

# Stable isotopes identify an ontogenetic niche expansion in Antarctic krill (*Euphausia superba*) from the South Shetland Islands, Antarctica

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Received: 6 November 2012 / Accepted: 8 January 2013 / Published online: 12 February 2013  
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**Abstract** Antarctic krill (*Euphausia superba*) occupy a key position in the Southern Ocean linking primary production to secondary consumers. While krill is a dominant grazer of phytoplankton, it also consumes heterotrophic prey and the relative importance of these two resources may differ with ontogeny. We used stable isotope analyses to evaluate body size-dependent trophic and habitat shifts in krill during the austral summer around the South Shetland Islands, Antarctica. We found evidence for an asymmetric, ontogenetic niche expansion with adults of both sexes having higher and more variable  $\delta^{15}\text{N}$  values but consistent  $\delta^{13}\text{C}$  values in comparison with juveniles. This result suggests that while phytoplankton likely remains an important life-long resource, krill in our study area expand their dietary niche to include higher trophic food sources as body size increases. The broader dietary niches observed in

adults may help buffer them from recent climate-driven shifts in phytoplankton communities that negatively affect larval or juvenile krill that rely predominately on autotrophic resources.

## Introduction

Antarctic krill (*Euphausia superba*) is a key species in the Southern Ocean that serves as a link between primary production and a diverse assemblage of secondary consumers (Laws 1985; Everson 2000). Because of their important position in the Southern Ocean food web, the foraging behavior and diets of Antarctic krill have been the focus of many investigations (Maciejewska 1993; Hamner and Hamner 2000; Meyer et al. 2010). Early dietary studies of Antarctic krill used primarily stomach content analysis (Barkley 1940), though more recently biomarker approaches such as stable isotope and fatty acid analyses have become commonplace (Atkinson et al. 2002; Schmidt et al. 2003, 2004, 2006). These methods rely on the principle that stable isotope ratios of carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) and the fatty acid composition of animal tissues are largely determined by their abundances in an animal's food web (DeNiro and Epstein 1978, 1981; Cripps and Atkinson 2000). Together, this body of research suggests that while Antarctic krill is commonly thought to be a grazer of phytoplankton, they are actually omnivorous and will consume heterotrophic prey such as copepods and protozoans in both experimental and wild settings (Atkinson and Snýder 1997; Perissinotto et al. 2000; Hernández-León et al. 2001). However, these studies have also identified a further need to examine ontogenetic variation in heterotrophic feeding by Antarctic krill (Atkinson et al. 2002; Ju and Harvey 2004; Schmidt et al. 2006).

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Communicated by A. Atkinson.

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There are three possible scenarios for how an organism's dietary niche may be affected by ontogeny (Werner and Gilliam 1984): Resource use may remain unchanged, niches may expand or contract as consumers expand or contract their foraging range and diets, or consumers may switch to completely different resources during ontogenetic development. Body size changes are a common determinant of niche dynamics during ontogeny, with size-related dietary shifts prevalent in many marine fishes (Scharf et al. 2000; Graham et al. 2007). Size-related niche shifts also have been observed in euphausiids: Park et al. (2011) used stable isotope analysis to document a shift from herbivory on microplankton to detritivory on large heterotrophic particles between juvenile and adult size classes of *Euphausia pacifica*.

Studies that have examined size class-related differences in the dietary niches of Antarctic krill have shown mixed results. Schmidt et al. (2006) used stomach contents, stable isotopes, and fatty acid techniques to examine the austral summer diets of Antarctic krill across the Scotia Sea in 2003. They found strong evidence of regional variation, but little evidence of ontogenetic-related differences in diets. In contrast, stable isotope data from South Georgia in austral summer 1996 and the Lazarev Sea in austral autumn 1999 suggest that adults likely foraged at a higher trophic level than juveniles (Schmidt et al. 2003, 2004). Furthermore, studies using both stomach contents and fatty acid analyses in the Lazarev Sea and Marguerite Bay during the austral autumn and winter of 1999 and 2001, respectively, yielded significant ontogenetic-related differences in the diet of krill with juveniles feeding mainly on phytoplankton and adults consuming both phytoplankton and small zooplankton (Atkinson et al. 2002; Ju and Harvey 2004). Therefore, there may be a significant spatial or temporal component to the prevalence of size class-related dietary niche differences in Antarctic krill.

Here, we expand on this previous research by examining ontogenetic differences in the diets of Antarctic krill collected around the South Shetland Islands and northern Antarctic Peninsula during austral summers of 2007 and 2009. Specifically, we focus on the stable isotope values of adult and juvenile size classes of krill collected over two years to test for inter-annual variation in the prevalence of ontogenetic dietary differences. Identifying both the magnitude and consistency of ontogenetic dietary differences in Antarctic krill is important as ontogenetic niche shifts can shape intra- and interspecific interactions and determine species-level resilience to environmental variability (Miller and Rudolf 2011; Rudolf and Lafferty 2011). The South Shetland Islands are an ideal location for this study for several reasons. The surrounding waters exhibit elevated phytoplankton biomass during the austral summer and act as an important area for krill growth and recruitment

(Hewes et al. 2009; Reid et al. 2002). In addition, the relatively high biomass of Antarctic krill and common co-occurrence of both adult and juvenile size classes in this region help to facilitate ontogenetic comparisons (Siegel et al. 2004; Reiss et al. 2008). Finally, relative to other regions in the Southern Ocean, there have been few studies that explicitly examined ontogenetic differences in the diets of Antarctic krill around the South Shetland Islands.

