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Winter preconditioning determines feeding ecology of *Euphausia superba* in the Antarctic Peninsula

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ABSTRACT: We examined the feeding ecology and lipid composition of Antarctic krill *Euphausia superba* around the northern Antarctic Peninsula from 2001 to 2012. We used lipid biomarkers to quantify feeding patterns and relate the variability in biomarkers to environmental conditions that structure the phytoplankton community. Fatty acid profiles varied among years, with some years dominated by lipids indicative of herbivory, while other years were indicative of greater omnivory. Principal component analysis of 60 fatty acids showed that 3 principal components (PCs) explained approximately 50% of the variability in fatty acid profiles. The first PC separated the fatty acid indicators along a herbivory–omnivory–carnivory gradient. Correlations between the gradient of herbivory and carnivory, as summarized by the first PC, were found with both winter sea ice extent ($r = 0.55$, $p < 0.01$) and with ENSO conditions the previous winter ($r = 0.88$, $p < 0.001$). These findings suggest that climatic conditions during the late winter precondition the pelagic ecosystem around the Antarctic Peninsula, impacting the trophic ecology of Antarctic krill the following summer.

KEY WORDS: Antarctic krill · Lipid biomarker · El Niño · Feeding ecology · Southern Ocean · Euphausiids

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INTRODUCTION

The feeding ecology of Antarctic krill *Euphausia superba* (hereafter krill) has been studied for many years because krill are the principal link between primary productivity and upper trophic levels in many parts of the Southern Ocean (Atkinson et al. 2009). Initial hypotheses suggested that krill fed mostly on diatoms and other phytoplankton to fuel growth and reproduction (Marr 1962). More recent hypotheses, however, propose a flexible feeding strategy that includes phytoplankton (Clarke 1980, 1984), in particular diatoms (Haberman et al. 2003), meso- and micro-zooplankton (Perissinotto et al. 1997), and detritus (Schmidt et al. 2011). It has also been demonstrated, using lipid fatty acid (FA) signatures, that krill feeding ecology is demographically and seasonally variable (Hagen et al. 1996, 2001).

Natural variability in FA profiles of krill can be used to examine their spatial variability in diets and determine relative levels of herbivory, omnivory, and carnivory (Pond et al. 1995, Mayzaud et al. 1998). Ratios of 20:5*n*-3/22:6*n*-3 (docosahexaenoic acid [DHA]/eicosapentaenoic acid [EPA]) have been related to levels of herbivory, and field studies have inferred that high ratios (>2) are indicative of diets rich in diatoms, while lower ratios (<1.5) are indicative of diets rich in flagellates (Stübing et al. 2003). Increased 18:1*n*-9/18:1*n*-7 and decreased saturated fatty acids (SFA)/polyunsaturated fatty acids (PUFA) ratios have been used to infer a relatively more carnivorous diet (Stübing & Hagen 2003). In field studies where diets were enhanced to increase consumption of heterotrophic prey, decreased SFA/PUFA ratios have been observed in both larval (Stübing et al. 2003) and post-larval krill (Cripps & Atkinson 2000).

Similarly, when diets of krill were artificially enhanced in laboratory feeding studies, FA profiles changed to reflect the dominant prey item consumed (Alonzo et al. 2003, Stübing et al. 2003). For example,

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Alonzo et al. (2003) showed that FA signatures of krill fed diatom- or dinoflagellate-enriched diets showed increased percentages of 20:5*n*-3, (EPA) and 22:6*n*-3 (DHA), respectively, and that krill fed cryptophytes had higher percentages of 18:1*n*-9. These general shifts in FA signatures show that relative levels of herbivory, omnivory, and carnivory can be spatially or temporally resolved and suggest that changes in diet can be detected, opening the possibility of relating variability in diet to interannual and long-term changes in environmental conditions.

Near the northern Antarctic Peninsula region, the magnitude and the timing of the spring bloom, which are functions of the extent and duration of sea ice the previous winter, have changed over the last 30 yr (Stammerjohn et al. 2008a,b). Sea-ice extent (SIE) and duration of ice cover have declined, driven by large-scale atmospheric teleconnections, including the El Niño-Southern Oscillation (ENSO) events (Stammerjohn et al. 2008b, Loeb et al. 2009) and the increasingly positive magnitude of the Southern Annular Mode (SAM) (Meredith et al. 2004). These climate modes have modified prevailing wind direction and intensity, resulting in increases in air and water temperature over the last 50 yr and driving the changes in sea ice. During ENSO, the water column during summer is colder and the mixed layer is deeper, negatively impacting overall primary production (Reiss et al. 2009). At other times (i.e. La Niña), summer water column temperatures are higher, the mixed layer shoals, and chlorophyll *a* (chl *a*) biomass is higher. This relationship between stratification and chl *a* biomass is also reflected in the size and structure of the phytoplankton community. During warm, more highly stratified periods, the phytoplankton community shifts toward smaller species such as cryptophytes and dinoflagellates, and away from larger diatoms (Moline et al. 2004, Montes-Hugo et al. 2008, 2009). Kozlowski et al. (2011) examined phytoplankton community structure over a 20 yr period using pigment biomarkers and showed that it varies in response to broad-scale atmospheric forcing, driven by the ENSO and SAM in the Antarctic Peninsula area.

The influence of seasonal physical forcing on the magnitude and timing of primary production and on phytoplankton community structure suggests that it could also influence the feeding ecology and nutritional condition of krill. In this study, we use FA profiles from krill collected near the northern Antarctic Peninsula over a 12 yr period to quantify feeding patterns of krill and relate the interannual variability in FA biomarkers to environmental conditions (ENSO, SAM, and SIE) that structure the phytoplankton community. We use principal component analysis (PCA) to examine patterns of FA signatures of krill among years. We then examine how interannual variability in principal component (PC) scores are correlated with climate indices previously shown to impact primary productivity (Reiss et al. 2009) and phytoplankton community structure (Kozlowski et al. 2011). The results are discussed with respect to krill productivity in response to climate variability.

MATERIALS AND METHODS

The US Antarctic Marine Living Resources Program (AMLR) Program conducts oceanographic surveys across approximately 125 000 km^2 of the waters around the South Shetland Islands as part of a long-term ecosystem monitoring study (Van Cise 2010). Surveys are conducted twice each austral summer in January and February. Samples in the present study were obtained from the surveys conducted in 2001, 2004, 2005, and 2008–2011 (Fig. 1). We also included data from 1 survey conducted in August of 2012 in order to contrast summer conditions with winter conditions.

