the spatial variability of seabird hotspots. First, we implemented a null spatial GAM with a smoothed spatial term and a season factor to assess how much spatial variation alone could explain seabird hotspots without additional covariates and to control for spatial autocorrelation (Dormann and others 2007). GAM_1 is $Seabird\ IPUE = te(Lon, Lat) + factor(season)$, where te is smoothed spatial interaction term. The second GAM implemented contained the spatial interaction and covariates. GAM_2 is $Seabird\ IPUE = s(Krill\ Biomass) + s(EKE) + s(SST) + s(Chl-a) + s(Distance\ to\ land) + factor(season)$, where s is a

smooth regression spline. GAMs for seabird *IPUE* were specified with a Quasi-Poisson distribution and a log-link function. We implemented GAMs using the *mgcv* package in the R statistical program (R Development Core Team 2016) and estimated smoothness parameters with generalized cross-validation (Zuur and others 2009). Adjusted pseudo R^2 and percent deviance explained were used to evaluate model performance. The effect of each covariate included in each GAM was plotted to visually inspect the functional form and assess seabird hotspots varying in relation to geospatial covariates (Dormann and others 2007; Zuur and others 2009).

RESULTS

Inter-Annual and Seasonal Variability of Relative abundance

Cape petrels were the numerically dominant species (by several orders of magnitude), followed by southern fulmars, black-bellied and Wilson's storm-petrels, and black-browed and grey-headed albatrosses (Table 1). Sighting frequencies and mean abundances of the two storm-petrel species were remarkably similar. Black-browed albatrosses were five times more abundant than grey-headed albatrosses (Table 1). Time series of standardized temporal anomalies showed high inter-annual variability, but there were not trends in species abundance (Figure S. 2). For example, southern fulmars and black-bellied storm-petrels displayed strong positive anomalies in 2005, and black-browed albatrosses showed a strong positive anomaly in 2003; all during late-summer. A paired sample t-test of the spatial mean abundance of each species in each grid cell during mid- and late-summer surveys suggests marked intra-seasonal variation in abundance. Relative abundance of cape petrels decreased from mid- to late-summer, while the relative abundance of black-bellied and Wilson's storm petrels and grey-headed albatrosses increased during late-summer (Table 1; Figure S. 2).

Distributions of Seabird Hotspots

Hotspots were observed for all species, but the locations of these hotspots varied between species within and between species groups (Figures 3, 4 and 5). For example, mid-summer cape petrel hotspots were located in the vicinity of the southern ACC front and its southern boundary in a nearly contiguous region of hotspots stretching north of Livingston Island to northern Elephant

Table 1. Species Sighting and Abundance (Spatial Mean and Standard Error) Summary per Mid- and Late-Summer Surveys; 2003–2011

Species	Total sightings	Total individuals	IPUE			IUCN status
			Mid mean \pm SE	Late mean \pm SE	Diff. t, p	
Cape Petrel	8,523	70,703	49.31 \pm 49.41	16.19 \pm 35.43	4.29, < 0.0001	Least concern
Southern Fulmar	5,955	34,700	18.78 \pm 34.52	22.35 \pm 96.9	-0.29, 0.77	Least concern
Black-bellied Storm Petrel	6,046	8,165	3.60 \pm 2.76	7.19 \pm 4.59	-7.00, < 0.0001	Least concern
Wilson's Storm Petrel	5,169	7,646	3.85 \pm 3.08	7.44 \pm 9.98	-2.82, 0.007	Least concern
Black-browed Albatross*	2,966	5,003	2.66 \pm 2.12	4.61 \pm 9.83	-1.51, 0.14	Endangered
Grey-headed Albatross*	844	966	0.37 \pm 0.37	0.37 \pm 1.01	-4.10, < 0.0001	Vulnerable

Diff. is the pairwise difference (t-test) between matched grid cells of standardized spatial mean abundance estimates during mid- and late-summer surveys; bold values indicate significance. International Union of Conservation and Nature (IUCN) status accessed on 9 March 2016.

*Indicates species breeds outside of the Antarctic Peninsula region.

Island, and two hotspots (medium and high) were located in southern Bransfield Strait near Trinity Island (Figure 3A). By comparison, there were far fewer cape petrel hotspots during late-summer (although these occurred in similar locations), indicating that cape petrels were less abundant, and also occurred in fewer large aggregations (Figure 3B). Hotspots of southern fulmar were located exclusively within coastal waters of Bransfield Strait (Figure 3C–D). These hotspots were located in southern Bransfield Strait during mid-summer, but shifted northeast during late-summer to near Elephant Island. Southern fulmar hotspots were located near presumed breeding colonies, such as Gibbs Island and Trinity Island, within Bransfield Strait. For the smallest species, the black-bellied and Wilson's storm petrels displayed complex distribution patterns (Figure 4A–D), with higher abundance during late-summer. These two species shared a single overlapping hotspot in mid- and late-summer south of Clarence Island. Black-bellied storm petrels displayed more hotspots within oceanic waters, compared to Wilson's storm petrels, which were mostly concentrated within Bransfield Strait, especially in the vicinity of the South Shetland Islands (Figure 4A–B). Black-bellied storm petrel hotspots were clustered around the southern ACC front and around the Elephant Island group (Figure 4C–D). Black-browed and grey-headed albatross displayed abundance hotspots within the ACC, near Elephant Island, and within Bransfield Strait (Figure 5A–D). During mid-summer, black-browed and grey-headed albatrosses were generally clustered around the southern ACC front (Figure 5A, C). Black-browed albatross also displayed increased abundance in southern Bransfield near Trinity Island and south of Clarence Island

(Figure 5A). During late-summer, the highest abundance hotspots of black-browed and grey-headed albatross are found in the vicinity of the insular shelf of Elephant Island (Figure 5B, D). Both species also displayed hotspots within coastal waters of southern Bransfield Strait during late-summer.