Our objective was to use stable isotope analyses to evaluate the presence of dietary differences in Antarctic krill according to body size, sex, and ambient environmental conditions. To address this objective, we first tested for relationships between body size and stable isotope values. In addition, we used the hypothesis-testing framework developed by Hammerschlag-Peyer et al. (2011) to examine differences in isotopic niche width, position, and overlap between ontogenetic size classes. This approach presents  $\delta^{15}\text{N}$  (diet) and  $\delta^{13}\text{C}$  (habitat) values as bi-plots which delineate an animal's isotopic niche (Newsome et al. 2007) that is a proxy of the n-dimensional niche space defined by Hutchinson (1957, 1959) to represent an animal's biotrophic (diet) and scenopoetic (habitat) use.  $\delta^{15}\text{N}$  values of tissue are used to infer an individual's dietary niche as they reflect the trophic level of consumers with a general increase in  $\delta^{15}\text{N}$  values by 3–5 ‰ per trophic level (Minagawa and Wada 1984). Therefore, we hypothesize that any size class-related dietary shifts toward heterotrophic prey will result in higher  $\delta^{15}\text{N}$  values in larger adults relative to smaller, juvenile krill. Similarly, tissue  $\delta^{13}\text{C}$  values in marine systems are used to infer an individual's benthic versus pelagic habitat use due to differences in  $\delta^{13}\text{C}$  fractionation during photosynthesis between benthic macro-algae and pelagic phytoplankton (France 1995; Cherel and Hobson 2007). However, factors such as temperature and the rate of primary production can also influence  $\delta^{13}\text{C}$  values in marine food webs independent of trophic or habitat shifts (Hinga et al. 1994; Schell 2000; Jaeger and Cherel 2011). Consequently, we used multiple regression approaches to determine whether inter-annual and spatial variation in factors related to resource abundance (zooplankton and primary producer biomass), habitat type (bathymetry), and physical conditions (temperature) affected the stable isotope values of Antarctic krill independent of body size-specific dietary trends.

## Methods

### Study site and sample collection

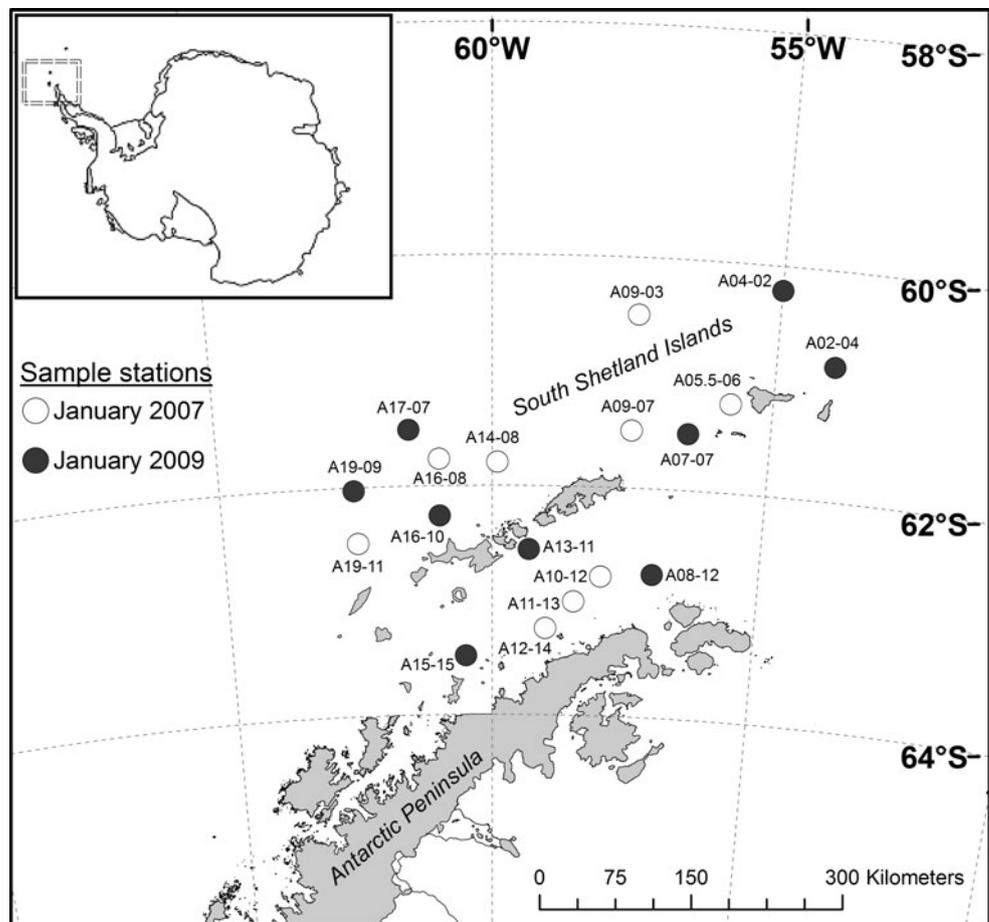
This study was conducted during January in the austral summers of 2007 and 2009 from the *R/V Yuzhmorgeologiya* as part of the U.S. Antarctic Marine Living Resources

(AMLR) program annual oceanographic survey of the area surrounding the South Shetland Islands and the northern Antarctic Peninsula (Fig. 1). At nine randomly selected stations in each year (18 total), we made hydrographic casts with a SBE Inc model 9/11 Conductivity, Temperature and Depth (CTD) instrument and collected water samples with attached 8 l Niskin bottles at discrete depths. Maximum bathymetric depth at each station was determined using ship sonar. These methods provided average water temperature within the upper mixed layer (approximately 0–40 m depth). Chl-a concentration ( $\text{mg m}^{-3}$ ) at each station was determined using a Niskin bottle triggered at a depth of 5 m via measurements of fluorescence (with acidification) after extraction in absolute, acid-free methanol (Holm-Hansen and Riemann 1978; Van Cise 2009). We also extracted monthly MODIS satellite-derived sea-surface temperature and Chl-a concentration data from  $50 \text{ km}^2$  grids centered on the nine stations in December and January of each austral summer (<http://reason.gsfc.nasa.gov/Giovanni/>). Satellite measurements of water temperature and Chl-a concentration at stations were positively correlated between months as well as with shipboard measurements confirming the

temporal stability of station-specific variation in these parameters ( $r = 0.60$  to  $0.89$ ,  $P = 0.001$  to  $0.008$ ). Therefore, in subsequent analyses, we used solely shipboard temperature and Chl-a data to remain consistent with other environmental parameters of interest that could not be estimated using satellite data.