Krill sampling and length measurement

Krill were sampled using a 1.8 m Isaacs-Kidd midwater trawl (IKMT) fitted with a 505 µm mesh net that was towed in a double oblique manner from the surface to 170 m or to within 10 m of the bottom where it was shallow. The volume of water filtered by the IKMT was estimated using a calibrated flow meter (Model 2030R, General Oceanics) mounted on the frame in front of the net. A pressure sensor provided real-time depth data for each tow. Tow speeds were approximately 2 knots and the average filtered volume was approximately 3850 m^3. The abundance of krill was standardized to ind. m^{-2}.

Immediately after retrieval of the IKMT trawl, post-larval krill were removed from samples and enumerated. As part of a larger demographic study, a subsample of up to 100 post-larval krill were measured for total length (TL, mm), sexed (male, female or juvenile), and staged for maturity. Krill reproductive maturity stage was determined using the classification scheme of Makarov & Denys (1981). TL was estimated by measuring the distance from the tip of the rostrum to the posterior tip of the uropods (Standard 1 as described by Mauchline 1980).

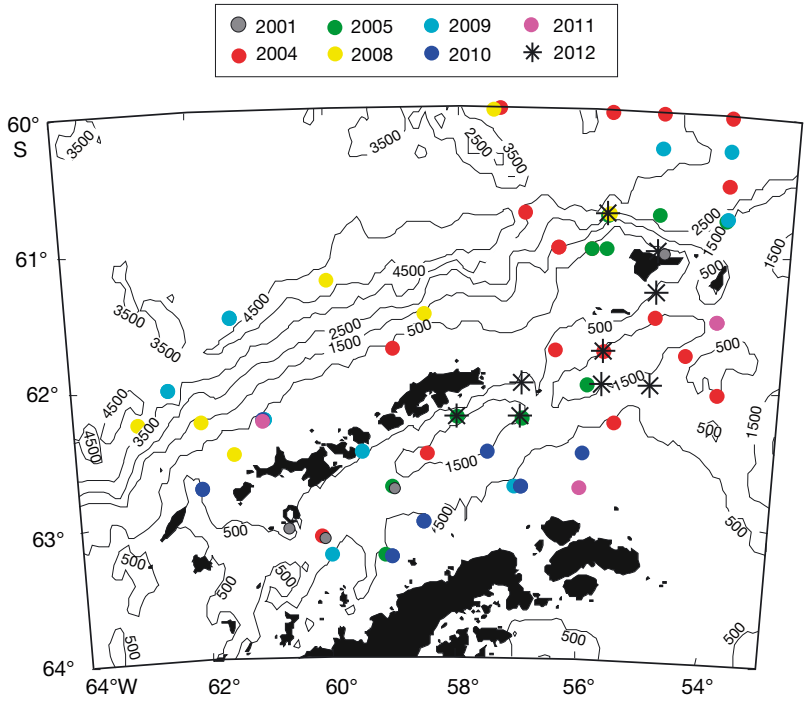

Fig. 1. The South Shetland Islands and sampling locations where Antarctic krill were collected for lipid analysis between 2001 and 2012

Fatty acid samples

From 2001 to 2008, post-larval krill >35mm TL (adults defined by sexual characteristics) were subsampled from the animals measured as part of the demographic study and were pooled without regard to sex or maturity and frozen for FA analysis. Beginning in 2009, krill used for FA analysis were measured for length, sexed, and pooled with individuals of the same sex and length from the same station to achieve the required sample mass for lipid extraction. Krill less than ~35 mm TL, and lacking diagnostic features, were classified as juveniles (Makarov & Denys 1981). Samples were placed in plastic bags and stored at −20°C (a −80°C freezer was not available.) Samples were analyzed as soon as possible after each cruise, and generally within 2 to 3 mo of collection to minimize the potential for FA oxidation. Some studies have found that such short-term storage has little effect on the major FA structure of lipids (Katan et al. 2003, Lind et al. 2012). Others have found that phospholipids degraded more than triglycerides, suggesting that much of the lipid structure used to analyze diets is adequately preserved (Kolakowska 1991).

FAs were analyzed from triacylglycerols (TAG), since TAG is the major lipid store in krill. TAG from 1.5 g aliquots of homogenized individuals were extracted according to Folch et al. (1957) and Budge et al. (2006). TAG was extracted using a 2:1 chloroform/methanol solution with 0.01% butylated hydroxytoluene (BHT). The TAG fraction in chloroform was dried using anhydrous sodium sulfate, and the chloroform solvent was evaporated under nitrogen (N-EVAP, Organomation). TAG was weighed to the nearest 0.001 g to determine percent TAG in each sample. For comparative purposes, percent wet mass values were then converted to percent dry mass using the conversion factor: dry mass = 0.216 × wet mass (Ikeda & Mitchell 1982, Hofmann & Lascara 2000).

Extracted TAG was then transesterified to form fatty acid methyl esters (FAME) according to Hilditch & Williams (1964). TAG was transesterified using a sulfuric acid catalyst, and FAME was then extracted in hexane, dried over anhydrous sodium sulfate, and the hexane solvent was evaporated under nitrogen. Hexane was added back to a concentration of 50 mg FAME ml^{-1} for gas chromatography analysis. FAME samples were analyzed on a Clarus 500 capillary gas chromatograph (Perkin-Elmer) with a flame ionization detector (GC-FID) using a fused silica column coated with 50% cyanopropyl methyl-polysiloxane (30 m length, 0.25 mm internal diameter, 0.25 µm film thickness; DB-23, Agilent Technologies), and using the oven program described in Budge et al. (2006). FAs were identified by comparing sample peaks to standard peaks, and area percents of peaks were determined using Total Chrom software (v.6.2.3, Perkin Elmer).