Determinants of Seabird Hotspots

By accounting for intra-seasonal variability and spatial effects, our models revealed that petrels, storm petrels, and albatross respond differently to geospatial variation in ocean physics, Chl-*a*, and krill biomass, thus indicating their preference for distinct habitat zones of the NAP ecosystem (Table 2; Figures 6, 7 and 8 and Figure S. 3–5). Overall, including a spatial term in GAMs greatly enhanced model performance and highlights the importance of accounting for spatial structure for assessing seabird hotspots in the NAP ecosystem (Table 2). Cape petrels are strongly correlated with krill biomass (Figure 6A), indicating that they are associated with krill hotspots in the oceanic region of the study area. Cape petrels are also linked to SST, and their response indicates association with temperatures between 1.5 and 2 °C (Figure 7A). Moreover, the functional relationship between cape petrel hotspots and distance to land indicates a complex spatial relationship with some hotspots occurring 100 km and 250 km from land (Figure S. 4a). The GAM for southern fulmar indicates they are moderately correlated with krill biomass, negatively correlated with SST, and positively correlated to EKE. The relationship between southern fulmars and SST indicates their association with temperatures ranging from 0.5 to 1.5 °C (Figure 7B). Southern fulmars are strongly linked

to EKE, indicating their hotspots are associated with high levels of EKE in the southern and northern coastal waters of Bransfield Strait (Figure 8A). Fulmars were negatively associated with surface Chl-*a* (Figure S. 3a). The response between fulmars and distance to land suggests their peak abundance occurs within 50-100 km from

land, possibly indicating their association with foraging ground close to breeding colonies (Figure S. 4b).

The GAM for black-bellied storm petrel performed poorly compared to other species (Table 2), and indicated that season was an important factor (increased sightings in late-summer), as well as SST

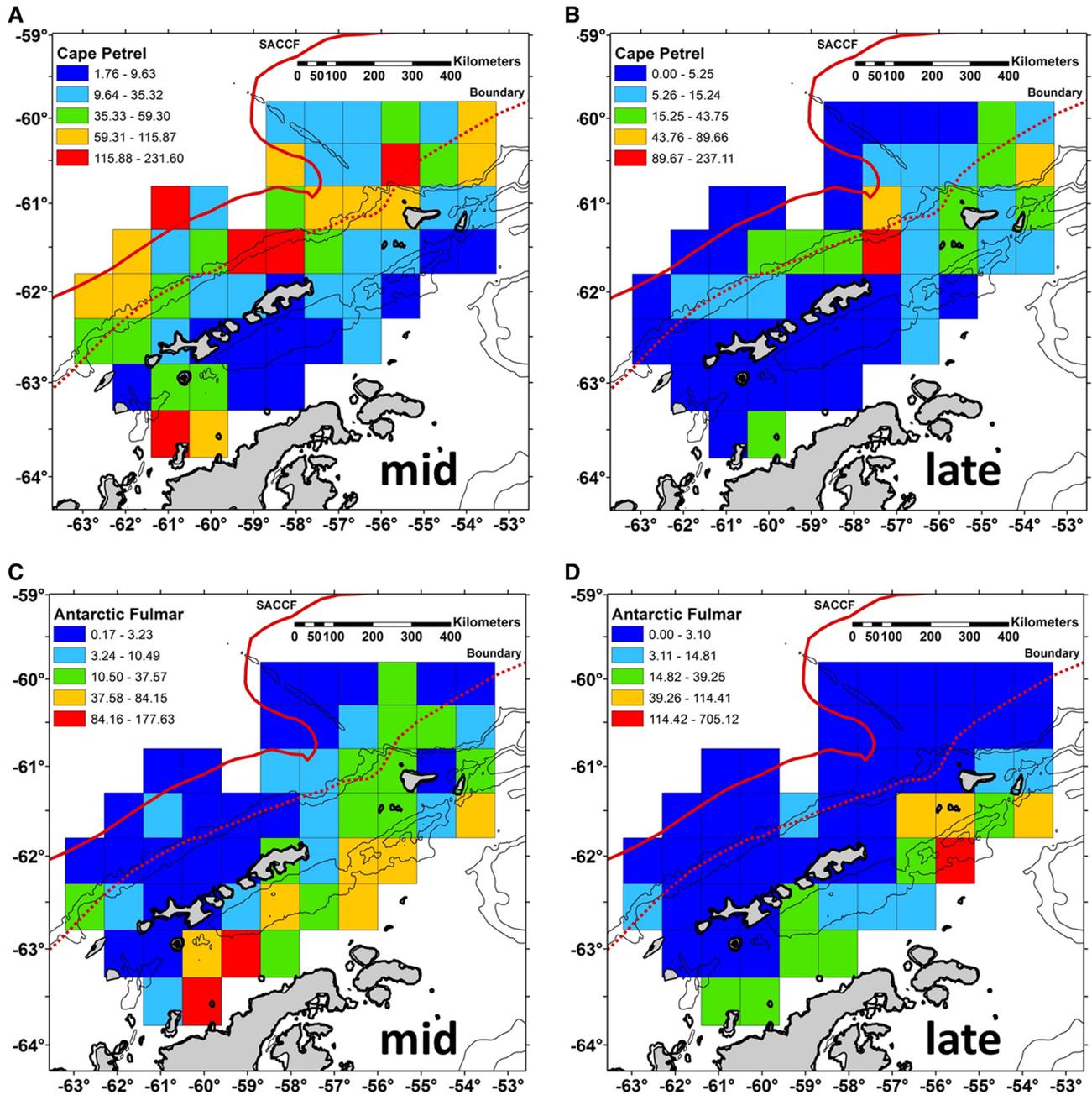


Figure 3. Cape petrel and southern fulmar hotspots during mid- and late-summer, illustrated as the long-term (2003–2011; 14 surveys) spatial mean of individuals-per-unit-effort (IPUE); hotspots are where the spatial mean is > 1 SD (orange) or > 2 SD (red). The average location of the southern Antarctic Circumpolar Current Front (SACCF) (red line) and the southern ACC boundary (red dashed line) are shown.