At each station, we collected krill and other zooplankton samples using a 1.8 m Isaacs-Kidd Midwater Trawl fitted with  $505\text{-}\mu\text{m}$  mesh plankton net fished obliquely from a depth of 170 m or to approximately 10 m above bottom in shallower waters. Flow volumes were measured using a calibrated General Oceanic (model 2030R) flow meter mounted on the frame in the front net. From each net tow sample, we randomly collected ten individual Antarctic krill for a total of 180 individual krill (90 krill in each year; Fig. 1). We measured the standard length (SL) of the krill to the nearest mm, from the anterior side of the eye to the tip of the telson. Krill  $\leq 35$  mm SL were considered juveniles and adult krill  $>35$  mm SL were visually sexed based on the presence or absence of the thelycum (Siegel and Loeb 1994; Miller and Trivelpiece 2007). Krill was kept frozen at  $-20^\circ\text{C}$  prior to isotopic analysis.

**Fig. 1** The 18 sampling stations (circles) near the South Shetland Islands and northern Antarctic Peninsula where Antarctic krill (*Euphausia superba*) samples and oceanographic data were collected in January 2007 and 2009



At each station, we also determined the total copepod abundance expressed in number per 1,000 m<sup>3</sup> water filtered as a proxy of heterotrophic prey availability. Previous studies have found copepods in the range of 1–3 mm are readily consumed by Antarctic krill (Atkinson and Snýder 1997). Copepod abundance in our study was dominated (77.3 % of total) by three taxa in this size range that have been previously identified in the diets of Antarctic krill (*Calanoides* spp., *Calanus* spp., and *Metridia gerlachei*; Atkinson and Snýder 1997; Hernández-León et al. 2001; Atkinson et al. 2002).

#### Sample preparation and isotopic analyses

Individual krill were homogenized and dried for 48 h in an oven at 60 °C. Lipids were then extracted from krill samples using a Soxhlet apparatus with a 1:1, petroleum-ether:ethyl-ether solvent mixture for 8 h (Seminoff et al. 2007). Lipid-extracted krill were not acidified prior to isotopic analysis. Approximately, 0.5 mg of each individual krill was loaded into separate tin cups and flash-combusted (Thermo-Finnigan elemental analyzer) and analyzed for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values via a Con-Flo II interfaced with a Thermo-Fisher Delta Plus XL continuous flow stable isotope ratio mass spectrometer (CFIRMS). Raw  $\delta$  values were normalized on a two-point scale using glutamic acid reference materials USGS-40 and USGS-41. Sample precision was 0.1 ‰ and 0.2 ‰, for  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values, respectively.

Stable isotope abundances are expressed in  $\delta$  notation in per mil units (‰), according to the following equation:

$$\delta X = \left[ \left( R_{\text{sample}} / R_{\text{standard}} \right) - 1 \right] \times 1,000$$

where  $X$  is  $^{13}\text{C}$  or  $^{15}\text{N}$ , and  $R$  is the corresponding ratio  $^{13}\text{C}/^{12}\text{C}$  or  $^{15}\text{N}/^{14}\text{N}$ . The  $R_{\text{standard}}$  values were based on the Vienna PeeDee Belemnite (VPDB) for  $\delta^{13}\text{C}$  and atmospheric  $\text{N}_2$  (AIR) for  $\delta^{15}\text{N}$ .

#### Statistical analysis

We tested for spatial (stations) and temporal (years) differences in the size of krill (SL) and their stable isotope values ( $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$ ) using separate nested ANOVA (Proc Nested) in SAS (version 9.1, SAS Institute 1999). We then used multiple linear regressions (Proc Reg) and model selection techniques to identify the biological and/or physical covariates which best explained the observed spatial and/or temporal variation in the stable isotope values of krill. We parameterized models as follows using the mean values at each station: krill  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values as response variables and krill body size (SL), chl-*a* concentration, copepod abundance, depth (log-transformed), and water temperature as covariates. We then determined the

most parsimonious models for krill  $\delta^{13}\text{C}$  or  $\delta^{15}\text{N}$  values by removing nonsignificant covariate terms from each full model using a backward, stepwise procedure based on minimizing the resulting model's Akaike's Information Criterion value (AIC; Akaike 1973). These five covariates were chosen to allow us to test several specific hypotheses. For example, krill body size and stable isotope values should be correlated if krill shift their diets and/or habitat during ontogeny. In addition, krill  $\delta^{15}\text{N}$  values should have a negative relationship with chl-*a* concentration and a positive relationship with copepod abundance if krill shift their diet in relation to the availability of these two prey groups. Krill  $\delta^{13}\text{C}$  values should be positively related to seawater temperature as lower temperatures increase  $\text{CO}_2$  (aq) fixation by diatoms that more effectively discriminate against  $^{13}\text{C}$  (Freeman and Hayes 1992; Hinga et al. 1994). A negative relationship between  $\delta^{13}\text{C}$  values and sample station depth is predicted as benthic macro-algae tend to have higher  $\delta^{13}\text{C}$  values than pelagic phytoplankton. Finally, as  $\delta^{13}\text{C}$  fractionation in marine phytoplankton is an inverse function of cell growth rate (Laws et al. 1995), we expected a positive relationship between krill  $\delta^{13}\text{C}$  values and chl-*a* concentration (a proxy for primary production) at sampling stations. If significant relationships between stable isotope values and body size were identified, we used simple linear regressions to graphically represent relationships at both the station and individual level.

To explicitly test for size class-related shifts in the dietary and habitat niche position and width of Antarctic krill, we examined  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in each year following the methods of Hammerschlag-Peyer et al. (2011) using Program R (version 2.14.1). First, we tested for differences in isotopic niche position by computing the Euclidean distance (ED) between group centroids ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bivariate means) of the three size classes of krill (juvenile, adult female, and adult male) following the methods of Turner et al. (2010). Isotopic niche positions were considered to be different if the ED between two size classes was significantly greater than zero after comparison with null distributions generated by a residual permutation procedure. If niche positions differed using this approach, we used ANOVA and Tukey–Kramer multiple comparison tests (Proc GLM) to determine which niche axis ( $\delta^{13}\text{C}$  and/or  $\delta^{15}\text{N}$ ) drove the observed shifts in niche position.

