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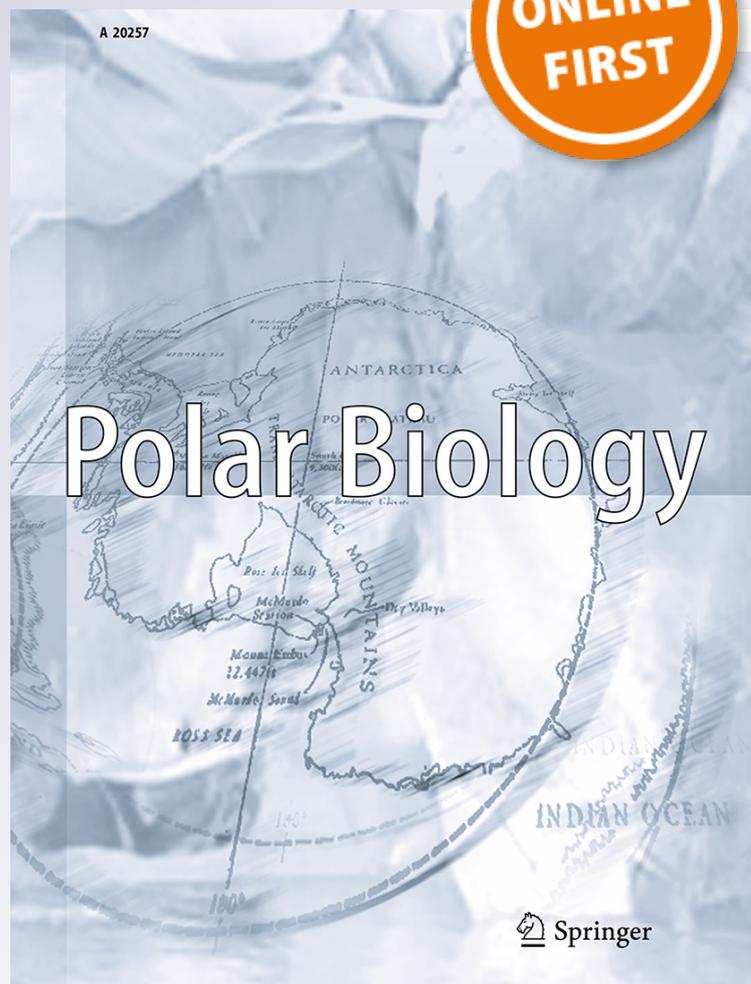
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Climate variability and multi-scale assessment of the krill preyscape near the north Antarctic Peninsula

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Abstract Antarctic krill (*Euphausia superba*) densities vary in space and time across multiple scales, with consequences for krill predators, the krill fishery, and management decisions. We use acoustic data collected from 1997 to 2011 around the South Shetland Islands near the northern Antarctic Peninsula to quantify spatiotemporal patterns in krill biomass, distribution, and patchiness both within and across years. Moreover, we evaluate potential climate drivers of krill biomass and spatial organization through comparison with seasonally lagged climate indices. Krill abundance varied by an order of magnitude throughout the study period, with mean biomass ranging from a high of 171.9 g m⁻² in 1997 to a low of 9.4 g m⁻² in 2002. We find that across years, krill abundance and variability are correlated with seasonally averaged measures of El Niño-Southern Oscillation at lags of approximately 2–2.5 years, which may correspond to strong reproduction and recruitment events. Krill biomass shows generally weak to moderate spatial autocorrelation and

high aggregation, with measures of spatial organization correlated with abundance in some habitats. Within years, there was an overall trend of declining krill abundance and/or detectability and contracted spatial distribution between midsummer and late summer, but this pattern was not consistent across all years. This synthesis provides the background to model krill prey landscapes in order to better understand regional foraging ecology of krill predators and fishery performance.

Keywords *Euphausia superba* · Acoustic survey · Spatial ecology · Climate · ENSO

Introduction

Antarctic krill (*Euphausia superba*, hereafter krill) are a keystone species in the Southern Ocean ecosystem and a major prey source for many species of fish, squid, seabirds, and marine mammals (Smetacek and Nicol 2005). Krill are the focus of the Southern Ocean's largest fishery by tonnage (Nicol et al. 2012), leading to concerns that harvesting, as well as climate-induced changes in distribution and abundance, may lead to decreased availability to predators (Hewitt et al. 2004; Flores et al. 2012). Krill are patchily distributed, and their abundance varies across a range of temporal and spatial scales, ranging from population-wide fluctuations that occur on the scale of years and thousands of kilometers, to variation at the concentration level that occur at the scale of months and hundreds of kilometers, to patch dynamics that occur at the scale of weeks and tens of kilometers (Murphy et al. 1988; Miller and Hampton 1989; Santora et al. 2012). These multi-scale orders of variation have important consequences to predators and the fishery at various levels. For example, inter-decadal changes in krill

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biomass have been linked to changing population trajectories of Chinstrap and Adélie Penguins breeding on the South Shetland Islands (Trivelpiece et al. 2011). At smaller temporal and spatial scales (e.g., months and 100 s of kilometers), krill availability during the breeding season has been linked to the reproductive success of seabirds and marine mammals at South Georgia (Croxall et al. 1999; Boyd and Murray 2001; Reid and Croxall 2001; Murphy et al. 2007). Moreover, spatial and seasonal overlap between the krill fishery and predator foraging has raised concerns that local fishery extraction may reduce the availability of krill to predators (Croll and Tershy 1998). For example, fishing vessels and predators such as blue whales may operate on similar spatiotemporal scales (Wiedenmann et al. 2011), raising the possibility of conflicts between human extraction and predator foraging needs, which can only be quantified with knowledge of the dynamics of the exploited stock. Thus, understanding the factors that underlie krill variability across space and time is important in the management of krill fisheries throughout the Southern Ocean ecosystem. We use a long-term acoustic data set collected from 1997 to 2011 around the Northern Antarctic Peninsula (NAP) region (Fig. 1) to elucidate intra- and inter-annual patterns in krill abundance and spatial organization and possible consequences for krill-dependent predators.

As revealed by acoustic and net data, krill populations exhibit inter-annual and decadal fluctuations in biomass and demography (Siegel and Loeb 1995; Reiss et al. 2008; Shelton et al. 2013). In the NAP region, periodic strong year classes produce cyclical patterns of krill biomass (Siegel and Loeb 1995; Hewitt et al. 2003). Krill

recruitment is tied to climatic factors, particularly the extent and duration of winter sea ice and El Niño–Southern Oscillation variability (Loeb et al. 1997; Quetin et al. 2007; Loeb et al. 2009). Although krill abundance and demography are linked to climate–ocean conditions (Loeb and Santora 2015), the consequences for both inter-annual and intra-seasonal spatial distributions have not been fully quantified. Previous work linking krill abundance and climate in this area has focused solely on net haul data (Loeb and Santora 2015), but these indices appear uncorrelated with acoustic data (Kinzey et al. 2015), raising the possibility that acoustic estimates of abundance may reveal different information about the influence of climate on the abundance and spatial organization of krill populations.

The hierarchical distribution of krill is the result of the interaction of physical processes that dominate at broad spatial scales (e.g., currents and fronts; 1000 s of km) and behavioral processes that facilitate concentration of krill within fine-scale (10 m–100 km) habitat favorable for successful feeding and reproduction (Atkinson et al. 2008). Advective processes such as the southern Antarctic Circumpolar Current (ACC) are thought to dominate in the open ocean, but small-scale behavioral responses to environmental cues (e.g., food availability) may alter krill advective trajectories (Lascara et al. 1999; Murphy et al. 2004). In addition, active krill migration may play an important role in krill distributions, particularly in areas with lower current velocities (Murphy et al. 2004; Richerson et al. 2015). Krill distributions near the NAP show patterns unlikely to result from advection alone, with clear segregation of size and maturity stages, suggesting that ontogenetic migrations may in part explain observed