Environmental indices

To evaluate how broad-scale environmental conditions influenced feeding ecology and FA signatures of krill, we chose 2 climate-based indices of winter environmental forcing and a measure of the winter SIE from satellite observations for comparison with summer feeding ecology of krill. The 2 climate

indices, the Bivariate ENSO index (BEST; Smith & Sardeshmukh 2000) and the SAM index (Marshall 2003), represent different spatio-temporal scales of climate forcing. The first is an index of ENSO, a global weather pattern with approximately 3 to 5 yr periodicities. ENSO has been shown to influence sea ice dynamics (Stammerjohn et al. 2008a), and has been correlated with summer phytoplankton biomass (Reiss et al. 2009) and recruitment dynamics of krill (Loeb et al. 2009). We also used a winter SAM index of climate forcing that is the primary extratropical climate mode in the Southern Hemisphere and has also been shown to influence the ocean and ecosystem dynamics of the Antarctic Peninsula region (Marshall et al. 2006). Monthly data from both indices were averaged for the austral winter period (June, July, and August). Additionally, we extracted monthly sea ice concentration data from the Special Sensor Microwave/Imager (SSM/I) data at the National Snow and Ice Data Center (www.nsidc.org) and generated a time series of winter SIE (km^2 of the 15% concentration) for the same winter months and years around the Antarctic Peninsula region (59 to 70° S; 50 to 70° W) to more directly measure the environmental conditions during winter prior to spring and summer bloom conditions. Because these indices are hypothesized to reflect environmental control of productivity, water-column structure and plankton community dynamics (Loeb et al. 1997), we used them to correlate with FA profiles as indicators of the feeding ecology of krill the following summer (e.g. winter 2000 climate index correlated with summer 2001 FA profile).

Statistical analysis

A potential impediment to attributing interannual differences in FA signatures or percent lipid to changes in the environment is that both can vary with sex and length of krill (e.g. Clarke 1980, Pond et al. 1995). If the variability in FA signatures is related more to the size or sex of krill in samples collected in a year than to environmental variability in feeding conditions, it would not be possible to resolve any relationships between climate forcing and changing FA signatures. Because of the random sampling scheme, not all sexes were sampled sufficiently in each year for balanced analyses, so we restricted some analyses to interannual comparisons in relation to length. We examined variability in FA signatures for years with length data using a 1-way ANCOVA with length as a covariate to examine sources of variability. We tested for a significant length effect and then examined interannual patterns using Tukey-Kramer multiple comparisons procedures.

To examine the temporal patterns in FA signatures of krill, we combined all data across stations and years in a PCA to determine if there were any common patterns in variability. A total of 60 FAs were identified and included in the PCA. We examined the first 3 PCs in relation to published FA signatures and FA ratios that have been used to infer herbivory, omnivory, or carnivory. We focused on relationships among several individual FAs: 16:0, 20:5*n*-3, 18:4*n*-3, 18:1*n*-9, 18:1*n*-7, 22:6*n*-3, 16:1*n*-7 and 16:4*n*-1. These FAs have previously been shown to reflect the relative consumption of diatoms and flagellates and to infer the degree of herbivory (Alonzo et al. 2003). We used the 18:4*n*-3 and 22:6*n*-3 isomers to indicate consumption of flagellates (Cripps et al. 1999), while we used 20:5*n*-3, 16:1*n*-7, and 16:4*n*-1 as diatom indicators (Pond et al. 2005). We used the FA ratios 16:1*n*-7/18:4*n*-3, EPA (20:5*n*-3)/DHA (22:6*n*-3), and SFA (16:0 and 14:0)/PUFA (20:5*n*-3 and 22:6*n*-3) to examine relative levels of herbivory (reviewed in Stübing & Hagen 2003) in krill and used the ratio 18:1*n*-9/18:1*n*-7 to infer relative levels of carnivory. These measures are imperfect and can be highly correlated with krill total lipid (percent of dry mass), length, and sex (Stübing & Hagen 2003). Where the data existed (2009 to present), we tested for any relationship between these FA signatures and length before comparing these measures of feeding ecology with climate indices. We compared interannual differences in PC scores and FA ratios using 1-way ANOVA to test whether the FA signatures varied between and among years, and correlated the first 3 PCs with the above biomarkers to examine how the variability in FAs was related to these measures of dietary preference. Strong loadings (positive or negative correlations) between FAs and PCs indicated the underlying relationships generating the PCs. We compared the PCs with climate indices to examine any potential relationships between the winter environment and the feeding ecology of krill the following summer.

RESULTS

Lipids and fatty acids

Krill lipid dry mass varied among individuals and years, and ranged from 3 to 39.7% over the course of the study (Fig. 2). The highest average lipid dry mass (20.6%) was found in 2010 and the lowest

(9.7%) was found in 2009 (Table 1, Fig. 2). Annual differences in lipid dry mass were significant (ANCOVA: $F_{4,73}$ = 15.08, p < 0.0001); however, length was not a significant covariate ($F_{1,4}$ = 0.17, p = 0.682). When length was not considered as a covariate, annual differences in lipid dry mass were still significant ($F_{7,112}$ = 9.3, p < 0.0001) (Fig. 2). Tukey-Kramer multiple comparisons showed that lipid content was lowest in summer 2009 and highest in winter 2012 (Fig. 2). Lipid dry mass percentages in 2004 and 2009 were significantly lower than in 2005, 2010, and winter 2012. Lipid dry mass in winter 2012 was significantly higher than summer values for all years except 2005, 2008, and 2010.

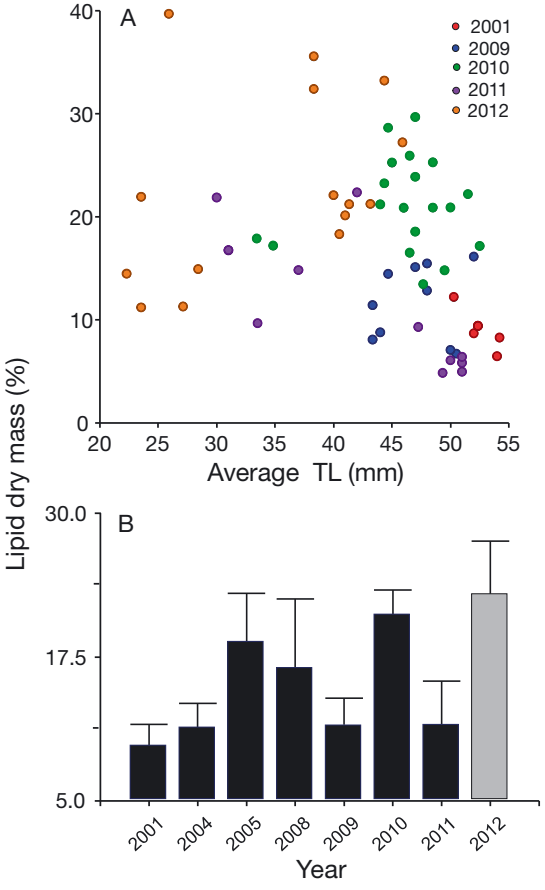

Fig. 2. (A) Relationship between length and lipid dry mass of Antarctic krill *Euphausia superba* color-coded by year of sample. (B) Lipid dry mass (mean +1 SE) by year of study. The bar for winter 2012 is shaded in gray; samples were collected in the austral summer in all other years

Ten FAs were dominant over the course of the study, comprising on average 88.9% of the 60 FAs resolved in the lipid extraction (Table 2). Three FAs (16:0, 20:5*n*-3, and 22:6*n*-3) each accounted for >15% of the FAs in krill during the study period. Three others (18:1*n*-9, 14:0, and 18:1*n*-7) contributed between 6.9 and 9.0% of the total, and 5 others (18:4*n*-3, 16:1*n*-7, 18:2*n*-6, 18:3*n*-3, and 18:0) made up between 1 and 5%. Each of the remaining FAs all made up <1% on average over the study.