We next tested for differences in niche width between size classes by computing the mean distance to centroid (MDC; a measure of dispersion) for each size class in each year separately (Turner et al. 2010). Using an analysis of nested linear models and residual permutation procedures, the absolute value of MDC differences was evaluated among groups with absolute values greater than zero indicating a difference in niche width among size classes. When pairwise comparisons indicated significant differences in

MDC and thus niche width, we used Bartlett’s tests to examine the homogeneity of variance of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among size classes in each year to determine which isotopic niche axis drove the observed differences in niche width. Last, we measured pairwise niche overlap between size classes by quantifying the percentage of individuals in each size class that were encompassed by a comparison size classes’ convex hull, the area of the smallest convex polygon that contains all individuals of a single size class in a  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  bi-plot (Layman et al. 2007).

Prior to analysis, all data were examined for normality and equal variance and transformed as detailed when necessary. Significance was assumed at the 0.05 level and all means are presented  $\pm$  standard deviation (SD).

**Results**

Variability between years and across sampling stations

Variation among stations (23.5–66.2 %) contributed more to the total variance in krill SL,  $\delta^{13}\text{C}$ , and  $\delta^{15}\text{N}$  values than did variation between years (0.0–5.7 %) with significant differences among stations (Table 1; SL:  $F_{16,180} = 20.63$ ,

$P < 0.001$ ;  $\delta^{13}\text{C}$ :  $F_{16,180} = 4.22$ ,  $P < 0.001$ ;  $\delta^{15}\text{N}$ :  $F_{16,180} = 17.32$ ,  $P < 0.001$ ), but not between years (SL:  $F_{16,180} = 0.04$ ,  $P = 0.839$ ;  $\delta^{13}\text{C}$ :  $F_{16,180} = 1.94$ ,  $P = 0.183$ ;  $\delta^{15}\text{N}$ :  $F_{16,180} = 1.84$ ,  $P = 0.194$ ). The most parsimonious model to explain spatial variation in  $\delta^{13}\text{C}$  values was one that included weak but significant effects of both body size ( $R^2 = 0.21$ ,  $P = 0.029$ ) and chl-a concentration ( $R^2 = 0.23$ ,  $P = 0.021$ ). Krill  $\delta^{13}\text{C}$  values increased in larger krill (Fig. 2) and at stations with higher chl-a concentration (Table 1). Similarly, spatial variation in krill  $\delta^{15}\text{N}$  values was best explained by a strong relationship with mean body size at stations ( $R^2 = 0.63$ ,  $P < 0.001$ ) as larger krill tended to have higher  $\delta^{15}\text{N}$  values (Fig. 2). We found no evidence for a relationship between  $\delta^{15}\text{N}$  values and any of the other biotic and abiotic covariates examined in this study.

Ontogenetic variation in isotopic niche position and width

Isotopic niche positions differed among size classes in each year, with the ED between juvenile and adult male and female krill group centroids ranging from 0.7 to 1.2 % (Table 2). Differences in niche positions were due to

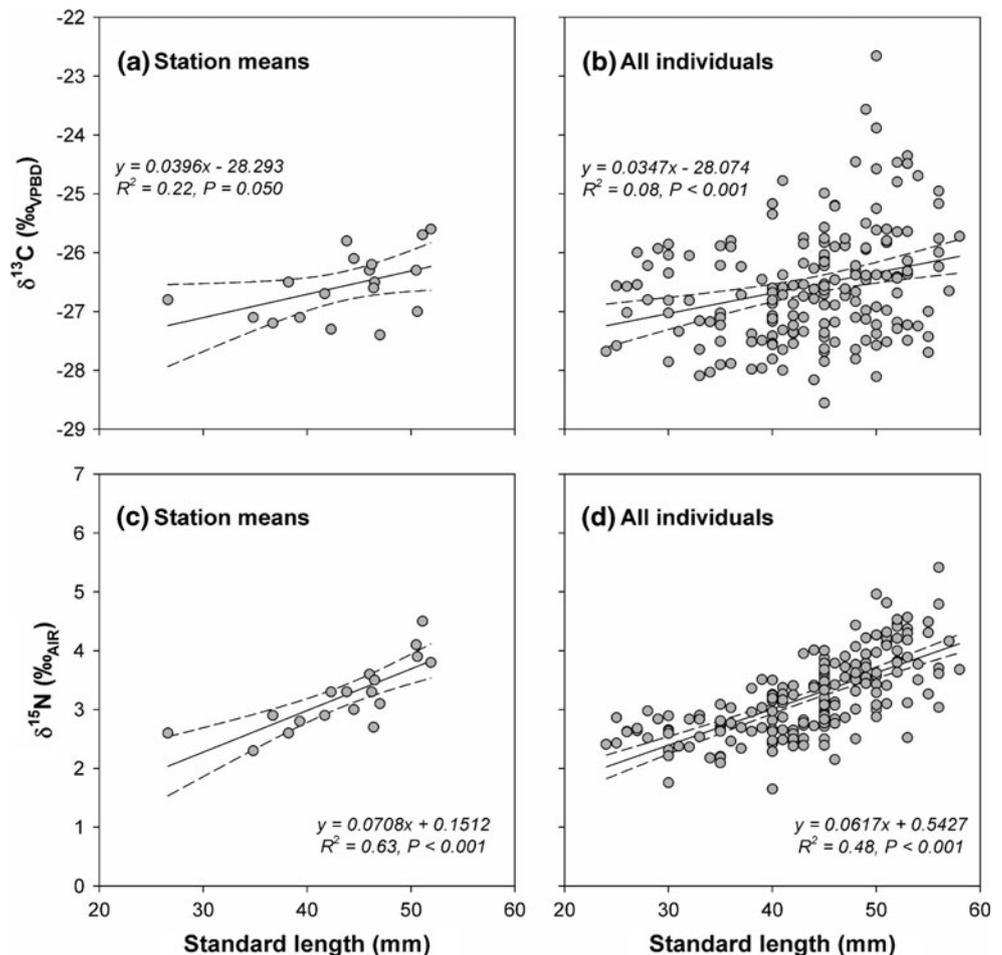
**Table 1** Mean ( $\pm$ SD) body size (SL), carbon-to-nitrogen ratio (C/N), stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of Antarctic krill (*Euphausia superba*), and selected abiotic and biotic oceanographic parameters at