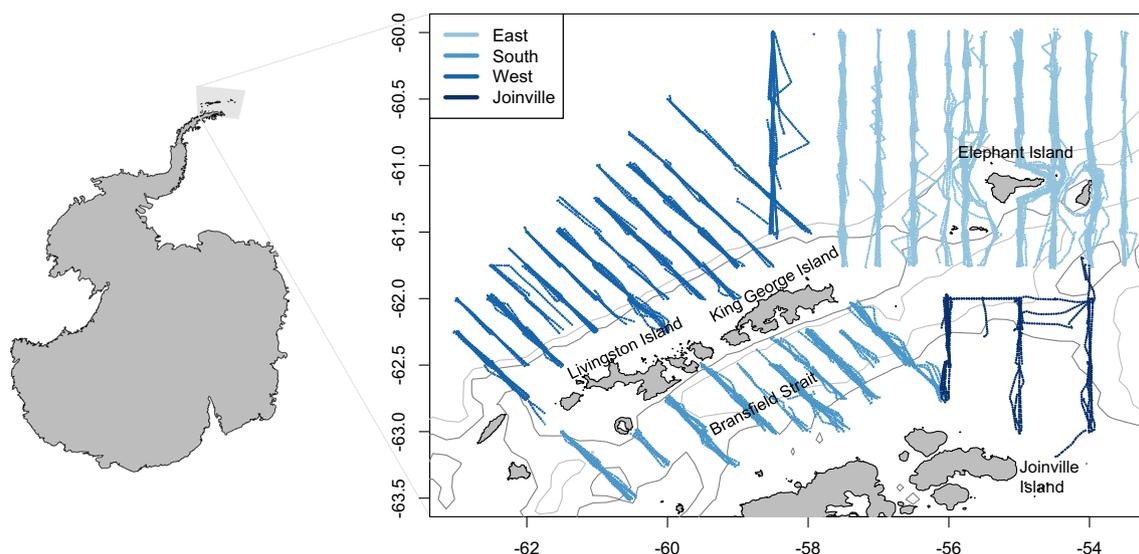


Fig. 1 All acoustic transect lines completed 1997–2011. Dark gray lines indicate the 500-m isobaths, and light gray lines indicate the 1000-m isobaths

spatial patterns (Watkins et al. 1992; Trathan et al. 1993; Siegel 1988; Lascara et al. 1999; Richerson et al. 2015). Krill also exhibit seasonal changes in habitat use, suggesting that behavior is responsible for seasonal variations in distribution (Lascara et al. 1999); however, a baseline of fine-scale changes in acoustically derived krill distribution has yet to be quantified.

Acoustic data from the United States Antarctic Marine Living Resources (US AMLR) Program collected around the South Shetland and Elephant Island areas provide an opportunity to investigate how krill distributions vary across both long (inter-annual) and short (monthly) time scales. Data were collected during austral summers of 1997–2011, with sampling repeated twice in 11 years, allowing comparisons of krill distributions early (January) and later (February) in the spawning season.

Using these data, we quantify: (1) inter-annual and intra-seasonal patterns in abundance and distribution, (2) measures of krill spatial aggregation and organization, and (3) connections between krill abundance and variability with indices of environmental forcing (El Niño–Southern Oscillation; ENSO and Southern Annular Mode; SAM). We conclude that climate fluctuations influence inter-annual fluctuations in krill abundance, while factors such as behavior and advection may drive intra-annual changes in krill abundance and distribution.

Methods

Survey area

The US AMLR Program study area is located around the South Shetland Islands, near the NAP (Fig. 1). This is an area of complex bathymetry and circulation, with contributions from the Antarctic Circumpolar Current (ACC), the Weddell Gyre, and the Antarctic Coastal Current (Thompson et al. 2009). The varied bathymetry of the area includes the continental shelf around the islands as well as deeper waters in the Bransfield Strait and Drake Passage. In addition, the southern ACC front, located north of the archipelago, is an important feature for concentrating krill (Atkinson et al. 2008; Santora et al. 2012). The survey area is also a major krill fishing ground (Jones and Ramm 2004) and home to large numbers of a variety of krill predators (Reiss et al. 2008; Santora and Veit 2013; Santora et al. 2014), making it of particular concern to conservation and management.

Survey methods

The US AMLR Program conducted annual surveys in the pelagic and coastal waters near the South Shetland Islands

during the austral summers (January to March) of 1988–2011.

These surveys occurred in a fixed sampling grid and collected a variety of oceanographic, biological, and acoustic data, with a focus on krill demographics, abundances, and distributions. Through 1996, all surveys were performed in the Elephant Island stratum, covering an area of 43,865 km². In 1997, the survey grid was expanded to two other strata: west (38,542 km² in area located north of King George and Livingston Island) and south (24,479 km² in the Bransfield Strait) (Fig. 1); thus, we focus the analyses on the years from 1997–2011 to assess the regional spatial organization of krill biomass. In 2002, a fourth area, Joinville Island (18,151 km² located northeast of Joinville Island), was added; however, total survey effort was low here. Transects in the Elephant Island and Joinville Island strata run north–south, while transects in the west and south strata run northwest–southeast (Fig. 1). In most years, two survey legs were completed approximately a month apart, with one in midsummer (typically January to early February) and one in late summer (typically February to early March). However, in 1997, 2006, 2007, and 2009 only the midsummer leg was completed, and in 2000 only the late summer leg was completed; see Table 1 for a summary.

The AMLR program uses multi-frequency echosounders (38, 70, 120, and 200 kHz) to survey the abundance and spatial distributions of krill in the upper 250 m of the water column within the study area (for full details of the acoustic survey, see Hewitt et al. 2003 and Reiss et al. 2008). Briefly, volume-backscattering strengths (S_v , Db) were recorded during daylight hours along survey tracklines. These data were converted into the integrated volume-backscattering coefficient (nautical area scattering coefficient or NASC, m² nautical mile⁻²) associated with krill, providing an index of krill abundance. NASC values are integrated over depth (250 m) and averaged over 1 nautical mile (1852 m). These values are then further processed into a depth-integrated estimate of krill biomass density (g m⁻²) using krill target strength and a weighted mean estimate of krill mass (Demer and Conti 2005). All values were produced using the Stochastic Distorted-Wave Born Approximation (SDWBA) model recommended by CCAMLR (SC-CAMLR 2010).

Krill time series and spatial variability indices

The spatial organization and abundance of krill affect predator foraging distribution and success (Santora et al. 2009); thus, we focused this analysis of the krill preyscape on measures of krill abundance (i.e., mean and standard deviation of biomass) and patchiness (i.e., spatial autocorrelation and aggregation). Since krill tend to show

Table 1 Details of US AMLR surveys

Year	Midsummer survey dates	Late summer survey dates	Strata surveyed, midsummer	Strata surveyed, late summer
1997	1/27–2/10	–	EI, S, W	–
1998	1/08–1/25	2/08–2/25	EI, S, W	EI, S, W
1999	1/15–1/28	2/10–2/23	EI, S, W	EI, W
2000	–	2/22–3/06	–	EI, S, W
2001	1/16–1/30	2/12–3/02	EI, S, W	EI, S, W
2002	1/16–1/29	2/24–3/08	EI, S, W, J	EI, S, W, J
2003	1/14–1/26	2/10–2/25	EI, S, W	EI, S, W
2004	1/16–1/31	2/20–3/06	EI, S, W	EI, S, W, J
2005	1/17–1/31	2/22–3/08	EI, S, W, J	EI, S, W, J
2006	1/16–2/01	–	E, S, W	–
2007	1/11–1/26	–	E, S, W	–
2008	1/18–2/03	2/27–3/07	EI, S, W, J	EI, S
2009	1/13–1/29	–	EI, S, W, J	–
2010	1/28–2/03	2/22–3/06	EI	S, W, J
2011	1/17–2/04	2/26–3/03	EI, S, W	S, J

EI Elephant Island, S South, W West, J Joinville Island

spatial segregation during the summer with juveniles concentrated on the continental shelf, adults near the shelf slope, and spawning females off-shore (Nicol 2006, Santora et al. 2010), we grouped observations by habitat type (on-shelf, <500 m depth, shelf slope 500–1000 m and off-shelf >1000 m). Table 2 shows the annual survey effort in each habitat. We calculated mean, variance, and standard deviation of krill biomass in midsummer and/or late summer in each habitat, as well annual values across the entire study area. We define a standardized abundance anomaly Z_y as

$$Z_y = \frac{x_y - \bar{x}}{s} \tag{1}$$

where x_y is the mean density in year y , \bar{x} is the long-term mean density, and s is the long-term standard deviation of density. These calculations and all other calculations below were done in R version 3.0.2 (R Development Core Team 2013).