Principal component analysis

The first 3 PCs of the PCA explained 54% of the variability in the krill FA profiles over the study period. PC1 explained 25% of the variability, while PC2 and PC3 explained 15.7 and 11.4%, respectively. Factor loadings (Pearson's correlations of the individual FA with the PC score) of the FAs showed that, of the 60 FAs, about half were significantly correlated with PC1 (Table 3). The most highly positively correlated (r > 0.75) FAs included 22:6*n*-3 (DHA), 20:4*n*-6, and 20:2*n*-6, the last 2 of which when combined summed to <1% of the total FAs over the study period. Other FAs that were positively correlated with PC1 included 20:5*n*-3 (EPA) and 16:4*n*-3 (r = 0.72 and 0.49, respectively). The FAs 22:1*n*-9, 12:0, 14:0, 16:0, and 16:2*n*-6 were highly negatively correlated with PC1 (r = –0.84, –0.87, –0.81, and –0.76, respectively).

Table 1. *Euphausia superba.* Krill length and lipid dry mass according to year and months of sampling. N = number of samples

Year	Month	Total length (mm)				Lipid dry mass (%)			
		N	Mean length (SD)	Min.	Max.	N	Mean (SD)	Min.	Max.
2001	Feb–Mar	7	52.5 (2.7)	44	59	8	9.8 (2.6)	6.5	14.8
2004	Jan–Feb	–	–	–	–	19	11.4 (4.5)	3.0	18.4
2005	Jan–Feb	–	–	–	–	14	18.9 (7.8)	5.9	32.4
2008	Jan–Feb	–	–	–	–	7	16.6 (7.9)	10.8	32.4
2009	Jan- Feb	18	46.4 (4.6)	35.0	52.0	18	9.7 (4.1)	4.4	16.1
2010	Jan- Feb	21	45.8 (5.4)	33.4	52.5	21	20.6 (4.9)	11.1	29.7
2011	Jan- Feb	12	42.0 (8.9)	30.0	51.0	12	11.6 (6.6)	4.8	22.4
2012	Aug	15	32.4 (7.1)	19.2	40.9	15	23.0 (8.9)	11.2	39.7

Table 2. *Euphausia superba.* Fatty acid content (%) of the top 25 of 60 fatty acids found in Antarctic krill over the period from 2001 to 2012 in samples (n = 132) collected around the South Shetland Islands, ranked from highest to lowest across all years

Isomer	Mean	SD	Min.	Max.
16:0	19.40	1.30	16.33	22.40
20:5*n*-3	19.17	2.92	11.12	27.50
22:6*n*-3	15.13	4.96	8.00	29.81
18:1*n*-9	9.04	1.83	5.89	14.58
14:0	7.80	2.39	1.47	12.73
18:1*n*-7	6.88	0.87	5.38	9.40
18:4*n*-3	4.11	1.92	0.97	9.16
16:1*n*-7	3.79	1.33	1.12	8.01
18:2*n*-6	2.08	0.42	1.17	2.97
18:3*n*-3	1.52	0.61	0.64	3.48
18:0	0.99	0.21	0.61	1.64
16:4*n*-1	0.69	0.35	0.15	1.97
21:5*n*-3	0.57	0.16	0.27	1.18
20:4*n*-6	0.55	0.26	0.17	1.36
16:1*n*-11	0.54	0.12	0.21	0.87
20:1*n*-11	0.53	0.20	0.20	1.22
7Mec16:0	0.52	0.18	0.18	1.06
22:5*n*-3	0.49	0.08	0.29	0.71
20:4*n*-3	0.47	0.10	0.20	0.68
16:4*n*-3	0.47	0.15	0.05	0.75
16:3*n*-6	0.44	0.16	0.16	0.91
18:1*n*-5	0.43	0.16	0.11	0.93
15:0	0.38	0.10	0.17	0.64
22:1*n*-9	0.36	0.18	0.05	0.95
17:1	0.28	0.08	0.11	0.46
20:1*n*-9	0.27	0.11	0.01	0.51

Table 3. *Euphausia superba.* Factor structure summary for the first 3 principal components (PCs) of Antarctic krill fatty acids based on a principal component analysis of 60 fatty acids (see Table 2). The percent contribution of each PC is shown in the respective column heading. Factor loadings with absolute values of >0.4 are considered important in the factor structure and are shown ranked from largest to smallest absolute values. **Bold** type marks fatty acids that are negatively correlated with the respective PC

PC1 (25.03%)	PC2 (15.73%)	PC3 (11.41%)
22:6*n*-3	17:1	**21:5*n*-3**
20:4*n*-6	**16:1*n*-5**	**18:4*n*-1**
14:0	7Mec16:0	**16:3*n*-4**
12:0	15:0	Iso15
16:0	**20:4*n*-3**	**18:2*n*-4**
20:2*n*-6	14:1*n*-9	22:4*n*-6
22:1*n*-9	**18:3*n*-4**	18:3*n*-3
16:2*n*-6	**18:3*n*-3**	20:3*n*-6
20:5*n*-3	18:1*n*-5	**18:4*n*-3**
18:1*n*-9	**18:0**	**16:4*n*-1**
16:1*n*-7	**16:2*n*-4**	**18:1*n*-9**
14:1*n*-5	**22:5*n*-3**	16:1*n*-7
16:3*n*-6	**Iso15**	**20:3*n*-3**
20:1*n*-11	**18:4*n*-3**	18:3*n*-1
18:1*n*-11	**13:0**	**18:1*n*-13**
16:4*n*-1	**20:1*n*-11**	**18:1*n*-7**
22:1*n*-7	**16:1*n*-9**	18:2*n*-6
18:2*n*-6	**16:1*n*-11**	15:0
16:1*n*-11	**16:4*n*-3**	
22:5*n*-6	18:2*n*-6	
22:5*n*-3	**14:1*n*-5**	
16:1*n*-9	18:2d5	
18:0	18:3*n*-1	
18:4*n*-3		
20:1*n*-9		
16:4*n*-3		
14:1*n*-9		
20:3*n*-6		
18:1*n*-13		

FAs that were strongly associated with PC2 included a number that have not typically been used as lipid biomarkers. Among these were 17:1, 15:0, 7Mec16:0, and 20:4*n*-3. Only one FA, 21:5*n*-3, was strongly associated with PC3. For all 3 PCs, however, a number of FAs were important in explaining the variability associated with factor scores.