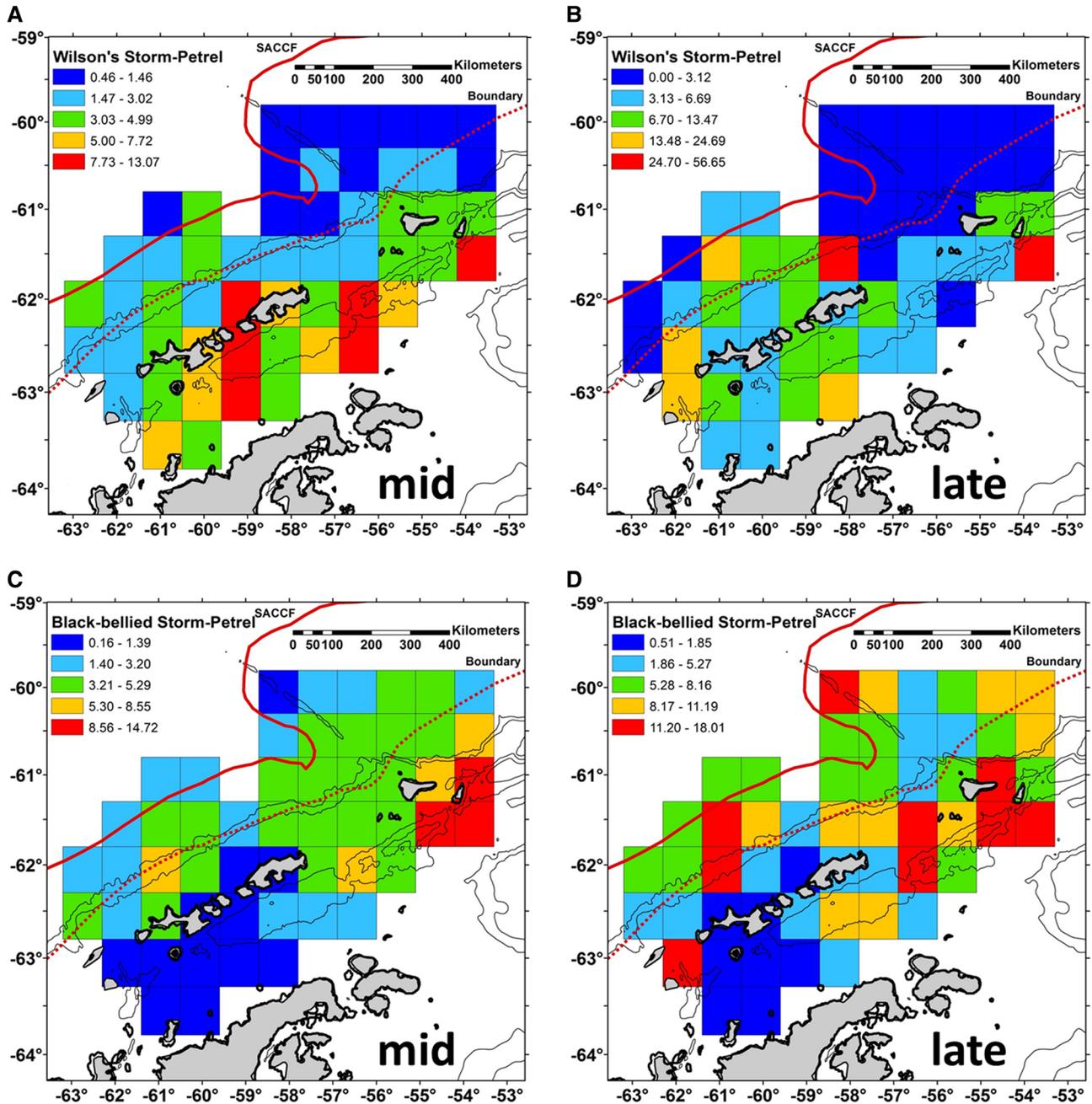


Figure 4. Black-bellied and Wilson's storm petrels abundance hotspots, during mid- and late-summer, illustrated as the long-term (2003–2011; 14 surveys) spatial mean of individuals-per-unit-effort (*IPUE*); hotspots are where the spatial mean is > 1 SD (orange) or > 2 SD (red). The average location of the southern Antarctic Circumpolar Current Front (SACCF) (red line) and the southern ACC boundary (red dashed line) are shown.

and distance to land, which displayed strongly linear responses with increased abundance offshore in warmer waters of the ACC (Figure 7C and Figure S. 4c). The model for Wilson's storm petrel also indicates season, but includes EKE and Chl-*a* as significant covariates. The relationship between

Wilson's storm petrel and surface Chl-*a* and EKE is negative and linear, suggesting their hotspots are located in low EKE and Chl-*a* waters (Figure 8B and Figure S. 3b).

The model for black-browed albatrosses included season (increase in late-summer), SST, EKE, and