To assess the inter-annual spatial organization of the krill preyscape, we calculated two measures of spatial distribution each year: global Moran's I and the negative binomial \hat{k} . Though both measures have been used to describe patchiness, they represent different measures of spatial structure (Fig. 2), with the negative binomial \hat{k} describing the degree of aggregation and Moran's I describing the degree of spatial autocorrelation. Moran's I (Moran 1950; Diniz-Filho et al. 2003) can take values between -1 and 1 , with positive values indicating a clustered distribution, negative values indicating dispersion,

and values near zero indicating random distribution. The statistic is

$$I = \frac{b}{\sum_i \sum_j w_{ij}} \frac{\sum_i \sum_j w_{ij} (X_i - \bar{X})(X_j - \bar{X})}{\sum_i (X_i - \bar{X})^2} \tag{2}$$

where b is the number of spatial units (indexed by i and j), X_i is the variable of interest at location i , and w is the spatial weights matrix such that w_{ij} is the spatial weight between locations i and j . We used the *ape* package (Paradis et al. 2004) to calculate this statistic in midsummer and/or late summer of each year. This package uses an inverse distance-weighted spatial weights matrix, so we used the *spdep* package (Bivand and Piras 2015) to compare the results to values of Moran's I calculated using binary and variance-stabilizing weighting methods. These results were very similar to values produced using the inverse distance-weighted matrix, so we did not report them here.

The negative binomial distribution (NBD) is commonly used to describe observations that are over-dispersed in space or time (Mangel 2006). If a discrete random variable N (for example, the number of krill swarms) follows the NBD, then

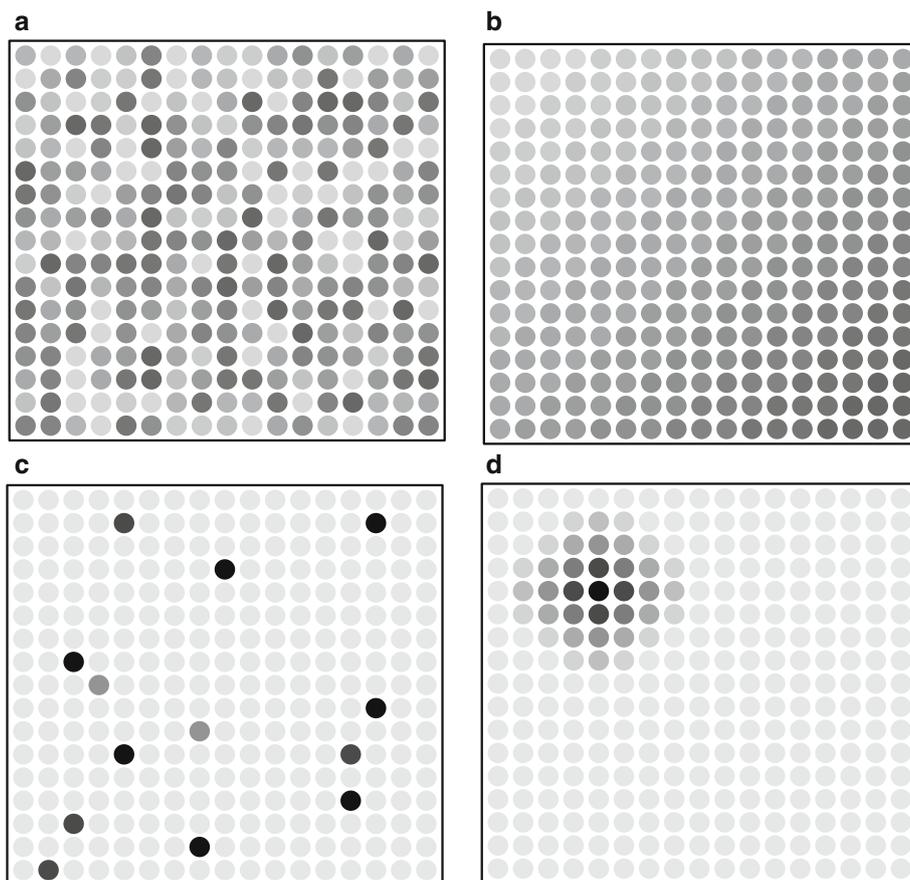
$$\Pr\{N = n\} = \frac{\Gamma(k + n)}{n!} \left(\frac{k}{k + m}\right)^k \left(\frac{m}{k + m}\right)^n \tag{3}$$

where m is the mean and k is the over-dispersion parameter (Mangel 2006). The NBD can also be thought of as a Poisson-gamma mixture; that is, the random variable follows a Poisson distribution where the Poisson parameter is drawn from a gamma distribution. The parameter k can be

Table 2 Annual and seasonal distance surveyed (nautical miles) in each habitat

Year	Midsummer			Late summer		
	Shelf slope	Off-shelf	On-shelf	Shelf slope	Off-shelf	On-shelf
1997	156	646	170	–	–	–
1998	185	820	238	166	786	152
1999	116	752	108	97	583	94
2000	–	–	–	120	663	173
2001	193	843	249	204	831	137
2002	203	719	284	189	522	241
2003	141	651	106	204	635	153
2004	217	719	212	228	745	192
2005	285	752	261	184	584	90
2006	200	622	180	–	–	–
2007	199	781	258	–	–	–
2008	218	838	370	148	333	155
2009	230	779	366	–	–	–
2010	55	244	81	113	172	92
2011	184	750	206	116	68	115

Fig. 2 Example spatial distributions of observations that are **a** random; **b** autocorrelated but not aggregated; **c** aggregated but not autocorrelated; and **d** both autocorrelated and aggregated



used as a measure of the degree of aggregation, with values below 1 describing observations that are highly aggregated (Mangel and Smith 1990; White and Bennets 1996;

Mangel 2006). As $k \rightarrow \infty$, the NBD converges to the Poisson distribution, and as $k \rightarrow 0$ it converges to a logarithmic series distribution. The variance is

$$\text{Var}[N] = m + \frac{m^2}{k} \quad (4)$$

so that the method of moments estimator for k is

$$\hat{k} = \frac{\bar{N}^2}{S^2 - \bar{N}} \quad (5)$$

where \bar{N} is the sample mean and S^2 is the sample variance. Using the mean and variance of krill biomass densities, we calculated \hat{k} for midsummer and/or late summer in each habitat in each year.

For mapping, we gridded the survey area into 1000-km² cells and calculated spatial mean and standard deviation of krill biomass density (g m⁻²) in each cell in each year, using the Raster package (Hijmans 2014). In years when surveys were done in both midsummer and late summer, we gridded the data for each survey separately. We also calculated mean krill biomass in each cell across years to examine overall trends and intra-seasonal variability.

SAM and ENSO indices

We examined several metrics of climate variability in the Southern Ocean to explore potential relationships between climate variability and krill abundance and distribution. The SAM describes the north–south movement of westerly winds around Antarctica, while the ENSO involves changes in temperature in the eastern and central Pacific, influencing winds and storm patterns around Antarctica. Both SAM and ENSO influence the extent and duration of sea ice around the Antarctic Peninsula, potentially impacting krill recruitment near the NAP (Loeb et al. 2009; Loeb and Santora 2015). We used two measures of ENSO: the Niño 3.4 Index, a measure of sea-surface temperature anomalies in the equatorial Pacific, and the Southern Oscillation Index (SOI), a measure of large-scale air pressure fluctuations that coincide with El Niño and La Niña events. We obtained SAM data from the British Antarctic Survey's Ice and Climate Division (<http://www.nerc-bas.ac.uk/icd/gjma/sam.html>). We obtained data on the El Niño 3.4 Index and SOI from the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>). For all analyses, we used 3-month rolling average values of climate variables in order to construct seasonal indices of climate conditions (Loeb and Santora 2015). We calculated correlations (Pearson) between krill time series (mean density, standard deviation of density, Moran's I , and \hat{k}) and climate indices lagged up to 36 months. We chose this range because krill are long-lived with a 6- to 7-year lifespan (Siegel 1987), and their reproduction is closely tied to ice extent, duration, and timing of retreat (Siegel and Loeb 1995; Quetin and Ross 2001). Thus, ice

conditions that promote preconditioning and enable early and multiple spawning events may show signatures in krill abundance and demography several years in the future.