18 sampling sites near the South Shetland Islands and northern Antarctic Peninsula in January 2007 and 2009

Years	Station No.	<i>E. superba</i> ( $n = 10$ per station)				Abiotic and biotic parameters			
		SL (mm)	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Max. depth (m)	Water temperature (°C)	Chl-a conc. ( $\text{mg m}^{-3}$ )	Copepod abundance (No. 1,000 $\text{m}^{-3}$ )
2007	A05.5-06	46.0 $\pm$ 5.0	3.4 $\pm$ 0.3	-26.3 $\pm$ 1.0	3.6 $\pm$ 0.4	122	0.8	0.75	995.3
	A09-03	46.5 $\pm$ 5.0	3.3 $\pm$ 0.2	-26.5 $\pm$ 1.0	3.5 $\pm$ 0.6	3622	1.7	0.09	62.1
	A09-07	50.5 $\pm$ 3.3	3.3 $\pm$ 0.3	-26.3 $\pm$ 0.9	4.1 $\pm$ 0.3	624	1.1	1.04	976.7
	A10-12	26.6 $\pm$ 1.8	3.4 $\pm$ 0.1	-26.8 $\pm$ 0.5	2.6 $\pm$ 0.2	760	1.7	1.41	160.1
	A11-13	36.7 $\pm$ 4.1	3.4 $\pm$ 0.1	-27.2 $\pm$ 0.8	2.9 $\pm$ 0.3	384	0.4	1.13	0.8
	A12-14	46.2 $\pm$ 2.9	3.6 $\pm$ 0.1	-26.2 $\pm$ 1.4	3.3 $\pm$ 0.7	130	0.3	0.87	42.1
	A14-08	51.1 $\pm$ 3.4	3.3 $\pm$ 0.0	-25.7 $\pm$ 0.5	4.5 $\pm$ 0.5	1640	1.5	2.42	303.1
	A16-08	43.8 $\pm$ 8.7	3.4 $\pm$ 0.1	-25.8 $\pm$ 0.6	3.3 $\pm$ 0.3	3430	1.5	1.59	1373.4
	A19-11	41.7 $\pm$ 5.4	3.3 $\pm$ 0.1	-26.7 $\pm$ 0.7	2.9 $\pm$ 0.4	780	1.1	1.36	121.6
2009	A02-04	44.5 $\pm$ 4.0	3.4 $\pm$ 0.0	-26.1 $\pm$ 1.5	3.0 $\pm$ 0.3	1806	0.9	0.75	38.8
	A04-02	51.9 $\pm$ 4.3	3.4 $\pm$ 0.1	-25.6 $\pm$ 1.0	3.8 $\pm$ 0.6	3315	2.4	2.05	1807
	A07-07	46.4 $\pm$ 4.0	3.4 $\pm$ 0.2	-26.6 $\pm$ 0.6	2.7 $\pm$ 0.3	503	1.5	0.91	264.5
	A08-12	38.2 $\pm$ 4.2	3.5 $\pm$ 0.1	-26.5 $\pm$ 0.7	2.6 $\pm$ 0.3	266	-0.2	1.17	83.7
	A13-11	39.3 $\pm$ 6.0	3.5 $\pm$ 0.1	-27.1 $\pm$ 0.3	2.8 $\pm$ 0.4	540	1.9	1.69	1817.8
	A15-15	34.8 $\pm$ 4.8	3.6 $\pm$ 0.2	-27.1 $\pm$ 0.6	2.3 $\pm$ 0.2	559	0.5	0.65	527.8
	A16-10	42.3 $\pm$ 4.5	3.7 $\pm$ 0.1	-27.3 $\pm$ 0.8	3.3 $\pm$ 0.4	4103	1.9	1.24	129.4
	A17-07	47.0 $\pm$ 5.7	3.6 $\pm$ 0.2	-27.4 $\pm$ 0.4	3.1 $\pm$ 0.7	3800	1.8	0.07	63.6
	A19-09	50.6 $\pm$ 3.3	3.4 $\pm$ 0.0	-27.0 $\pm$ 0.5	3.9 $\pm$ 0.4	4654	1.9	0.67	123.3

Values reflect lipid-extracted material

**Fig. 2** The relationship between body size and stable isotope values ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) in Antarctic krill (*Euphausia superba*) collected from 18 sampling stations near the South Shetland Islands and northern Antarctic Peninsula in January 2007 and 2009. Linear regression lines, 95 % confidence intervals, and test statistics are provided for relationships at both the station (a, c mean values) and individual levels (b, d all values). Individual-level test statistics are for reference only due to the sampling of multiple krill at each station



juveniles having lower  $\delta^{15}\text{N}$  values relative to adult males and females which were similar (Table 3;  $F_{2,180} = 7.09$ ,  $P = 0.005$ ). These trends were similar in both years with no significant size class\*year interaction ( $F_{2,180} = 0.13$ ,  $P = 0.876$ ). Mean krill  $\delta^{13}\text{C}$  values did not differ among groups (i.e., juveniles, males, and females; Table 3;  $F_{2,180} = 0.57$ ,  $P = 0.576$ ) or exhibit a significant size class\*year interaction ( $F_{2,180} = 0.57$ ,  $P = 0.573$ ).

We found consistent differences in the niche width of juveniles versus adult males and females in both years (Fig. 3). Mean MDC was significantly higher (+0.3 to +0.4 ‰) in both adult males and females relative to juveniles (Table 2). Broader niches in adults were driven by larger variance in  $\delta^{15}\text{N}$  values of both adult male and females relative to juveniles in each year (2007:  $K^2 = 23.02$ ,  $df = 2$ ,  $P < 0.001$ ; 2009:  $K^2 = 8.85$ ,  $df = 2$ ,  $P = 0.012$ ). In contrast, the degree of variation in krill  $\delta^{13}\text{C}$  values did not differ among size classes (2007:  $K^2 = 2.45$ ,  $df = 2$ ,  $P = 0.294$ ; 2009:  $K^2 = 3.04$ ,  $df = 2$ ,  $P = 0.217$ ). Niches of individual juvenile krill overlapped substantially with niche width of either adult females or males (44.4–88.7 %; Table 2). Niche area overlap between adult females and males was also high (53.3–90.6 %). In

contrast, only 11.1–34.4 % of either adult male or female individuals were encompassed by the convex hull (i.e., isotopic niche area) of juveniles.