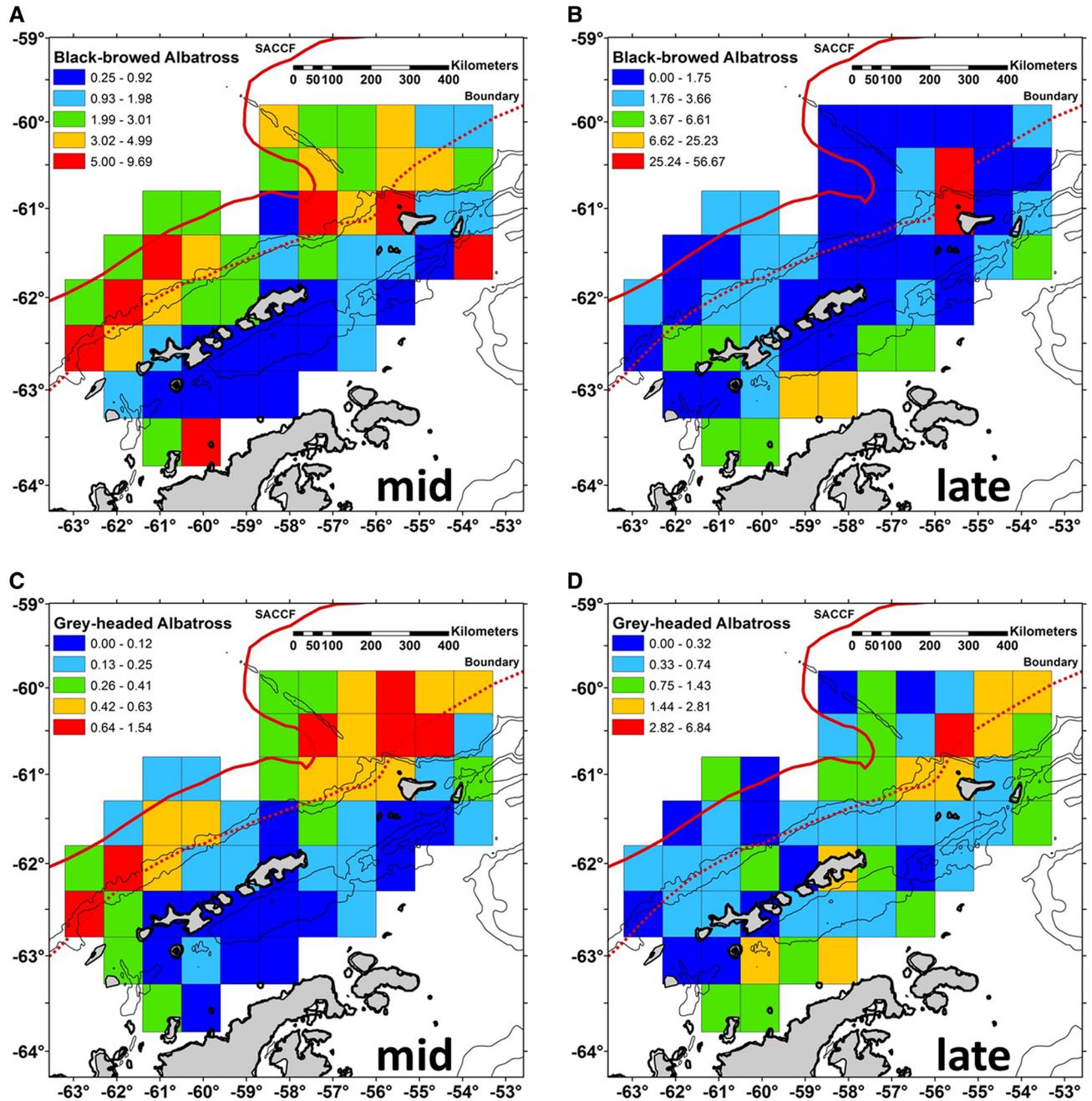


Figure 5. Black-browed and grey-headed albatross abundance hotspots during mid- and late-summer, illustrated as the long-term (2003–2011; 14 surveys) spatial mean of individuals-per-unit-effort (*IPUE*); hotspots are where the spatial mean is > 1 SD (orange) or > 2 SD (red). The average location of the southern Antarctic Circumpolar Current Front (SACCF) (red line) and the southern ACC boundary (red dashed line) are shown.

distance to land as significant covariates. Black-browed albatrosses were negatively associated with SST and distance to land (Figure 7D and Figure S. 4d). The functional response between black-browed albatrosses and EKE revealed a positive asymptotic relationship, indicating albatross hot-

spots are associated with EKE ranging from 40 to 80 $\text{cm}^2 \text{s}^{-2}$ (Figure 8C). The model for grey-headed albatrosses included season, SST, EKE, and Chl-*a* as significant covariates. Grey-headed albatrosses were negatively correlated to SST (Figure 7E) and positively related to EKE, also indicating an affinity

Table 2. Results of Generalized Additive Models for Assessing the Spatial Distribution Pattern and Functional Response Among Seabirds, Krill, and Environmental Covariates

Species	Season		Krill biomass		SST		EKE		Chl- <i>a</i>		Dist.Land		<i>te</i> (Lon, Lat)		% Dev.	<i>r</i> ²	GCV
	<i>t</i> , <i>p</i>	Edf., Res.df	F, <i>p</i>	Edf., Res.df	F, <i>p</i>	Edf., Res.df	F, <i>p</i>	Edf., Res.df	F, <i>p</i>	Edf., Res.df	F, <i>p</i>	Edf., Res.df	F, <i>p</i>	(Null)	(Null)	(Null)	
Cape Petrel	-2.18	2.41	7.49	5.75	2.25	7.46	1.65	1.00	1.25	8.13	3.79	11.55	3.61	76.6 (28.8)	0.65 (0.21)	26.92 (39.64)	
	0.03	2.91	< 0.001	6.78	0.04	8.32	0.12	1.00	0.26	8.73	< 0.001	13.32	< 0.001				
Southern Fulmar	0.14	2.73	5.87	3.63	4.80	2.94	5.25	1.00	13.24	2.72	4.02	18.33	2.27	89.1 (77.5)	0.95 (0.66)	16.06 (24.42)	
	0.54	2.92	0.00	4.17	0.00	2.99	0.05	1.00	< 0.001	2.90	0.01	19.85	0.01				
Wilson's Storm Petrel	0.47	4.90	1.47	7.62	1.14	3.36	5.95	1.32	8.40	1.00	1.20	13.97	1.58	79 (50)	0.72 (0.36)	2.79 (3.77)	
	0.01	5.91	0.19	8.37	0.34	4.13	< 0.001	1.54	0.00	1.00	0.27	16.33	0.09				
Black-bellied Storm Petrel	0.51	1.00	0.16	1.00	3.64	1.00	6.59	1.00	0.03	1.00	10.29	10.22	2.55	46.1 (31.6)	0.29 (0.21)	2.33 (2.42)	
	0.01	1.00	0.69	1.00	0.05	1.00	< 0.001	1.00	0.86	1.00	0.00	11.44	0.01				
Black-browed Albatross	0.97	3.38	1.27	1.00	15.49	2.29	2.79	1.44	0.48	1.00	12.60	13.19	2.62	65.1 (45.2)	0.62 (0.35)	3.31 (4.22)	
	< 0.001	4.17	0.28	1.00	< 0.001	2.86	0.04	1.73	0.59	1.00	< 0.001	15.69	0.00				
Grey-headed Albatross	2.09	1.79	0.79	1.00	39.12	5.09	13.55	1.00	10.43	3.10	1.45	14.88	2.90	77.1 (34.7)	0.79 (0.29)	0.27 (0.47)	
	< 0.001	2.21	0.46	1.00	< 0.001	6.12	< 0.001	1.00	0.00	3.78	0.23	16.72	< 0.001				

SST is sea surface temperature, EKE is eddy kinetic energy, Chl-*a* is Chlorophyll-*a*, Dist. Land is distance (km) to land from grid cell centroid, and *te*(Lon, Lat) is spatial component that includes a smoothed interaction term between longitude and latitude. Edf. is estimated degrees of freedom, Res. df is residual degrees of freedom, % Dev. is percent deviance explained, and GCV is generalized cross-validation. Null refers to the performance of GAM, which includes effects of season and a spatial component.