Results

Inter-annual variability

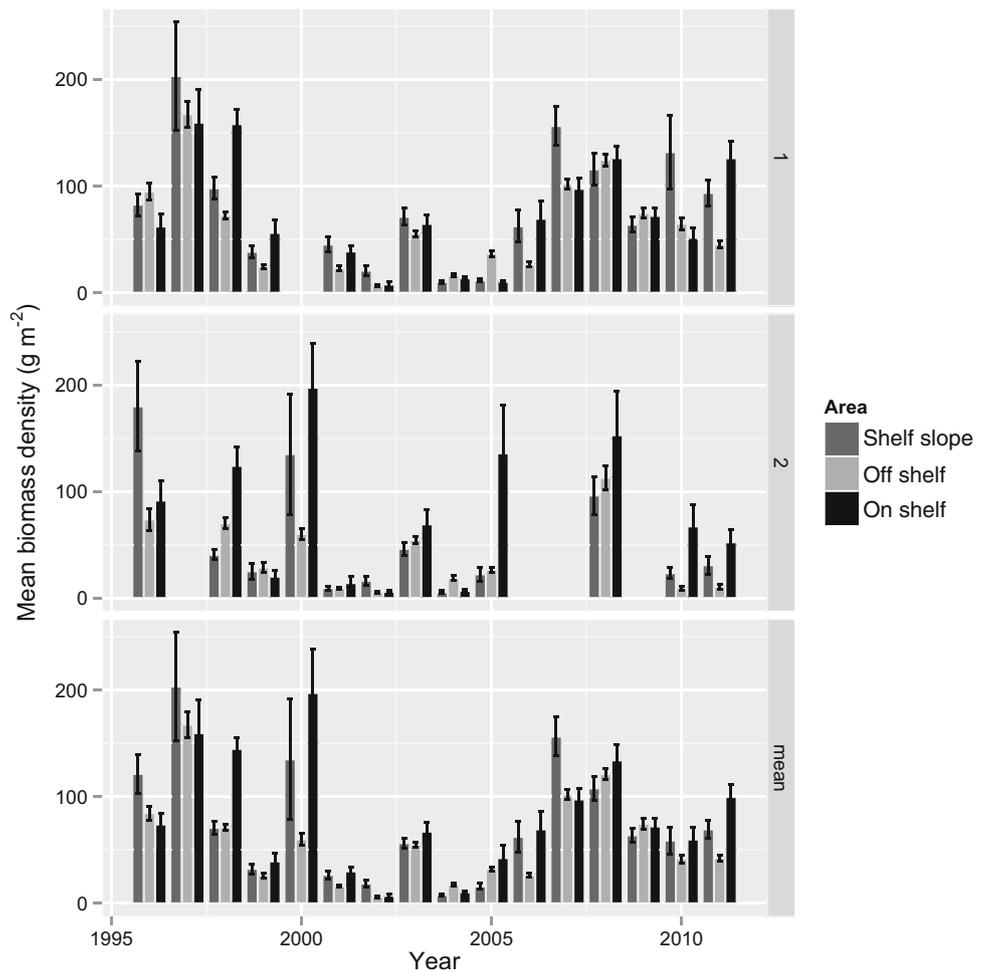
Mean krill density varied greatly during 1997–2011, from a high of 171.9 g m⁻² in 1997 to a low of 9.4 g m⁻² in 2002 (Fig. 3). Anomalies of krill abundance indicate relatively high overall krill abundance in years 1997, 1998, 2000, 2007, 2008, and 2009; lower abundance appeared in years 1999, 2001, 2002, 2004, 2005, and 2006 (Fig. 4). In some years, there was considerable variation across habitats and within the summer season. For example, in 2011, the on-shelf anomaly was 0.27 in midsummer, but –0.12 in late summer, and in 1997, the off-shelf anomaly was nearly three times that on-shelf.

Moran's I was consistently positive, indicating some spatial autocorrelation in acoustic observations, but showed considerable variation across time (Fig. 5). It ranged from essentially 0 (–0.0099) in 1999 to 0.50 in 2007, indicating that the degree of spatial aggregation varied by over an order of magnitude across years. However, Moran's I was generally less than 0.2, indicating modest to weak spatial autocorrelation in most years and habitats. The NBD dispersal parameter \hat{k} showed a similar degree of variation, ranging from 0.2 in 2002 to 0.65 in 2008 (Fig. 6). Values were always <1 (often <0.5) indicating a high degree of aggregation. Estimates of Moran's I and \hat{k} were uncorrelated, suggesting that these indices characterize patchiness in different ways and that the degree of spatial autocorrelation is not related to the degree of aggregation (Fig. 7).

Seasonal variability

Mean densities in midsummer and late summer across all years combined were significantly different (Welch two-sample t test, $t = 7.76$, $p < 0.001$), indicating that the overall abundance and/or detectability of krill tended to decrease as summer progressed. However, this pattern was not consistent across years. In Fig. 8, we show mean biomass in midsummer versus late summer, with values falling below the identity line indicating years with declining mean biomass across the season. In 9 of the 10 years in which the area was surveyed in both midsummer and late summer, mean krill density declined across surveys, but the decrease was significant in only 4 of these years (Table 3). In one year (2005), there was a significant increase in mean

Fig. 3 Mean krill (*Euphausia superba*) biomass in midsummer (*top*), late summer (*center*) and averaged across both legs (*bottom*). Vertical bars represent standard error



density across the season. On average, the greatest krill biomass was found north and west of Elephant Island, the southern part of the Bransfield Strait, and along the north side of the South Shetland Islands (Fig. 9). Average distributions of krill biomass appear to contract across the season, with larger areas with low biomass density values and a few areas with very high biomass density (Fig. 9).

Relationships between patchiness and abundance

We found significant positive linear relationships between Moran's I and mean biomass density in midsummer in the shelf slope habitat ($p = 0.013$, $R^2 = 0.39$, Fig. 10); however, there was no relationship in the on-shelf or off-shelf habitats in midsummer or in any habitat in late summer (regressions shown in Online Resource 1, Online Resource 2). In contrast, \hat{k} and density were positively correlated in the off-shelf habitat in both midsummer and late summer ($p = 0.028$, $R^2 = 0.29$ and $p = 0.007$, $R^2 = 0.57$, respectively; Fig. 10), but not in the on-shelf or shelf slope habitats (Online Resource 1, Online Resource 2).

Correlations with environmental indices

We found that some features of krill biomass were linked with measures of ENSO (Niño 3.4 anomaly and SOI) at approximately 2- to 2.5-year lags. In particular, we found that mean krill biomass was significantly ($p < 0.05$) negatively correlated with SOI lagged 27–28 and 30–33 months and that the standard deviation of krill biomass was negatively correlated with SOI lagged 23–33 months. Niño 3.4 was significantly positively correlated with the standard deviation of biomass at 22- to 33-month lags. We found a significant correlation between SAM and mean biomass at 25- to 26-month lags and standard deviation of biomass at a 26-month lag. There was no significant correlation between Moran's I or \hat{k} and Niño 3.4, SOI, or SAM. The large number of correlations tested raises the possibility of spurious correlations. However, the consistent direction and magnitude of correlations between krill abundance and ENSO indices (SOI and Niño 3.4) lagged approximately 2–2.5 years indicate that these relationships are unlikely to be the result of chance.