Four of the 5 FA ratios examined showed strong relationships with PC1 (Fig. 3). Three of the ratios (EPA/DHA, SFA/PUFA, and 18:1*n*-9/18:1*n*-7) were negatively correlated with PC1 (Fig. 3), while 16:0/16:1*n*-7 was positively correlated with PC1. Only one commonly used feeding ratio (16:1*n*-7/18:4*n*-3) was uncorrelated with PC1. Winter 2012 FA ratios were negatively correlated with PC1 across almost all samples.

Interannual variability

Significant differences in prevalent FAs, as inferred from average PC scores, were evident among years (2012 was removed from this analysis, as it was significantly different from all other years; Table 4). ANOVA of PC1 showed significant differences in the magnitude of the PC scores among years ($F_{6,96}$ = 3.53, p < 0.0035). Multiple comparisons showed that the PC score for 2010 was lower than 2001 and 2011. PC2 scores for 2004, 2005, and 2008 were lower than for 2001, 2009, and 2011, while the PC2 score for 2011 was also higher than for 2010 ($F_{6,96}$ = 21.09, p < 0.0001). PC3 scores for 2010 and 2011 were lower than for 2009 ($F_{6,96}$ = 3.02. p < 0.0099).

Similarly, all FA ratios showed significant variability over time, and each exhibited some differences among years except for 18:1*n*-9/18:1*n*-7. EPA/DHA in 2001 was significantly lower than in 2010 (ANOVA: $F_{6,96}$ = 2.92, p < 0.0112). In 2011, 16:0/

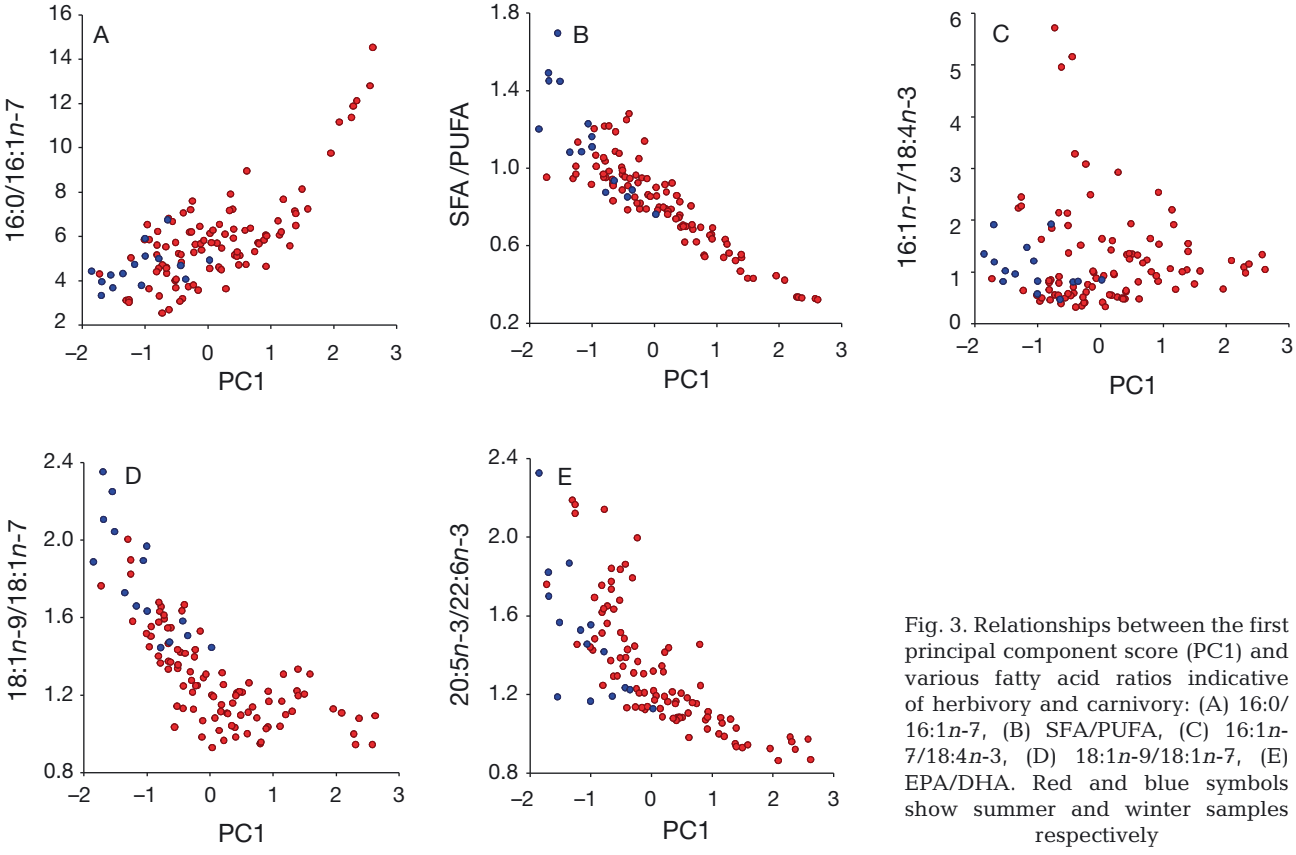

Fig. 3. Relationships between the first principal component score (PC1) and various fatty acid ratios indicative of herbivory and carnivory: (A) 16:0/16:1*n*-7, (B) SFA/PUFA, (C) 16:1*n*-7/18:4*n*-3, (D) 18:1*n*-9/18:1*n*-7, (E) EPA/DHA. Red and blue symbols show summer and winter samples respectively

16:1*n*-7 was greater than in 2004, 2009, and 2010 ($F_{6,96}$ = 3.94, p < 0.0015). In 2001 and 2011, SFA/PUFA was lower than in 2005 and 2010 ($F_{6,96}$ = 5.18, p < 0.0002). In 2009, 16:1*n*-7/18:4*n*-3, the only ratio not correlated with PC1, was higher than in all other years ($F_{6,96}$ = 5.66, p < 0.0001).