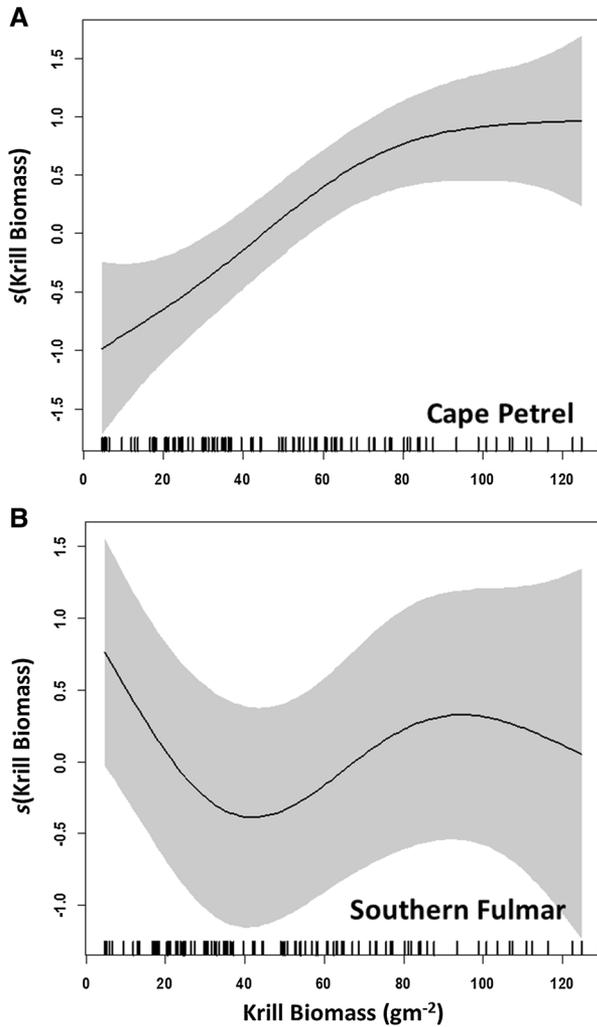


Figure 6. GAM results illustrating the functional relationship of krill biomass and **A** cape petrel, and **B** southern fulmar; shaded area indicates 95% confidence intervals and ticks above x -axis indicate data availability.

for EKE ranging from 40 to 80 $\text{cm}^2 \text{s}^{-2}$ (Figure 8D). Grey-headed albatrosses were the only species that were strongly associated with enhanced surface Chl- a waters (Figure S. 3c).

DISCUSSION

Our synthesis on the ecosystem oceanography of seabird hotspots resolved specific abiotic and biotic conditions underlying the formation of hotspots within coastal and oceanic waters (Figure 9). These hotspots reflect physical features conducive to concentrating prey resources within recurrent localized areas. Hotspots located near known breeding colonies should be considered as critical foraging habitat for successful population growth. Moreover, interspecific responses to environmental

conditions for this species group indicate their life history is important for understanding the spatial organization of hotspots within the ecosystem. Overall, no long-term trends were apparent in seabird temporal anomalies, but there seem to be correlated seasonal fluctuations that indicate abrupt changes in trophic interactions. We discuss the generalizations of our ecosystem oceanography approach and how it may be extended to understand drivers of biological hotspots in other pelagic ecosystems. We also discuss the implications of Antarctic seabird hotspots as ecosystem indicators of (a) mesoscale dynamics within coastal and oceanic waters, (b) seasonal variation, (c) krill biomass, and for (d) ecosystem-based management within an important krill fishing ground.

Generalizations

Identification of seabird hotspots provides a means of summarizing information on ecosystem function as it integrates over large numbers of multiple species of top level predators and environmental conditions (Sigler and others 2012; Suryan and others 2012; Santora and Veit 2013). Thus, our approach allows for the relatively quick identification of ecosystem fluctuation across multiple spatial and temporal scales. Although our study focused on a pelagic ecosystem of the Southern Ocean, our ecosystem oceanography approach, involving data integrations of satellite ocean conditions and at sea measurements of prey biomass for identifying drivers of seabird hotspots, is easily extendable to other ecosystems. This is especially true for pelagic upwelling ecosystems, which are similarly structured by strong bathymetric steering of currents, the presence of hydrographic fronts and eddies, and dense forage fish species aggregations (Bakun 1996; Cury and others 2008). Through a comparison of similar ecosystems, our understanding of the stability and variability of environmental determinants of biological hotspots will improve and benefit our ability to assess their susceptibility to climate change and fishery overexploitation (Sydemann and others 2006; Cury and others 2011; Hazen and others 2013). Moreover, trophic connections of pelagic ecosystems involving keystone forage fish species are often similarly structured; therefore, comparing ecosystems may illuminate universal approaches for managing forage fish (Plagányi and Essington 2014; Pikitch and others 2014). Regarding spatial structure and trophic interactions, advancing ecosystem-based management of forage fish predators will benefit from understanding where, when, and how predator