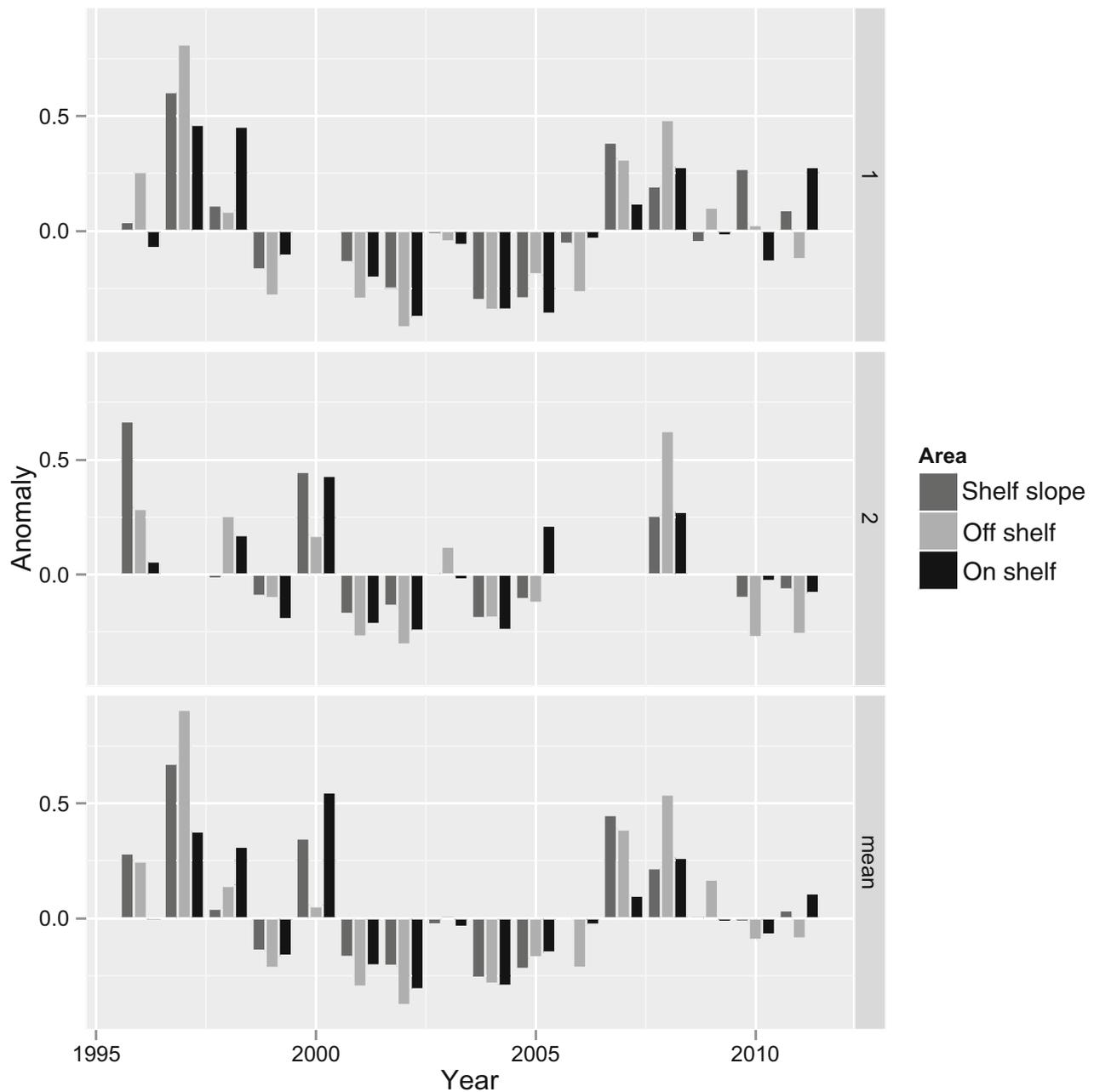


Fig. 4 Krill (*Euphausia superba*) anomaly in midsummer (*top*), late summer (*center*) and averaged across both legs (*bottom*)

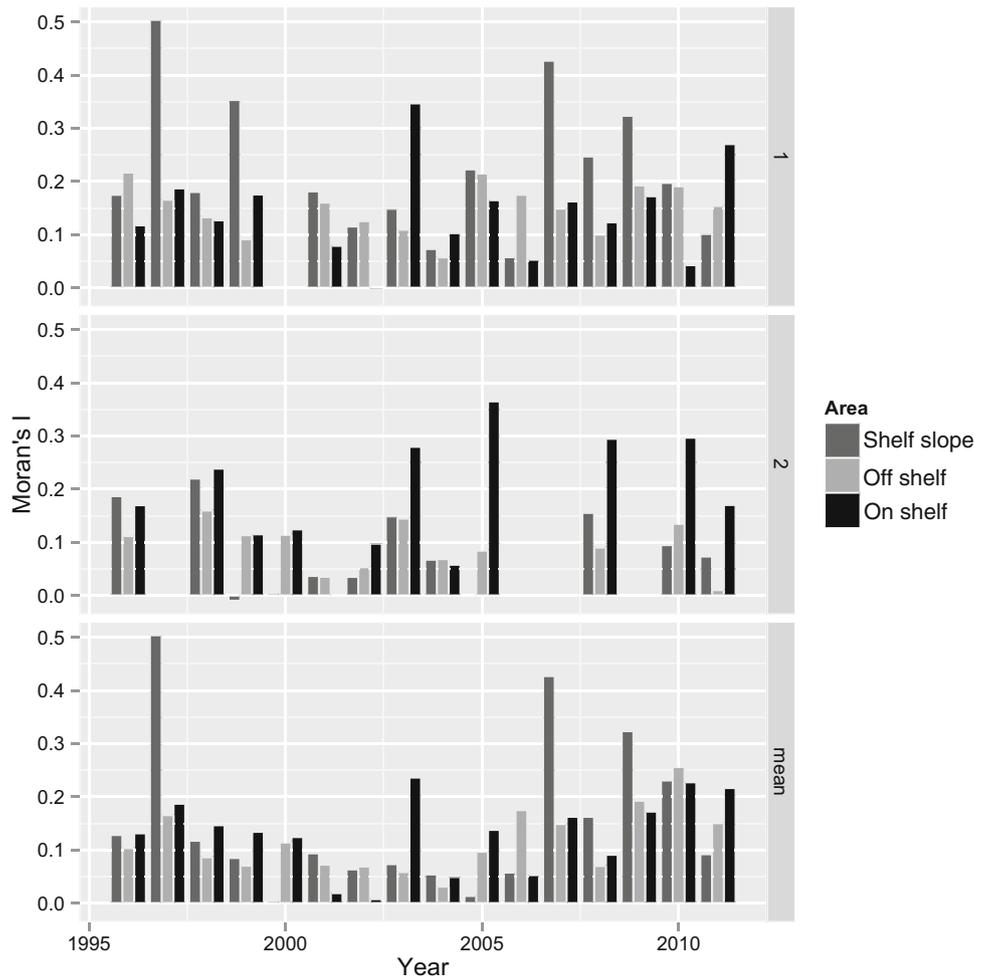
Discussion

Intra-annual variability

Krill distributions near the Antarctic Peninsula show marked changes across seasons, suggesting the possibility of differential habitat use across time (Lascara et al. 1999). In summer, krill in the West Antarctic Peninsula are abundant, found in dense aggregations, and located high in the water column, while in the autumn and winter

abundance and density decrease and krill move deeper in the water column (Lascara et al. 1999; Ashjian et al. 2004; Lawson et al. 2004). Although the surveys examined in this study cover a small portion of the year, the late summer data may capture the beginning of an autumnal change in habitat selection by krill (Santora et al. 2014). Krill biomass was on average lower in late summer than in midsummer, indicating either fewer krill in the area, fewer krill in the upper 250 m of the water column where they are detectable by acoustics, or both. Benthic foraging has been

Fig. 5 Moran's I in midsummer (*top*), late summer (*center*) and averaged across both legs (*bottom*)



observed in krill (Gutt and Siegel 1994; Schmidt et al. 2011), and there is evidence that adult krill may overwinter closer to the sea floor (Gutt and Siegel 1994; Lawson et al. 2004). Thus, the decrease in abundance in late summer may be due to krill utilizing deeper habitat out of reach of acoustics; or alternately leaving the study area entirely through advection, mortality, or migration. However, this decrease was not consistent across years, indicating that other factors are influencing intra-seasonal movement of krill in the study area. Krill spawn in the summer, with spawning aggregations concentrated in off-shelf and oceanic waters, and the particular environmental conditions of a particular year may influence when these aggregations form and disperse.

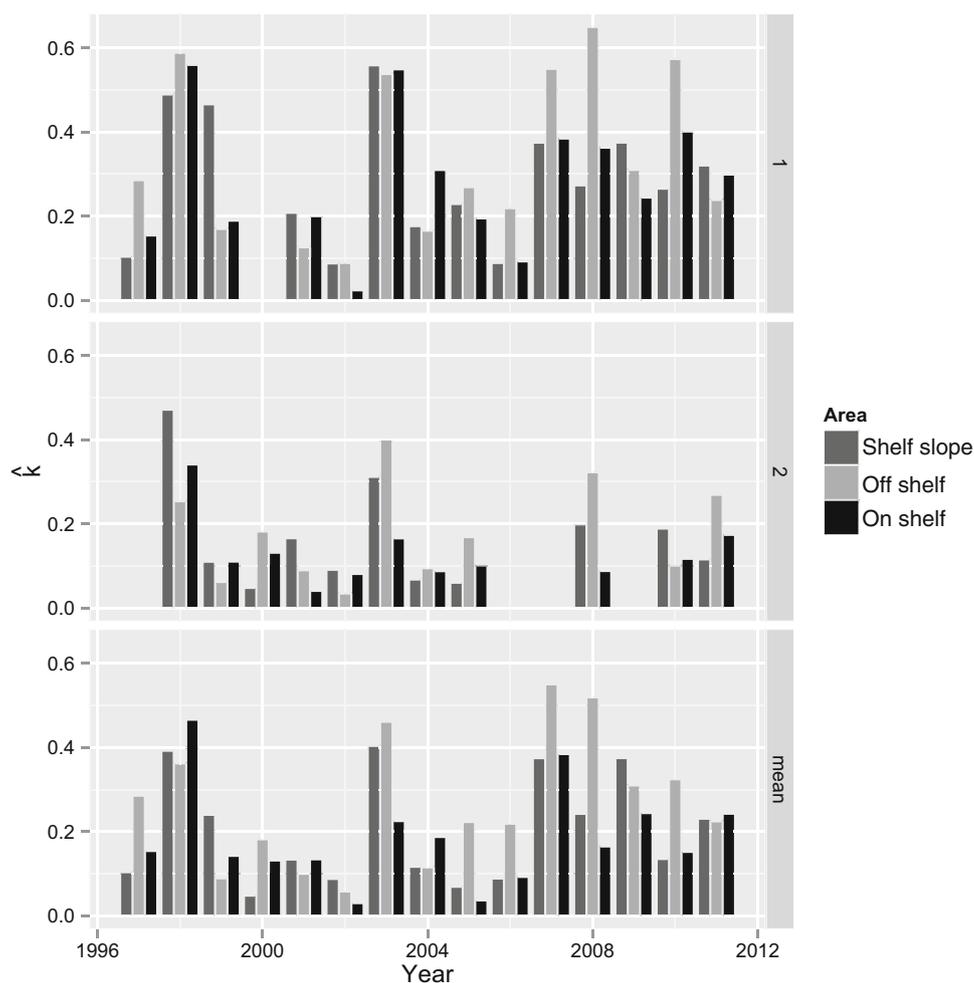
The relationship between spatial autocorrelation and mean density also varied across midsummer and late summer, with a significant positive correlation between global Moran's I and mean density in midsummer shelf slope habitat, but not late summer. However, the relationship between \hat{k} and biomass was consistent across midsummer and late summer in the off-shelf habitat.