## Discussion

We found that  $\delta^{15}\text{N}$  values and to a lesser extent  $\delta^{13}\text{C}$  values of Antarctic krill in our study were positively related to body size. In addition, spatial variation in krill stable isotope values was best explained ( $\delta^{15}\text{N}$ ), or explained in part ( $\delta^{13}\text{C}$ ), by similar variation in the size of krill around the South Shetland Islands. Higher  $\delta^{15}\text{N}$  values in larger krill suggest an increased consumption of heterotrophic prey. While relatively weaker, a positive relationship between  $\delta^{13}\text{C}$  values and body size indicates that larger adult krill may also have increased access to benthic foraging habitats where higher trophic prey such as copepods are more commonly consumed (Schmidt et al. 2011).

When examining the stable isotope values of krill by specific size classes, we found higher and more variable  $\delta^{15}\text{N}$  values in adults of both sexes relative to juveniles. This trend was consistent across both years of our study

with the isotopic niche width of adult males and females being larger, but generally encompassing the niche of juveniles. Together, these results provide clear evidence of a classic asymmetric dietary niche expansion between juvenile and adult size classes of Antarctic krill (Werner and Gilliam 1984; Hammerschlag-Peyer et al. 2011). While we cannot fully quantify the diet compositions of each size class, the range of krill  $\delta^{15}\text{N}$  values observed in our study (1.7–5.4 ‰) suggests krill in the South Shetland Islands are likely foraging between two trophic levels. We can infer this because of a general increase in tissue  $\delta^{15}\text{N}$  values by 3–5 ‰ per trophic level (Minagawa and Wada 1984). Therefore, while phytoplankton likely remained an

important resource during the austral summers of 2007 and 2009, in both years most adults expanded their dietary niche to include heterotrophic food sources such as small zooplankton. It is possible that while both adult and juvenile krill use compression filter feeding to consume phytoplankton (Hamner 1988), adult krill might be relatively more selective or adept at raptorial capture of larger heterotrophic particles (Granéli et al. 1993).

Our study provides evidence of inter-annually consistent, size class-specific differences in the summer dietary niches of Antarctic krill around the South Shetland Islands. Nonetheless, previous studies in other regions during the austral summer have shown mixed results (Table 4).

**Table 2** Pairwise differences in isotopic niche position and width and the relative degree of niche overlap between juvenile, adult female, and adult male Antarctic krill (*Euphausia superba*) collected near the South Shetland Islands and northern Antarctic Peninsula in January 2007 and 2009

Metric, year	Size class	Juvenile	Adult female	Adult male
Niche position and width differences (‰)				
2007	Juvenile	–	1.2 (<0.001)	0.9 (0.004)
	Adult female	0.4 (0.015)	–	0.3 (0.250)
	Adult male	0.3 (0.075)	0.1 (0.567)	–
2009	Juvenile	–	0.9 (0.004)	0.7 (0.028)
	Adult female	0.4 (0.033)	–	0.3 (0.257)
	Adult male	0.4 (0.036)	0.1 (0.949)	–
Niche overlap (% individuals)				
2007	Juvenile	–	44.4	72.2
	Adult female	11.1	–	53.3
	Adult male	25.9	85.2	–
2009	Juvenile	–	66.7	88.7
	Adult female	27.9	–	83.7
	Adult male	34.4	90.6	–

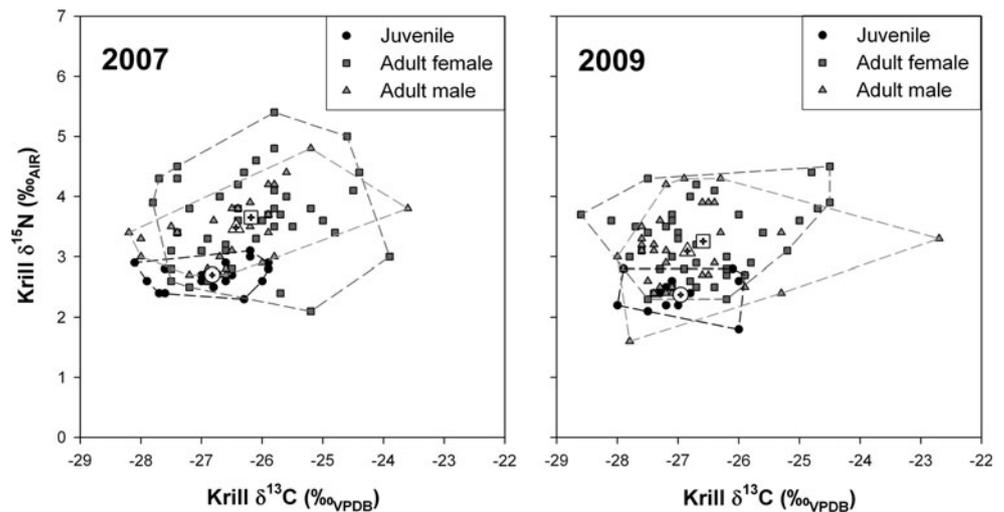
Differences in isotopic niche position (listed above the diagonal for each year) are the Euclidean distance between group centroids. Isotopic niche width comparisons (below the diagonal for each year) reflect differences in the mean distance to centroid among groups. *P* values are provided in parentheses. Niche overlap reflects the percent of individuals in each size class (rows) that are encompassed by the convex hull of comparison size class (columns) for each year

**Table 3** Sample size (*n*), mean ( $\pm$ SD) carbon-to-nitrogen ratio (C/N), and whole-body  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values of juvenile, adult female, and adult male Antarctic krill (*Euphausia superba*) collected near the South Shetland Islands and northern Antarctic Peninsula in January 2007 and 2009