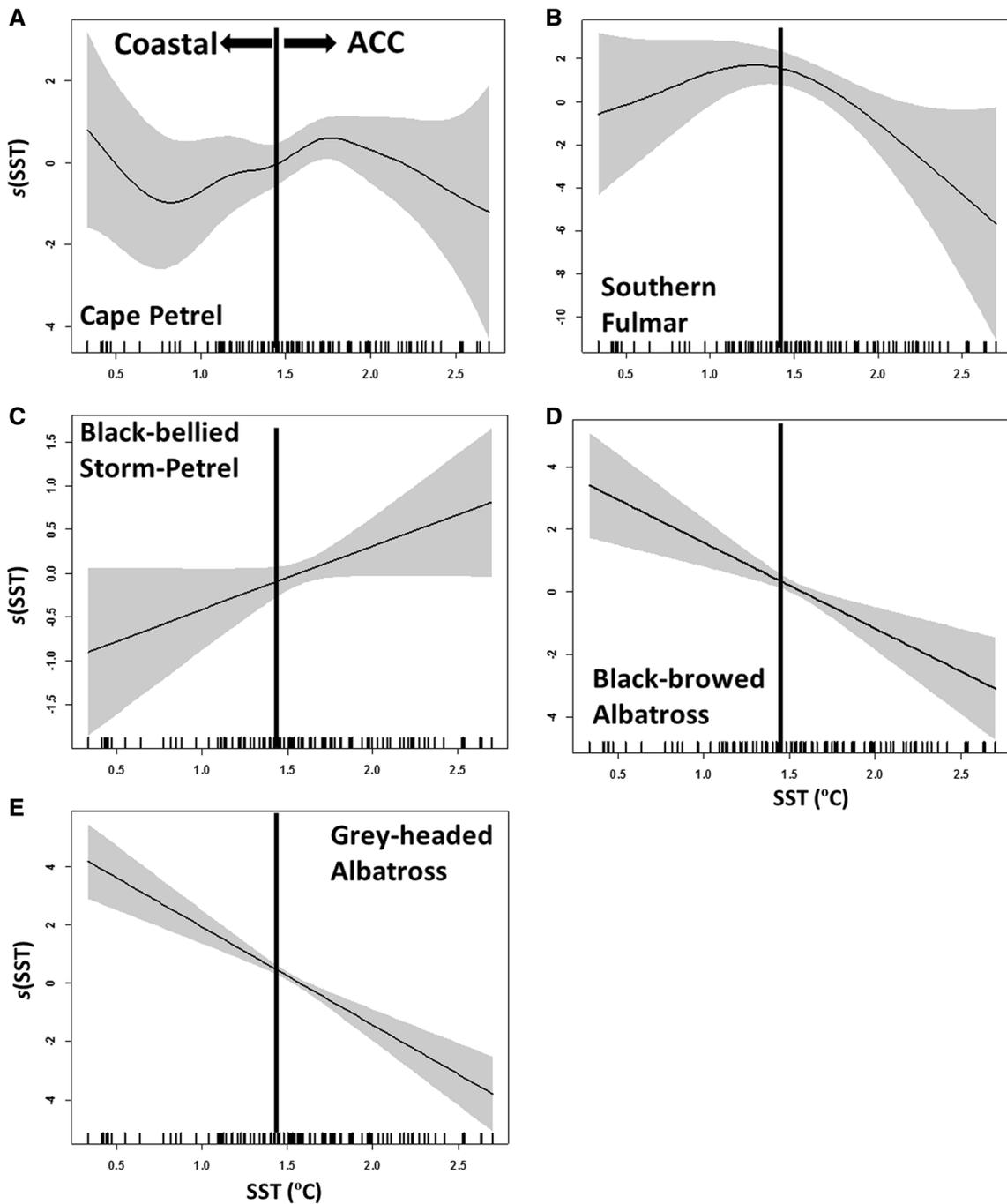


Figure 7. GAM results illustrating the functional relationship of sea surface temperature (SST) and **A** cape petrel, **B** southern fulmar, **C** black-bellied storm petrel, **D** Black-browed albatross, and **E** grey-headed albatross; shaded area indicates 95% confidence intervals and ticks above x -axis indicate data availability. *Black arrows/lines* indicate oceanic and coastal habitats; ACC is Antarctic Circumpolar Current.

and forage species hotspots may form, as well as estimating how much prey biomass is consumed by species, and extracted by fisheries within hotspots. More generally, our study provides a procedure for

assessing the mesoscale variability of biological hotspots and how (a) physical ocean conditions interact with a schooling forage species, whose biomass and recruitment are environmentally dri-

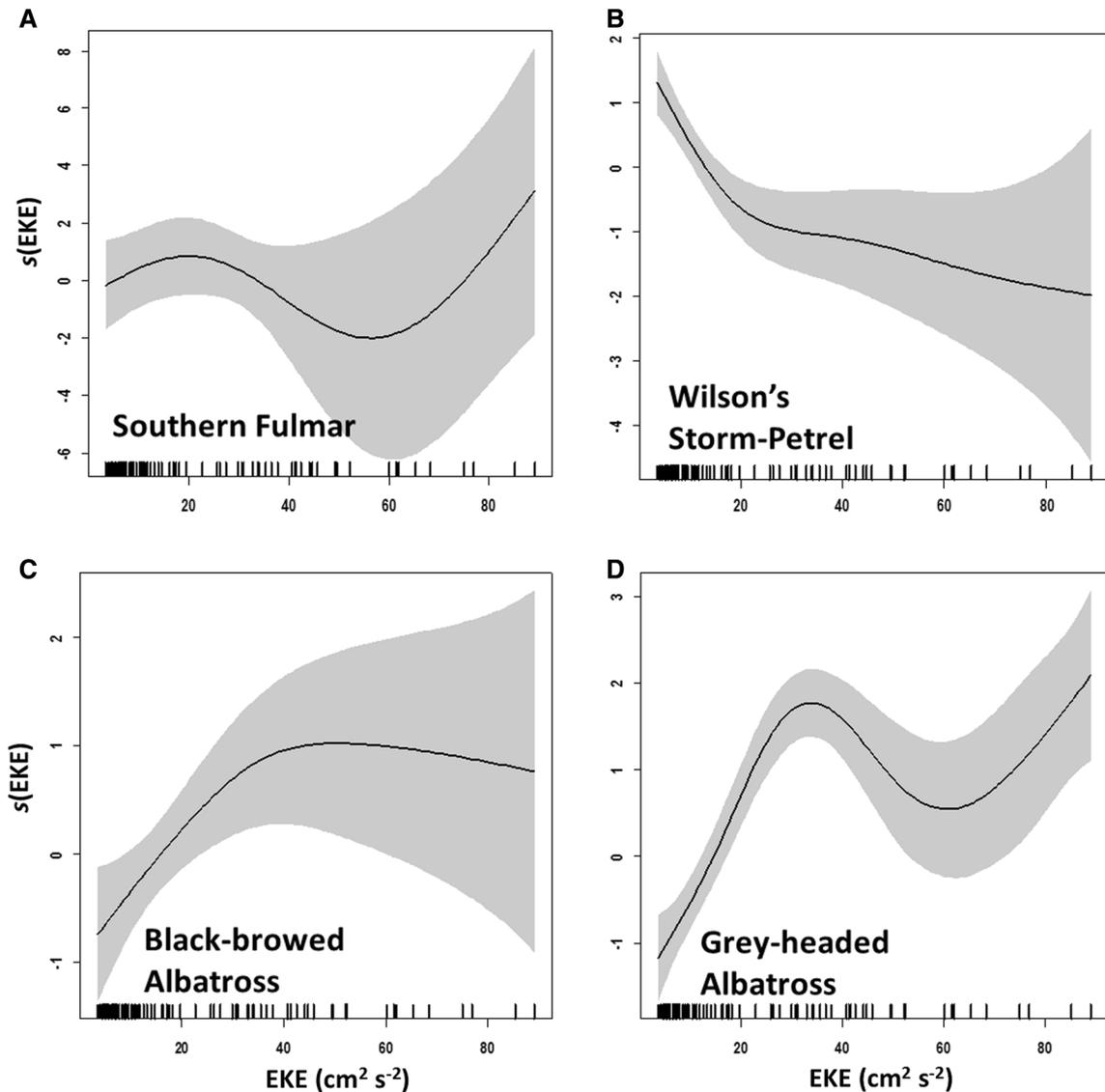


Figure 8. GAM results illustrating the functional relationship of eddy kinetic energy (EKE) and **A** southern fulmar, **B** Wilson's storm petrel, **C** black-browed albatross, and **D** grey-headed albatross; shaded area indicates 95% confidence intervals and ticks above x -axis indicate data availability.

ven (similar to other pelagic ecosystems), and how the abundance and distribution of wide-ranging predators reflect the spatial organization of marine ecosystems; and (b) similar predator species respond differently to prey availability and ocean conditions, and we should expect that in other ecosystems. Indeed, one of the fundamental lessons of ecosystem ecology is that we should anticipate multiple causes and explanations, and this is especially true in highly dynamic pelagic systems where many predators utilize a common forage species.