This indicates that the relationship between some measures patchiness and biomass at the habitat scale may change across the summer season; however, this is only true for patchiness as measured by spatial autocorrelation (Moran's I).

Inter-annual variability

Our results show strong inter-annual variability in both krill biomass and patchiness, consistent with other studies in this area (Reiss et al. 2008; Santora et al. 2009). When only considering data from midsummer, the years with the largest mean anomaly occurred in 1997–1998, 2003, and 2007–2008, generally consistent with the 5- to 6-year cycles of krill populations in the West Antarctic Peninsula suggested by Quetin and Ross (2003) (note that the area was only surveyed in late summer in 2000). However, averaging over both midsummer and late summer surveys presents a less clear picture, with positive anomalies in 1997–1998, 2000, 2003, and 2007, 2008, and 2009. Though survey effort was not always consistent across

Fig. 6 Negative binomial distribution \hat{k} in midsummer (*top*), late summer (*center*) and averaged across both legs (*bottom*)



years or seasons, making comparisons difficult, it is possible that seasonal changes in habitat use (Lascara et al. 1999) may alter the abundance of krill measurable by these surveys across the midsummer to late summer season.

Spatial variability

Spatial organization (i.e., the degree of aggregation) of krill also varied across years. In years of higher krill biomass, there was a tendency toward greater spatial autocorrelation (higher Moran's I) and lower aggregation (higher negative binomial \hat{k}), but this relationship was not consistent across habitats or season. This indicates that under some conditions, krill biomass and patchiness are linked, with important consequences for krill-dependent predators. This may also have implications for net-based sampling programs, which may be biased by varying levels of aggregation, especially if they have limited spatial coverage. The apparent lack of a relationship between Moran's I and \hat{k} , and the difference between the patchiness–biomass

relationships calculated with these two statistics indicate that they describe spatial aggregation differently. This is unsurprising because Moran's I uses a spatial weights matrix to describe how observations near in space relate to each other relative to more distant observations. In contrast, \hat{k} is an estimator for the shape parameter of the NBD, which can arise when organisms are distributed over a landscape according to a Poisson distribution with a mean drawn from a gamma distribution (Anscombe 1950). In other words, Moran's I describes the form of krill distributions across the landscape, while the negative binomial \hat{k} describes the intensity of their aggregation. Thus, the NBD offers a convenient model for the distribution of krill aggregations across space and the probability a foraging predator might encounter a patch with a given density of krill. Predator foraging success depends on both abundance and distribution of krill (Mangel and Switzer 1998), and in years with low krill abundance, more aggregated krill may alter foraging costs, compounding the consequences of low krill years for predators. Estimates of \hat{k} could be used to

Fig. 7 Relationship between the negative binomial distribution \hat{k} and Moran's I across all habitats, seasons, and years

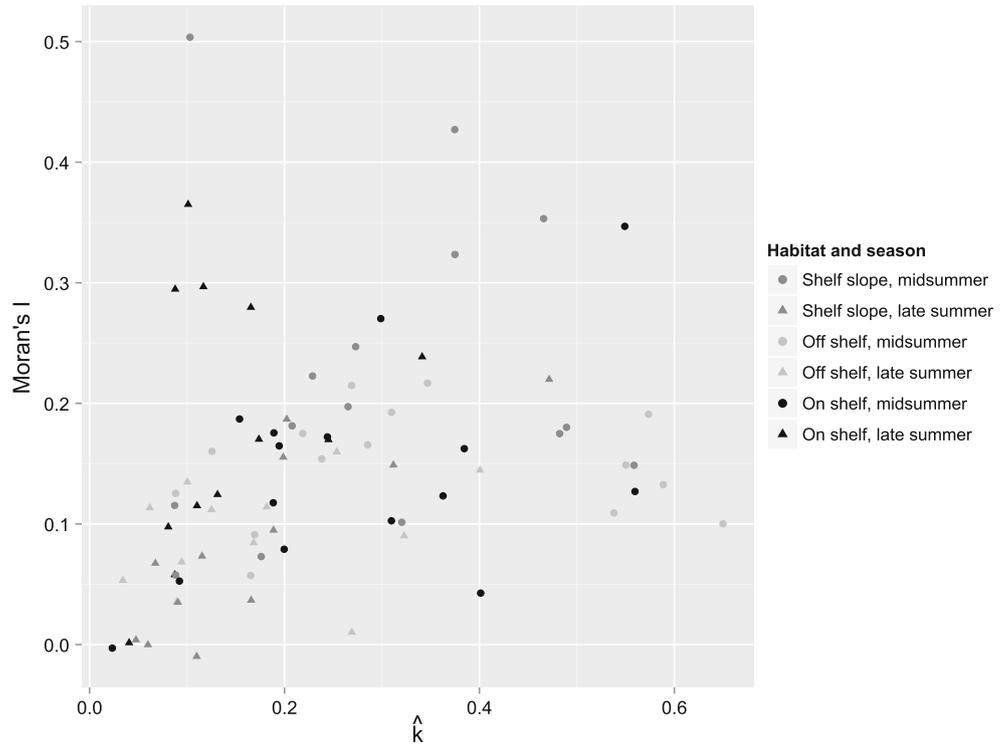
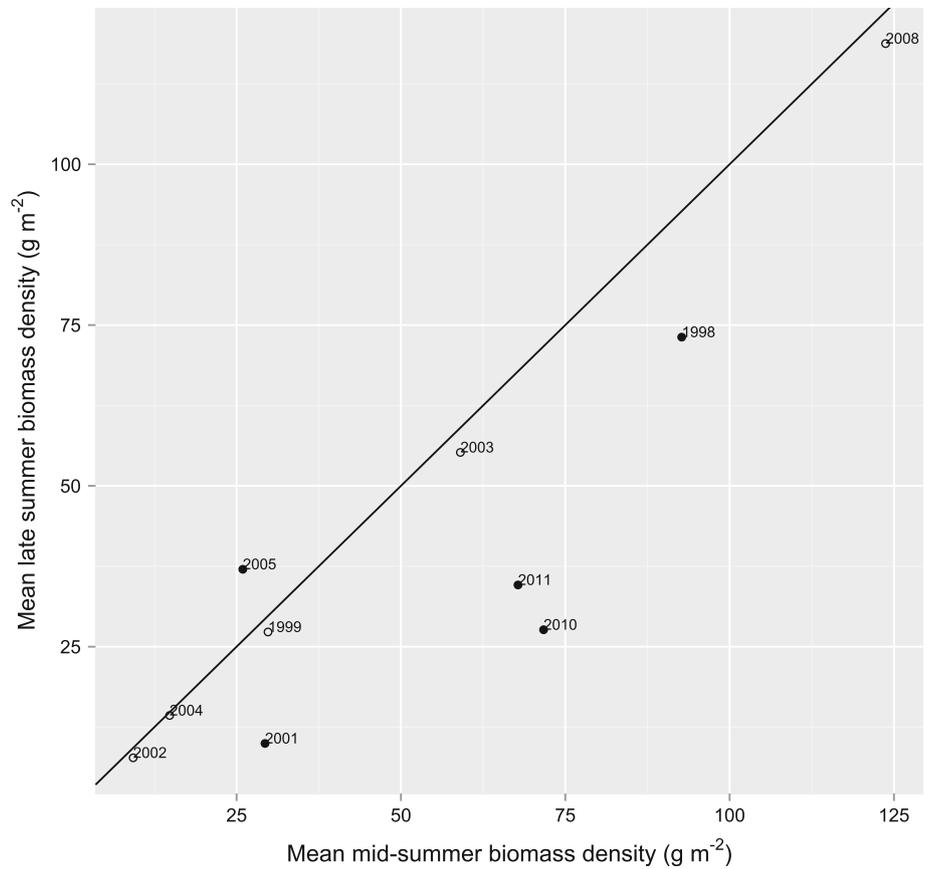


Fig. 8 Mean krill (*Euphausia superba*) biomass in midsummer and late summer, with observations falling below the identity line indicating years with lower mean density later in the summer. Filled circles represent statistically significant differences across a season (Welch two-sample t test, $p < 0.05$)



inform models of predator foraging under differing krill conditions. For example, one could generate a number of krill preyscapes representing the range of conditions (from low abundance higher aggregation to high abundance lower aggregation) and explore foraging behavior and consequences for predators (e.g., Cresswell et al. 2008). This has the advantage of incorporating the effects of both krill abundance and spatial distribution on predator performance.