Environmental correlations

Two of the 3 climate and environmental metrics were strongly correlated with average PC1 scores (Fig. 4). Both the index of winter SIE and the BEST index were negatively correlated with PC1 (r = –0.57, p < 0.05; r = –0.78, p < 0.001, respectively). The SAM index was not correlated with any PC (not shown).

DISCUSSION

Primary production and phytoplankton community composition in the Antarctic Peninsula are strongly affected by interannual and long-term variability in sea-ice retreat and water-column stratification, the timing of which are affected by the major climate modes influencing the Antarctic Peninsula region (i.e. ENSO and SAM) (Moline et al. 2004, Montes Hugo et al. 2008, Stammerjohn et al. 2008a, Hewes et al. 2009, Reiss et al. 2009, Kozlowski et al. 2011). These climate-linked changes in primary production and phytoplankton community structure result in annual differences in the quantity and quality of food available to grazers during the summer (Reiss et al. 2009, Kozlowski et al. 2011, Venables et al. 2013, Saba et al. 2014) These direct links among atmospheric forcing, SIE, and the feeding ecology of a principle grazer in the Antarctic were evident in the variable FA signatures of Antarctic krill over the 12 yr study period (Fig. 4).

Lipid biomarkers and feeding ecology during ENSO

The correlation of FA signatures with ENSO and winter SIE suggests that winter conditions affecting the summer phytoplankton community structure are reflected in the diets and the feeding ecology of krill. Three of the 5 FA ratios examined (16:0/16:1*n*-7, SFA/PUFA, and EPA/DHA) indicated a shift away

Table 4. *Euphausia superba*. Fatty acid sample size and mean (SD) annual PC scores for the first 3 PCs of all 60 fatty acids (combined) found in Antarctic krill during the study period, and the mean (SD) of the fatty acid ratios used to examine levels of herbivory (EPA/DHA) and carnivory (16:0/16:1*n*-7, 16:1*n*-7/18:4*n*-3, 18:1*n*-9/18:1*n*-7, and SFA/PUFA) in krill collected between 2001 and 2012

Year	Sample size	PC1	PC2	PC3	EPA/DHA	16:0 /16:1*n*-7	16:1*n*-7 /18:4*n*-3	18:1*n*-9 /18:1*n*-7	SFA/ PUFA
2001	10	0.78 (0.56)	0.57 (0.33)	0.03 (0.22)	1.05 (0.09)	6.01 (1.19)	1.21 (0.32)	1.20 (0.08)	0.08
2004	19	0.08 (0.69)	−0.71 (0.60)	−0.20 (0.84)	1.39 (0.34)	5.36 (1.10)	0.89 (0.48)	1.22 (0.21)	0.21
2005	14	−0.14 (0.83)	−0.79 (0.85)	−0.13 (0.63)	1.26 (0.20)	6.42 (1.60)	0.83 (0.54)	1.29 (0.20)	0.20
2008	7	0.60 (0.32)	−1.00 (0.48)	0.17 (0.74)	1.10 (0.07)	7.12 (1.06)	0.86 (0.60)	1.17 (0.10)	0.10
2009	19	0.26 (0.90)	0.15 (0.55)	0.27 (1.53)	1.36 (0.33)	5.39 (2.12)	2.02 (1.70)	1.32 (0.22)	0.22
2010	34	−0.39 (0.61)	−0.11 (0.85)	−0.27 (1.08)	1.44 (0.20)	4.98 (0.98)	1.06 (0.65)	1.30 (0.24)	0.24
2011	14	0.92 (1.61)	1.49 (0.70)	−0.48 (0.46)	1.31 (0.51)	8.41 (4.21)	1.41 (0.58)	1.26 (0.37)	0.37
2012	15	−1.07 (0.55)	0.40 (0.98)	0.99 (0.45)	1.49 (0.33)	4.60 (0.88)	1.08 (0.44)	1.80 (0.30)	0.30

from carnivorous or omnivorous feeding toward herbivorous feeding when ENSO conditions were prevalent. This same dietary shift towards herbivory was also evident with respect to increased winter SIE (Fig. 4). The positive relationship between ENSO and sea-ice dynamics at the tip of the peninsula indicates that the abundance of larger phytoplankton species

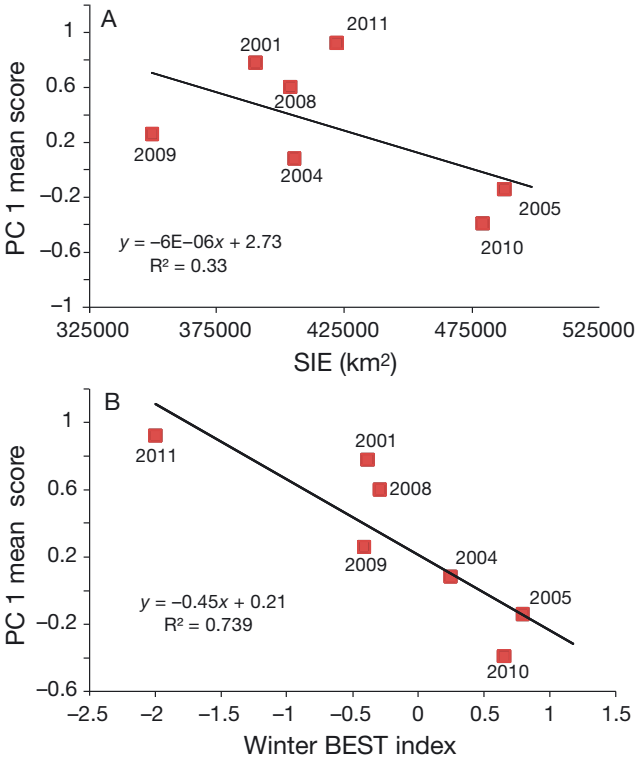

Fig. 4. Relationship between magnitude of the first principal component score (PC1) and (A) mean winter sea ice extent (SIE) and (B) winter bivariate ENSO (BEST) index. In both cases, low values are related to a more omnivorous diet as inferred from fatty acid profiles of Antarctic krill around the Antarctic Peninsula region of the Southern Ocean. Results from winter 2012 are not included in the plots

such as diatoms increases when sea ice is persistent and the upper mixed layer of the water column is deep relative to non-ENSO periods (Montes-Hugo et al. 2008, Reiss et al. 2009). The patterns of the aforementioned FA ratios are consistent with other findings (e.g. Schmidt et al. 2006) that krill feed on large diatoms (rich in 20:5*n*-3 and 16:1*n*-7) when they are present and shift their diet when algal biomass is low or is dominated by smaller species, such as flagellates or cryptophytes (Schmidt et al. 2006). The similarity between spatial patterns of FAs across the Scotia Sea found in some studies (Mayzaud et al. 1998, Cripps & Atkinson 2000) and the temporal variability in FA ratios found in this study suggests that krill exhibit a flexible feeding strategy that reflects ecosystem variability resulting from seasonal atmospheric forcing.