Ecosystem Oceanography of Seabird Hotspots

The importance of physical ocean features (for example, hydrographic fronts and eddies), their stability in space and time, and resulting effect on forage species aggregations likely makes such features universally important for predicting biological hotspots. Our models indicate that seabird hotspots are structured by mesoscale environmental gradients of EKE, SST, Chl- a , and distance to land that reflect different ocean conditions between coastal

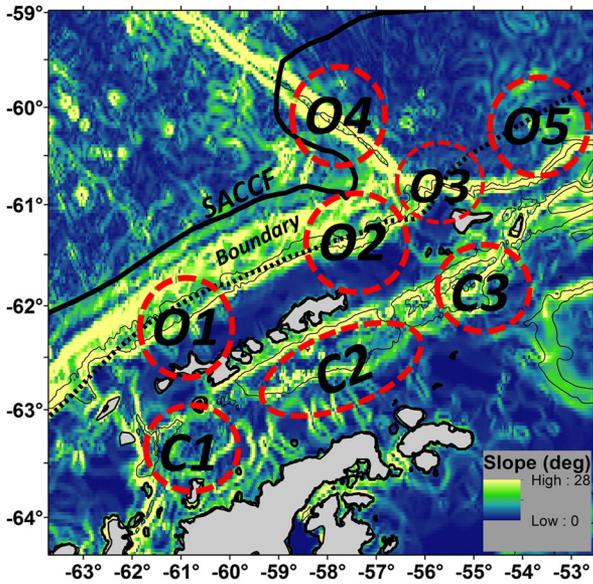


Figure 9. Summary of mesoscale hotspot zones as indicated by relationships among seabirds, krill biomass, and environmental characteristics that together reflect oceanic (O1–5) and coastal (C1–3) mesoscale ocean processes. Dashed circles indicate that hotspots are considered dynamic and do not represent fixed boundaries. Contoured bathymetric slope (degrees; data derived from ETOPO-1) illustrates the importance of bathymetry on water circulation and hotspot location. SACCF is southern Antarctic Circumpolar Current front and Boundary is the southern ACC boundary. See Figure 1 for land references.

and oceanic waters. Seabird hotspots within the oceanic domain, represented by cape petrel, black-bellied storm petrel and both albatross species, are influenced by the prevailing West Wind Drift of the ACC, and enhanced EKE is associated with the southern ACC front, which meanders along the continental shelf break north of the archipelago, generating mesoscale eddies near islands and on either side of the Shackleton Fracture Zone (Kahru and others 2007; Zhou and others 2010; Venables and others 2012). Cape petrels are clearly linked to the mesoscale variability of krill biomass throughout the oceanic domain (see below). Our results indicate at least 5 important mesoscale hotspot zones in the oceanic domain that are critical for top predators: (O1) waters north of Livingston Island overlapping with a submarine canyon system, (O2) the area between north King George Island and Elephant Island, the waters north of Elephant Island near the (O3) Seal Islets and (O4) Shackleton Fracture Zone, and the (O5) high EKE zone to the northeast of Elephant Island (Figure 9). These productive waters support dense krill hotspots that

are associated with enhanced EKE and linearly related to distance to the shelf break and the southern ACC front (Santora and others 2012). Our models indicate that albatross hotspots are associated with enhanced EKE, especially near islands in the oceanic domain. Their positive relationship with EKE suggests they seek regions with increased turbulence that may influence the concentration of prey from days to weeks. Therefore, the formation and maintenance of biological hotspots within the oceanic domain are likely sensitive to changes in the position and intensity of the southern ACC front (Figure 2) and the concentration of krill aggregations within eddies along the shelf-break region.

When compared to oceanic domain, water circulation within coastal domain is considerably more complex owing to multiple source water inputs combined with rugged coastal bathymetry (Zhou and others 2006; Thompson and others 2009). The hydrographic variability of the coastal domain is influenced by the location of deep basins with Bransfield Strait and upstream input from the Antarctic coastal current, which flows northeast along southern edge of the South Shetland Islands, and from the Weddell Sea, which enters from the east in the study area (Figure 1). Coastal seabird hotspots, represented by southern fulmars, Wilson’s storm petrel, and both albatross species, also indicate at least three important mesoscale hotspot zones: (C1) western Bransfield Strait where waters from the Antarctic coastal current and Gerlache Strait converge over complex bathymetry, (C2) central Bransfield Strait associated with deep basins and (C3) eastern Bransfield Strait south of Elephant Island where there eddies are associated with complex bathymetry and confluence of waters from the Antarctic coastal current, ACC, and Weddell Sea (Figure 9; Thompson and others 2009). Southern fulmar hotspots are associated with krill in coastal waters, positively related to EKE and situated over deep coastal basins. During summer, Bransfield Strait contains smaller krill (<34 mm), so perhaps fulmars are selecting such foraging areas, where krill may be concentrated by eddies, or perhaps facilitated to the surface by humpback whales, which are also densely concentrated there during summer (Santora and others 2010). Alternatively, fulmar hotspots may relate to forage fish, such as the Antarctic silverfish (*Pleuragramma antarctica*), which may be more concentrated in coastal waters closer to the Antarctic Peninsula (Ainley and others 1992; Barrera-Oro 2002). Our assessment of black-browed and grey-headed albatrosses indicates that their

hotspots overlap and occur in both domains. Since they are seasonal visitors to the NAP, restricted by the distance traveled from their breeding colonies (for example, Diego Ramirez; Robertson and others 2007) and have similar diets, feeding strategies, and morphology, it is not surprising that albatrosses select similar foraging grounds.