It should also be noted that indices of spatial autocorrelation and aggregation used here are dependent on the scale upon which the data are collected. Krill are

distributed at multiple scales, from swarms that may span tens or hundreds of meters, to patches and larger concentrations that may span hundreds of kilometers (Murphy et al. 1988). Our measurements are taken on the scale of 1 nautical mile, capturing relatively fine-scale spatial patterns on the magnitude of patches; however, they are unlikely to capture smaller swarm-level dynamics.

Climate variability

Environmental forcing is theorized to affect krill abundance by influencing winter sea ice (Wiedenmann et al. 2009). Negative phases of the SOI (which may be amplified by increasing SAM) are associated with an earlier advance and longer duration of sea ice, which results in greater primary production and better larval krill survival (Quetin et al. 2007). In the West Antarctic Peninsula, strong recruitment events observed in 1991–1992, 1995–1997, and 2000–2003, 2006–2007, and 2010–2011 were linked to positive chlorophyll *a* anomalies the previous year, which in turn were linked to a negative SAM phase the preceding spring (Ducklow et al. 2013; Saba et al. 2014). These peaks at least roughly correspond to the pattern of positive krill anomalies observed in the data, with peaks in 1997–1998, 2000, 2003, and 2007–2008–2009. However, we found that SOI appears to have a more extensive influence on krill than SAM. In the north Antarctic Peninsula, Loeb et al. (2009) found a significant relationship between 1-year lagged El Niño 3.4 anomaly and krill abundance taken from net hauls. In contrast, we found suggestion of links between mean krill and standard

Table 3 Mean biomass density (g m^{-2}) of krill in midsummer and late summer for years with two surveys

Year	Midsummer	Late summer	Percent change
1998	92.7	73.1	-21.1 (<0.001)
1999	29.8	27.3	-8.4 (0.57)
2001	29.3	10.0	-66.0 (<0.001)
2002	9.3	7.7	-16.7 (0.35)
2003	59.0	55.2	-6.5 (0.37)
2004	14.8	14.3	-3.4 (0.78)
2005	25.9	37.0	42.7 (0.048)
2008	123.7	118.8	-4.0 (0.71)
2010	71.7	27.6	-61.5 (<0.001)
2011	67.8	34.6	-49.0 (<0.001)

Years with similar spatial coverage are highlighted in italic; bolditalic values indicate significant changes assessed by Welch two-sample *t* test

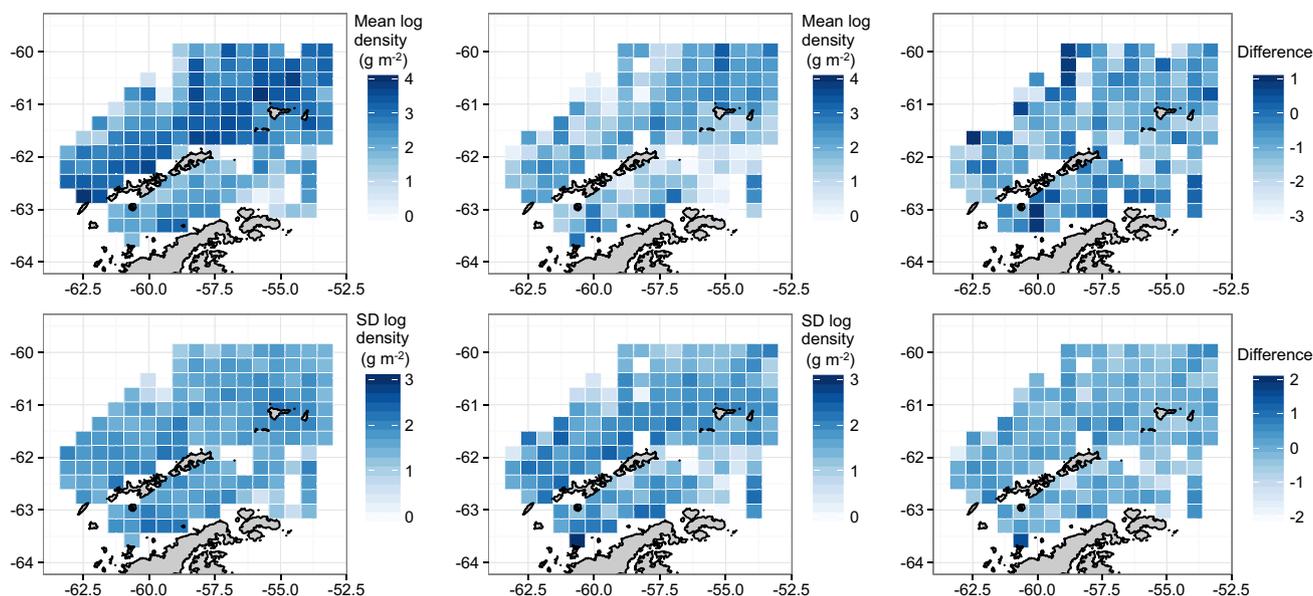


Fig. 9 Mean and standard deviation of log krill (*Euphausia superba*) density, averaged over available years 1997–2011 in midsummer (left) and late summer (center). The difference between midsummer and late summer is shown on the right

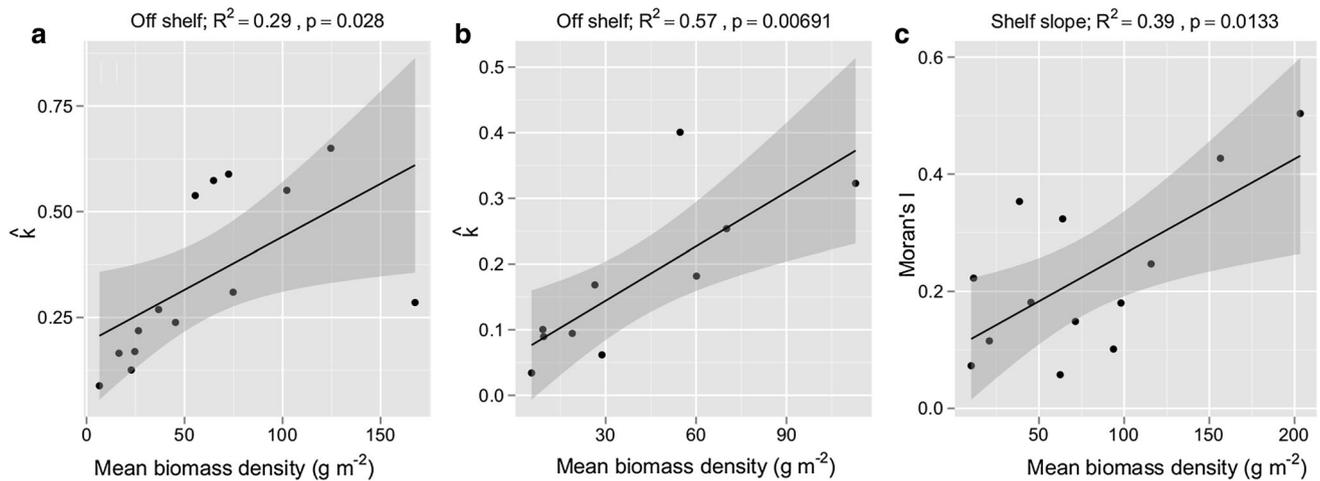


Fig. 10 Relationships between mean biomass and **a** \hat{k} in the off-shelf habitat in midsummer, **b** \hat{k} in the off-shelf habitat in late summer; and **c** Moran's I in the shelf slope habitat in midsummer

deviation of krill abundance and ENSO indices lagged approximately 2–2.5 years. This is the first study to our knowledge to link acoustic indices of krill in the NAP and large-scale environmental forcing, indicating that data from predator stomach samples (Saba et al. 2014), nets (Loeb et al. 2009; Loeb and Santora 2015) and acoustics (this study) may provide different information about climate and krill. For example, large numbers of krill in net samples may indicate strong recruitment the previous spring, while high biomass in acoustic surveys may indicate strong recruitment 2 years in the past, as biomass has increased through growth. In addition, the links between climate fluctuations and krill vary across the Southern Ocean, with SAM dominating further south off the peninsula (Saba et al. 2014) and no apparent direct effect of SAM or ENSO on acoustic measures of krill at South Georgia (Fielding et al. 2014), though this area is thought to be linked to the Antarctic Peninsula by transport across the Scotia Sea and predator performance at South Georgia has been linked to ENSO (e.g., Forcada et al. 2005).