Not all FAs or FA ratios that have been associated with omnivorous and carnivorous feeding strategies were less prevalent during ENSO conditions. One ratio, 18:1*n*-9/18:1*n*-7, which has been traditionally used to evaluate relative levels of carnivory (Stübing & Hagen 2003), exhibited the opposite trend and seemed to indicate a shift toward increased omnivory or carnivory during ENSO conditions. The FA 18:1*n*-9 is more characteristic of marine animal lipid relative to phytoplankton lipid (Falk-Petersen et al. 2000) and it is often highly correlated with total lipid content (Hagen et al. 2001, Schmidt et al. 2006). This suggests that factors other than diet may influence the levels of this FA in krill. For example, this FA can be synthesized de novo from saturated FA precursors (Falk-Petersen et al. 2000, Hagen et al. 2001) and its presence may be confounded by krill metabolic processes (Stübing & Hagen 2003). Additionally, laboratory feeding experiments found that 18:1*n*-9 is not selectively assimilated by krill when krill are fed diets high in this FA, as demonstrated by the high

levels of 18:1*n*-9 in the recovered fecal matter (Stübing et al. 2003).

Although the origin of 18:1*n*-9 in krill may be difficult to definitively resolve and should therefore be used with caution as a trophic indicator, high levels of this FA may still be useful for inferring the consumption of some food resources. While several studies have found that high levels of 18:1*n*-9 are consistent with a carnivorous diet (e.g. Phleger et al. 2002, Stübing & Hagen 2003), others have found that high levels of 18:1*n*-9 are consistent with a cryptophyte diet (Alonzo et al. 2005). The results of the present study suggest that the high ratio of 18:1*n*-9/18:1*n*-7 associated with a low PC1 score (Fig. 3) and therefore with ENSO conditions and increased herbivorous feeding (Fig. 4) reflected increased feeing on cryptophytes rather than heterotrophs, particularly during the summer of 2010.

Although the physical environmental characteristics of ENSO (i.e. persistent SIE and a cold, deep upper mixed layer) are usually not conducive to supporting large blooms of cryptophytes (Moline et al. 2004, Montes-Hugo et al. 2008), a study in the Bransfield Strait during the summer of 2010 found that despite prevalent ENSO conditions during which diatoms would typically be favored, cryptophytes were the dominant phytoplankton group (Mendes et al. 2013). These authors speculated that a moderate ENSO event delayed the seasonal succession cycle of phytoplankton in the Antarctic Peninsula region by reducing the amount of sea ice melting and hindering the diatom bloom that usually precedes the appearance of cryptophytes. In fact, the anomalous conditions during the winter of 2009 and the following summer (2010) are well documented and reflect changing ocean–atmosphere teleconnections (Lee et al. 2010). A warm pool of water in the south central Pacific Ocean associated with a persistent anticyclone increased the amount of warm air directed over the Bellingshausen Sea and Antarctic Peninsula ecosystem. This may have confounded the normal ENSO conditions, resulting in localized glacial melting that stratified the water column in this area (Mendes et al. 2013). While cryptophytes are not considered a preferred food source for krill (Haberman et al. 2003, Moline et al. 2004), the absence of alternative resources during an unusual summer may have driven the increased consumption of cryptophytes and the increased levels of 18:1*n*-9 in krill during otherwise ENSO-like conditions. Other studies have suggested that krill could obtain 18:1*n*-9 from ingesting large amounts of *Phaeocystis* spp. (Virtue et al. 1993). However, *Phaeocystis antarctica* is not generally abundant within the South Shetland Islands, as it comprises <10% of the phytoplankton community in this region (Mendes et al. 2013). Moreover, Haberman et al. (2003) found that krill demonstrated a high selectivity for diatoms over *P. antarctica*, even when diatoms were scarce. These authors suggested that krill reject *P. antarctica* outright during the filtration process, possibly because it is a suboptimal food resource. Both diet and physiological mechanisms may play a role in the levels of certain FAs in krill, but environmental conditions may also affect the quality and the FA composition of the food consumed by krill, and also the ability of krill to modify certain FAs.

Diatoms may be more adaptable to the summer conditions during ENSO, such as reduced light availability due to increased mixing of surface waters (Reiss et al. 2009, Petrou & Ralph 2011) and an extended supply of soluble iron released into surface waters from persistent sea-ice melting into the summer months (Montes-Hugo et al. 2008, van der Merwe et al. 2011). Iron, while essential for primary production, also affects total lipid content of phytoplankton. Chen et al. (2011) found that algal cells grown in an iron-enriched medium had significantly higher total cellular FA concentrations than algal cells grown in an iron-deficient medium, and that the percentage of 16:1*n*-7 increased over tenfold in the diatom *Thalassiosira oceanica* between the iron-deficient and the iron-enriched media. These authors suggested that the increase in 16:1*n*-7 is the result of desaturation of 16:0 by the enzyme fatty acid desaturase, of which iron is an essential component. In the present study, the low ratio of 16:0/16:1*n*-7 in krill may be indicative of diatom grazing during ENSO conditions, in general. It is unknown whether krill can use ingested iron to synthesize fatty acid desaturase, but the high ratio of 18:1*n*-9/18:1*n*-7 during ENSO conditions, while a possible result of cryptophyte feeding, may also indicate increased levels of de novo synthesis of 18:1*n*-9 while feeding on other iron-rich algae. However, further testing of this hypothesis is required.