Years	Group	<i>n</i>	SL (mm)	C/N	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)
2007	Juvenile	18	28.9 $\pm$ 3.4	3.4 $\pm$ 0.1	–26.8 $\pm$ 0.7	2.7 $\pm$ 0.2
	Adult female	45	47.8 $\pm$ 4.5	3.4 $\pm$ 0.2	–26.2 $\pm$ 1.0	3.6 $\pm$ 0.7
	Adult male	27	45.2 $\pm$ 5.1	3.4 $\pm$ 0.2	–26.4 $\pm$ 1.0	3.5 $\pm$ 0.6
2009	Juvenile	15	33.1 $\pm$ 2.1	3.6 $\pm$ 0.2	–27.0 $\pm$ 0.7	2.4 $\pm$ 0.3
	Adult female	43	47.2 $\pm$ 5.5	3.5 $\pm$ 0.1	–26.6 $\pm$ 1.0	3.3 $\pm$ 0.6
	Adult male	32	44.6 $\pm$ 5.1	3.5 $\pm$ 0.2	–26.8 $\pm$ 1.0	3.1 $\pm$ 0.6
Both years	Juvenile	33	30.8 $\pm$ 3.5	3.5 $\pm$ 0.2	–26.9 $\pm$ 0.7	2.6 $\pm$ 0.3
	Adult female	88	47.5 $\pm$ 5.0	3.4 $\pm$ 0.2	–26.4 $\pm$ 1.0	3.5 $\pm$ 0.7
	Adult male	59	44.9 $\pm$ 5.0	3.5 $\pm$ 0.2	–26.7 $\pm$ 1.0	3.3 $\pm$ 0.6

Values reflect lipid-extracted material

**Fig. 3**  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values (closed symbols), mean isotopic niche positions (open symbols), and total isotopic niche area (dashed lined convex hulls) of juvenile, adult female, and adult male Antarctic krill (*Euphausia superba*) collected near the South Shetland Islands and northern Antarctic Peninsula in January 2007 and 2009. See Table 2 for the results of detailed ontogenetic comparisons of isotopic niche metrics



Schmidt et al. (2006) found little evidence of ontogenetic-related differences in summer diets of krill sampled throughout the Scotia Sea in a study focused primarily on regional variation. However, due to the large spatial scale, wide spectrum of temperature, nutrients and phytoplankton conditions and limited juvenile sample sizes, ontogenetic-related differences may have been less apparent in their study (Table 4). In contrast, similar to our findings, Schmidt et al. (2004) reported higher  $\delta^{15}\text{N}$  values in adult male and female krill relative to juveniles near South Georgia in January 1996. Similarly, Stowasser et al. (2012) found a positive relationship between  $\delta^{15}\text{N}$  values and body mass in Antarctic krill collected in the Scotia Sea in January and February 2008. Unfortunately, many previous studies have not provided body size, age and/or sex information when reporting the stable isotope values of post-larval Antarctic krill (Table 4). In addition, such comparisons are further complicated across and within studies as growth and turnover of body tissues slow in larger krill with the stable isotope values of adults likely reflecting a longer dietary window relative to juveniles (Frazer et al. 1997; Siegel and Nicol 2000; Schmidt et al. 2003). These turnover differences with age may result in a slight temporal mismatch in our ontogenetic comparisons. However, there is growing evidence from stable isotopes and other methods to suggest that adults consume a relatively greater proportion of heterotrophic prey than juveniles in the austral summer, corresponding to similar trends in the austral autumn and winter (Table 4; Atkinson et al. 2002; Ju and Harvey 2004).

Nonetheless, it is likely that small krill consume some proportion of zooplankton (e.g., Hernández-León et al. 2001), as phytoplankton intake alone may not meet their energetic requirements (Pakhomov et al. 1997). In addition, there is ample evidence from our study and others that autotrophic resources remain an important food source of

adult krill (Maciejewska 1993; Schmidt et al. 2003, 2006). Therefore, temporal or spatial variability in the availability of autotrophic versus heterotrophic food sources is likely to influence the relative degree of ontogenetic differences in krill diets. Even so, we found no evidence for relationships between krill  $\delta^{15}\text{N}$  values and either of two indices of resource availability (chl-a concentration and copepod abundance). One possible explanation for this absence may be a temporal mismatch. Isotopic signatures of whole-body krill reflect diets over at least the previous month and krill stable isotope values can be slow to change in response to a new food environment (Frazer et al. 1997; Schmidt et al. 2003). While shipboard and satellite-derived measurements of Chl-a concentration suggested that variation in the relative abundance of primary producers across stations was consistent in the months before and during krill sampling, we could not similarly confirm this fact for zooplankton prey. If the spatial pattern (i.e., differences across stations) of relative copepod abundance varied dramatically prior to when we sampled krill, it could have confound the comparisons conducted here. In addition, this analysis may have benefited from abundance data on tintinnids or heterotrophic dinoflagellates that in some cases may be better indicators of zooplankton prey availability for krill (Schmidt et al. 2003).

Factors other than a dietary niche expansion also may have influenced the general increase in  $\delta^{15}\text{N}$  values we observed in adult krill. Rapid somatic growth can lower tissue  $\delta^{15}\text{N}$  values because the ratio of nitrogen incorporated into body tissue, relative to nitrogen loss, is higher in growing than in nongrowing animals (Martínez del Río and Wolf 2005; Trueman et al. 2005; Reich et al. 2008; Sears et al. 2009). While daily growth rates of Antarctic krill decrease with size (Siegel and Nicol 2000), the magnitude of growth-related  $^{15}\text{N}$  depletion in tissues is small ( $\leq 0.5\text{‰}$ ; Sears et al. 2009) relative to the range of  $\delta^{15}\text{N}$

**Table 4** Previously published stable isotope values (mean  $\pm$  SD) for post-larval Antarctic krill (*Euphausia superba*)