Conclusions

Both the abundance and spatial organization of krill are important to krill-dependent predators (Santora et al. 2009, 2012). Krill are patchily distributed at multiple scales (Murphy et al. 1988; Siegel 2005), and krill recruitment, abundance, and population structure vary across years (Quetin and Ross 2003). Understanding the processes underlying krill variability across space and time is crucial to our conception and management of the Southern Ocean ecosystem. This unique long-term data set provides a

window into some of the patterns underlying krill variability in an ecologically and commercially important area of the Southern Ocean. Knowledge of the complex interactions between environmental conditions (both local-scale and broad-scale) and krill abundance and distribution highlighted by this study will be important in our understanding and management of the NAP. For example, while krill catch limits in this area are set to be allocated among small-scale management units in order to facilitate ecosystem-based management, the proposed allocations do not account for climate-driven variations in abundance and distribution. Knowledge of the drivers of these fluctuations could benefit management actions that account for the interactions between climate, fishing, krill, and predators. Future work should further explore the forces that underlie inter-annual changes in krill abundance and distribution and this area and relationships with dynamics both further south along the Antarctic Peninsula as well as across the Scotia Sea (Brierley et al. 1999). For example, more local-scale fluctuations in oceanographic conditions such as the location of the southern boundary of the Antarctic Circumpolar current and eddy kinetic energy may affect krill distributions (Tynan 1998; Santora et al. 2012). In addition, much work remains in quantifying and explaining seasonal changes in krill abundance and distribution, and potential connections to behavior, species interactions, and advection. Finally, the consequences of variation in krill abundance and spatial organization for predator performance are not fully understood. Future modeling studies can use the NB \hat{k} to generate krill preyscapes to explore drivers of aggregations of krill and their predators, thus enhancing our knowledge of how climate variability may affect higher trophic levels through changes in krill abundance and aggregation.

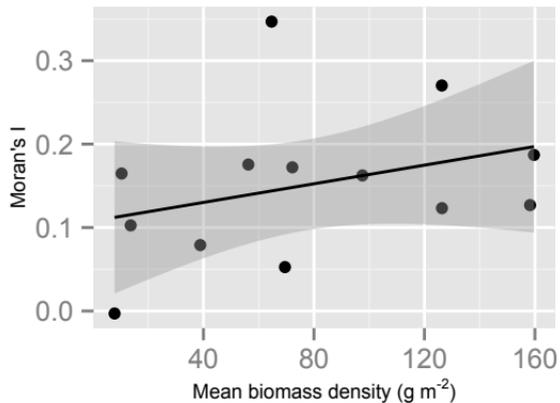
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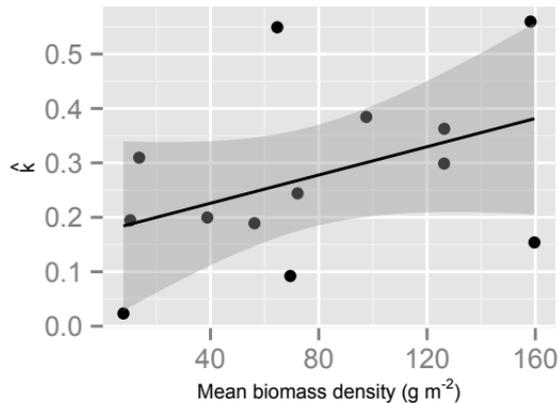
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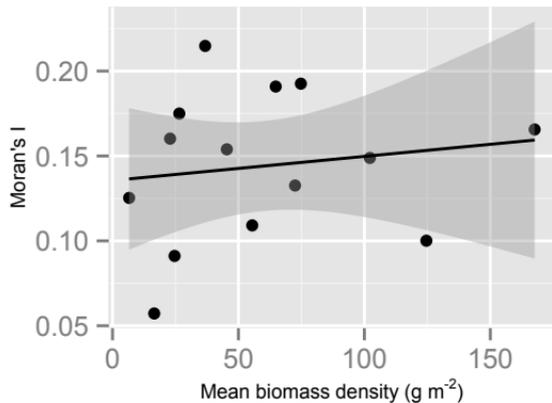
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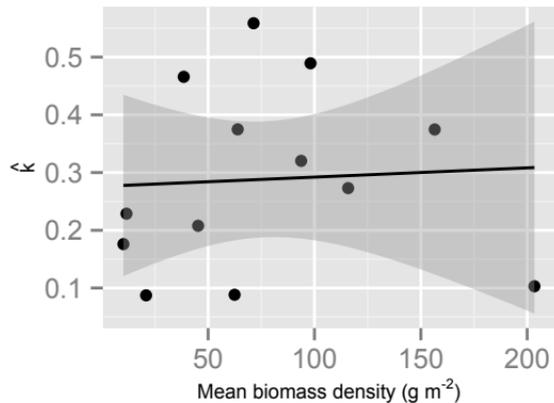
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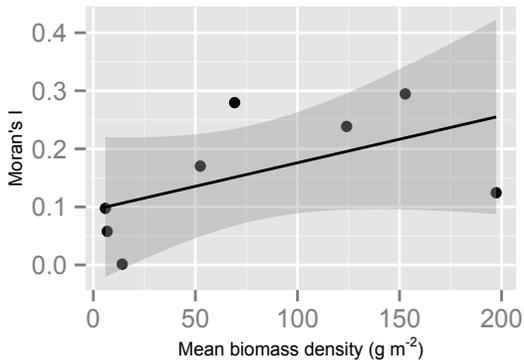
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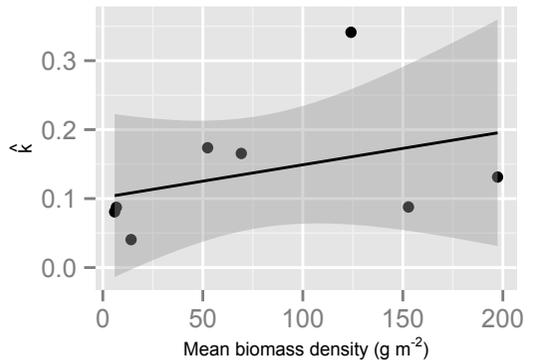
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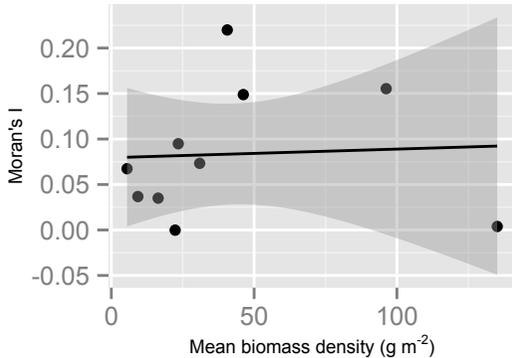
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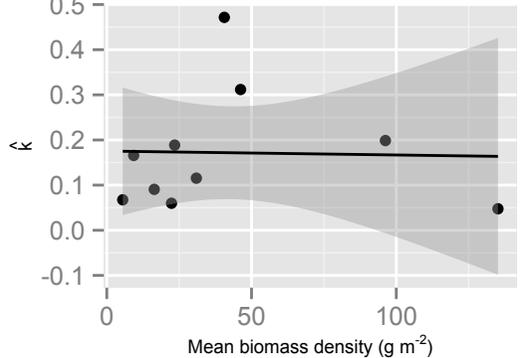
On shelf; $R^2 = -0.0073$, $p = 0.367$



Shelf slope; $R^2 = -0.12$, $p = 0.88$



Shelf slope; $R^2 = -0.12$, $p = 0.941$



Off shelf; $R^2 = 0.072$, $p = 0.229$