The ratio of 16:1*n*-7/18:4*n*-3 was uncorrelated with PC1. This ratio has been used to resolve relative consumption of diatoms and flagellates in a number of studies in the Scotia Sea (Cripps et al. 1999, Schmidt et al. 2006). Values of the 16:1*n*-7/18:4*n*-3 ratio during the current study ranged from <1 to ~6. Schmidt et al. (2006) found that the range of this ratio varied from <1 to >14. The highest ratios were from high chl *a*, diatom-dominated stations north of South Georgia, and within high chl *a* (>3 µg l^{-1}) bloom areas in the

Weddell Sea. Schmidt et al. (2006) also showed that the change in the magnitude of the ratio was largely due to the very high values of 16:1*n*-7 in chl *a* bloom areas. Such diatom-dominated and high chl *a* concentrations are rarely found in the open waters around the South Shetland Islands, suggesting that the diatoms and autotrophic dinoflagellates were present in relatively equal proportions (Mendes et al. 2013). The lack of correlation between 16:1*n*-7/18:4*n*-3 and PC1 is likely the result of lower 16:1*n*-7 levels in the current study area, and reflects the substantially more diverse feeding environment in this region of the Southern Ocean. This suggests that the16:1*n*-7/18:4*n*-3 ratio is less useful as a trophic marker in this particular area of the Southern Ocean compared to other areas where individual taxa dominate the plankton community (e.g. South Georgia; Cripps et al.1999).

Winter conditions are thought to be a critical period for krill (Hagen et al. 1996). The paucity of water-column production and the necessity of foraging on sea-ice algae or on micro-zooplankton associated with ice might suggest that the FA signatures during winter could be very different from those of summer (Flores et al. 2012). The findings here show that while some winter FA ratios were at times elevated compared to summer, they remained within the observed ranges of summer samples.

There are other factors that may have affected our ability to more clearly discern patterns with respect to some FAs. We stored our samples in the dark at −20°C prior to analysis. Some studies have indicated that lipid samples should be stored at −80°C in a nitrogen environment to prevent or minimize oxidation. Several laboratory studies that have examined the effect of storage temperature and duration (e.g. Katan et al. 2003, Lind et al. 2012) on seal blubber and human adipose samples have shown minimal changes in the fatty acids profiles over short time scales (months) at a variety of suboptimal temperatures (−20 to 20°C). The effects of storage temperature and duration are associated mostly with phospholipids, not triglycerides (Kolakowska 1991). Given the consistent treatment of our samples among years and the short time between collection and analysis we believe that any lipid oxidation which may have occurred would not have impacted the principal findings of this study.

Comparisons to other studies

Our findings of interannual differences in krill FA signatures and dietary shifts along a herbivory–omnivory gradient are consistent with patterns observed during a variety of other field studies conducted throughout the Southern Ocean. Clear spatial differences in FA profiles have been related to levels of productivity (Pond et al. 1995, Mayzaud et al. 1998, Cripps et al. 1999), to interannual differences in lipid storage (Phleger et al. 2002, Stübing & Hagen 2003), and to the composition of prey items consumed by krill (Cripps et al. 1999, Cripps & Atkinson 2000, Schmidt et al. 2006). Despite these demonstrated relationships, inferring diets of krill and the contributions from various prey types is complicated and dependent on a broad understanding of the productivity of the system, the available alternate prey, and the resulting combination of FA signatures (Alonzo et al. 2003, Stübing et al. 2003). The process is often complicated by several factors, including the mixed diets available to krill (e.g. Haberman et al. 2003), potential de novo synthesis of some FAs and associated metabolic processes, and selective mobilization and retention of certain FAs within an organism (Budge et al. 2006) that can modify the FA signature when compared to the signatures of the prey. Our ranges for EPA/DHA and 16:1*n*-7/18:4*n*-3 are much lower than the ranges of these same ratios observed in other studies (e.g. Cripps & Atkinson 2000, Stübing et al. 2003, Schmidt et al. 2006). Yet, the amount of lipids in krill from these previous studies and the current study was similar. We propose that the diets of krill in the South Shetland Island region reflect the environmental variability resulting from atmospheric forcing and that krill here consume a more diverse diet than krill in other regions of the Southern Ocean. This in part explains the lack of correlation between some measures of herbivory that have been observed in other areas of the Scotia Sea (Schmidt et al. 2006), but supports the similar conclusion drawn by other studies in the Peninsula region (e.g. Phleger et al. 2002). Our results also suggest that regional differences in foraging environments throughout the Southern Ocean heavily influence krill feeding ecology and must be understood and accounted for when drawing conclusions about krill diets and condition.

Implications for the future

Continued warming of the Antarctic Peninsula over the next decades will further impact the seasonal sea-ice dynamics that are critical to the overwinter survival and year-class strength of krill (Loeb et al. 1997, Atkinson et al. 2004, Saba et al. 2014). The demon-

strated positive relationship between increasing global temperatures and the SAM, which is negatively related to ENSO (Wang & Cai 2013), will impact the timing and the magnitude of the spring blooms. Under these modified climate conditions, Hill et al. (2013) have projected the impact of temperature and chl *a* concentration on the growth of krill and have suggested that areas of high quality habitat will change. The flexible feeding strategy demonstrated by krill suggests that they may be relatively adaptive, and in the South Shetland Islands region, where large diatoms are not dominant and water temperature may not increase as much as in other areas (e.g. South Georgia) because of the influence of the cold Weddell Sea outflow, the short-term impact on krill populations may be less than hypothesized (Hill et al. 2013). If warming persists or strengthens with continued climate change, or the frequency and intensity of climatic events change (Lee et al. 2010), then the phytoplankton community composition, krill density, and distribution in some areas of the Southern Ocean will change. The resulting shift in the spatial distribution of krill could negatively impact krill predators, specifically central-place foragers, by potentially increasing foraging distances during the breeding season, or affecting their energetic intake. The transition to warmer water and smaller phytoplankton species may also facilitate increased populations of salps, which have already increased up to twofold in the Antarctic Peninsula region over the last decade (Atkinson et al. 2004).

CONCLUSIONS

This study demonstrates that krill exhibit flexible feeding strategies with changing environmental conditions, and that in the South Shetland Islands, krill diets are substantially more diverse than in more productive areas. This suggests that simple projections regarding the impact of climate change on krill biology and ecology may be more complicated than assumed (Hill et al. 2013). Although this study of feeding ecology of krill is longer in duration than other studies, it is still relatively short for a time series. Given the nature of correlative studies in general and the current frequency of ENSO events, we suggest that the study be expanded and repeated where possible, to further examine our results. Our data suggest that studies on winter preconditioning may be a fruitful avenue to better understand the impact of climate change on those aspects of krill life history likely to be influenced by moderating winter conditions.

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