Seasonal Variation of Seabird Hotspots

Changes in the intensity and distribution of top predator hotspots suggest that they are indicators of seasonal change in the physical and biological structure of NAP marine ecosystem. Antarctic fur seal (*Arctocephalus gazella*) and fin whale (*Balaenoptera physalus*) hotspots also increase in intensity and shift poleward between seasons in the NAP and are associated with changes in krill availability and ocean conditions (Santora 2013; Santora and others 2014). Collectively, changes in hotspot intensity and distribution indicate a major reorganization of the top predator community and potential shift of vertebrate biomass into the NAP ecosystem in autumn. Decreases in cape petrel hotspot intensity may indicate that their aggregations reflect seasonal changes in physical ocean conditions within the oceanic domain. Storm petrel and albatross species displayed seasonal abundance increases and albatrosses shifted distribution, with increases closer to land, including near the insular shelf of Elephant Island and within coastal waters of Bransfield Strait. The impact of these abundance changes and distribution shifts should be further explored in ecosystem and food-web models for the NAP (Murphy and others 2013; Watters and others 2013).

Seasonal variation of seabird hotspots provides ecosystem indicators of biophysical ocean conditions that likely relate to energetic demands of breeding and time allocated to foraging and raising young. Seabirds generally schedule their annual breeding cycle to coincide with the peak abundance and availability of their prey (Schreiber and Burger 2001). Their breeding season is partitioned into discrete phases regarding mating, egg laying, incubation, and chick provisioning, which all influence the amount of time spent foraging at sea. Therefore, a possible explanation for seasonal abundance increases, and distribution shifts in hotspots locations may be due to changes in parental duties regarding the schedule of egg incubation, brood guard, and chick rearing behaviors (Croxall and Prince 1980; Schreiber and Burger 2001). During early summer, it is more likely that parents are incubating eggs and are limited in their

ability to undergo extended foraging trips. When provisioning their chicks, parents will spend considerably more time foraging, but are limited in the how far they can travel to collect sufficient prey (that is, central place foragers). This extends to storm petrels and albatrosses, which displayed increase hotspot intensity during late-summer. Storm petrels are locally breeding species, and we detected increases in abundance in the vicinity of several islands, possibly indicating more birds foraging within radii of their presumed breeding locales. Furthermore, increases in albatross abundance may indicate that either they are toward the end of their chick rearing cycle and have more time to undergo longer trips, or may indicate an influx of individuals that failed at breeding (Croxall and Prince 1980; Reid and others 2005; Cherel and others 2002). The closest major black-browed and grey-headed albatross breeding colonies are on the Diego Ramirez Archipelago, the Falkland Islands (Isla Malvinas), and South Georgia (Croxall and others 1997; Robertson and others 2007). The occurrence and strong seasonal variation of albatross hotspots reported here clearly indicate the NAP ecosystem is an important feeding ground for albatrosses.

Of Krill and Cape Petrels

Our study indicates that cape petrel hotspots are strongly associated with krill biomass. Cape petrels are a CCAMLR Ecosystem Monitoring Program (CEMP) species with respect to their breeding biology, and our data indicate their foraging hotspots may be valuable indicators of krill availability. Previously, it was demonstrated that the inter-annual spatial variability of cape petrels and krill is also linked, and during years with low krill biomass, both petrels and krill are concentrated in fewer patches, suggesting a coherence of krill and seabird patchiness (Santora and others 2009). During summer, large (>44 mm) sexually mature krill occur in high abundance offshore in proximity to the southern ACC front (Atkinson and others 2008; Loeb and Santora 2015), overlapping with cape petrel hotspots. Therefore, aggregations of cape petrels in oceanic waters may relate to the occurrence of mating and spawning behavior of postlarval krill within the ACC, and could also provide information about multi-scale characteristics of krill aggregations in oceanic waters. Cape petrels also respond to finer-scale (km) changes in horizontal and vertical distribution of krill biomass within the submarine canyon system north of Livingston Island (Santora and Reiss 2011). In summary, cape petrel hotspots are an important

indicator of the availability of krill biomass across multiple spatio-temporal scales, and, more generally, they provide critical information about the mesoscale variability and key habitats within the Antarctic Peninsula marine ecosystem.

Implications for Conservation and Fishery Management

Our ecosystem oceanography assessment of seabird hotspots provides reference points for conservation plans (for example, marine protected areas; MPA) that are easily extendable to other pelagic ecosystems containing similar predators and schooling forage species. By identifying important environmental factors associated with seabird hotspots, these patterns may help resolve potential interactions between seabirds and the commercial forage fisheries, especially the krill fishery that operates near the NAP (Croll and Tershy 1998; Nicol and others 2012). The seasonal distribution shifts of top predators, within or among hotspots, may help define temporal windows of potential vulnerability for seabirds. Such changes in hotspot use could be useful in defining temporal windows of protection in spatial management schemes (that is, when MPAs might be opened or closed; Hooker and others 2011; Lascelles and others 2012). For example, move-on rules and timed closures could be implemented in fishery management strategies to shift fishing vessels away from seabird hotspots to avoid potential conflict with seabird hotspots (Babcock and others 2005; Dunn and others 2014). Furthermore, the spatially explicit estimates of seabird abundance, combined with their physiological requirements (for example, basal metabolic rates; Hodum and Weathers 2003), and krill age- or size-based estimates of krill biomass (Reiss and others 2008; Loeb and Santora 2015) may be used to develop regional estimates of krill consumption and size-dependent predation (Hunt and others 2000) to better inform fishery management and conservation planning. Due to the inaccessibility of the nesting locations, satellite tracking of small petrels remains a challenge; therefore, consideration of their sea abundance hotspots may provide the best estimate of their population-level requirements at regional scales in this sector of the Southern Ocean.

The distributions of hotspots quantified here may inform delineation of Important Bird and Biodiversity Areas (IBAs) near the NAP (Figure 9; Harris and others 2015). Black-browed and grey-headed albatross are species of conservation concern (Table 1; Rodrigues and others 2006).

Therefore, the albatross hotspots near the NAP during summer indicate an important population-level feeding ground for these species. Such hotspots could become areas of increased interaction for these species of concern if the krill fishery targets coastal and oceanic hotspots near islands. These hotspots should be monitored to evaluate their importance to the conservation of albatrosses in Antarctic waters and where possible compared with satellite telemetry to understand behavior within hotspots. Last, although we quantified the environmental determinants of the distribution of flying seabird hotspots, future integration of field and numerical studies is needed to understand the physical mechanisms that facilitate the formation and maintenance of biological hotspots (Dorman and others 2015). Physical mechanisms that influence the residence time of krill patches within seabird and fishing hotspots should be explored using regional ocean (for example, particle tracking) models (Hofmann and Murphy 2004; Piñones and others 2013) to determine drivers of the distribution and persistence of multispecies hotspots. Furthermore, evaluation of historical fishing extraction patterns within krill-predator hotspots should be explored to assess sensitivity of the ecosystem to fishing pressure and climate change.

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