Region	Collection Date	n	Age/Sex	Tissue	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	Notes <sup>a</sup>	Source <sup>b</sup>
South Georgia	Jan. 1996	20	Juvenile	Whole	-26.3 $\pm$ 1.5	3.5 $\pm$ 0.6	MC	1
	Jan. 1996	3	Adult female	Whole	-22.6 $\pm$ 1.0	4.0 $\pm$ 0.3	MC	1
	Jan. 1996	3	Adult male	Whole	-22.7 $\pm$ 2.3	5.3 $\pm$ 0.4	MC	1
Scotia Sea	Summer 2002	10	Unknown	Whole	-18.3 $\pm$ 0.6	6.2 $\pm$ 0.3	LE,SC	2
	Jan.–Feb. 2003	4	Juvenile	Muscle	-27.2 to -25.2 $\pm$ 0.4 <sup>c</sup>	3.3 to 3.4 $\pm$ 0.3 <sup>c</sup>	NE	3
	Jan.–Feb. 2003	19	Adult female	Muscle	-27.6 $\pm$ 1.1 to -19.6 $\pm$ 0.5 <sup>c</sup>	3.0 $\pm$ 0.2 to 5.6 $\pm$ 0.2 <sup>c</sup>	NE	3
	Jan.–Feb. 2003	30	Adult male	Muscle	-27.7 $\pm$ 0.8 to -20.4 $\pm$ 0.4 <sup>c</sup>	3.2 $\pm$ 0.5 to 5.7 $\pm$ 0.5 <sup>c</sup>	NE	3
South Shetland Is.	Jan.–Feb. 2008	20	Unknown	Whole	-22.3 $\pm$ 3.1	4.3 $\pm$ 1.0	LE	4
	Mar. 2000	9	Juvenile	Whole	-25.1 $\pm$ 0.9	4.2 $\pm$ 0.4	MC	1
	Mar. 2000	9	Adult female	Whole	-28.3 $\pm$ 0.7	2.9 $\pm$ 0.4	MC	1
	Jan. 2008	10	Adult	Whole	-26.5 $\pm$ 0.4	3.2 $\pm$ 0.4	LE	5
	Jan. 2007 & 2009	33	Juvenile	Whole	-26.9 $\pm$ 0.7	2.6 $\pm$ 0.3	LE	6, 7, 8, 9
Antarctic Peninsula	Jan. 2007 & 2009	88	Adult female	Whole	-26.4 $\pm$ 1.0	3.5 $\pm$ 0.7	LE	6, 7, 8, 9
	Jan. 2007 & 2009	59	Adult male	Whole	-26.7 $\pm$ 1.0	3.3 $\pm$ 0.6	LE	6, 7, 8, 9
	Mar. 1989	12	Adult	Muscle	-29.8 $\pm$ 0.6	3.6 $\pm$ 0.2	NE	10
	Mar. 2000	6	Adult	Whole	-28.2	4.9	MC	11
	Apr. 1999	23	Juvenile	Whole	-31.1 $\pm$ 0.7	2.1 $\pm$ 0.9	MC	1
Lazarev Sea	Apr. 1999	20	Adult	Whole	-31.3 $\pm$ 0.7	3.6 $\pm$ 0.4	MC	1
	Winter/Spring 2002	12	Unknown	Whole	-25.8 $\pm$ 0.4	5.5 $\pm$ 0.4	LE,A,SC	12
Adélie Land	Summer 2002	10	Unknown	Whole	-25.4 $\pm$ 0.6	5.3 $\pm$ 0.5	LE,A,SC	12
	Jan. 1984	Unknown	Juvenile	Whole	-28.1	1.0	NE	13
East Antarctica	Jan. 1984	Unknown	Adult	Whole	-29.3	2.7	NE	13
	Summer 2001–2003	9	Adult	Whole	-24.8 $\pm$ 0.9	3.0 $\pm$ 0.8	LE,SC	14
	Summer 2002–2003	10	Unknown	Whole	-25.0 $\pm$ 0.3	4.0 $\pm$ 0.2	LE,A	15

<sup>a</sup> MC values mathematically corrected for lipid content, LE chemically lipid extracted, A acidified, NE not lipid extracted, SC recovered from predator stomach

<sup>b</sup> 1) Schmidt et al. 2004, 2) Anderson et al. 2009, 3) Schmidt et al. 2006, 4) Stowasser et al. 2012, 5) Polito and Groebel 2010, 6) This study, 7) Polito et al. 2009, 8) Polito et al. 2011a, 9) Polito et al. 2011b, 10) Dunton 2001, 11) Schmidt et al. 2003, 12) Cherel 2008, 13) Wada et al. 1987, 14) Tierney et al. 2008, 15) Hodum and Hobson 2000

<sup>c</sup> Range of stable isotope values across individual maturity stages and five sampling stations in the Scotia Sea

values observed in our study (1.7–5.4 ‰). Also, growth effects are not likely to lead to the observed increased variability in adult krill  $\delta^{15}\text{N}$  values that are more convincingly explained by an ontogenetic trophic-niche expansion. Ontogenetic differences in tissue composition may have also had the potential to influence the isotopic signatures of krill in our study. For example, carbon isotope values in zooplankton can be skewed to lower values by gut contents that typically have lower  $\delta^{13}\text{C}$  values compared to body tissues (Hill and McQuaid 2011). Also, the chitinous exoskeletons of zooplankton exhibit low  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values relative to whole-body isotope values (Gorokhova and Hansson 1999). Lastly, a previous study found tissue-specific differences in  $\delta^{15}\text{N}$  values between reproductively active male and female Antarctic krill driven by variations in the relative proportions and  $\delta^{15}\text{N}$  signatures of amino acids in these tissues (Schmidt et al. 2004). Therefore, we cannot discount the possibility that size class or sex-related isotopic trends, or the lack thereof, may be due in some small part to differences in tissue composition. Regardless, the magnitude of the bias introduced by these caveats would be small relative to the range of size-related differences found in our study. For example, based on the calculations of Fach et al. (2008), the protein-to-chitin ratio of juvenile and adult krill in our study differed by less than 0.1 % and is therefore very unlikely to drive body size-related differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values. Therefore, shifts in krill  $\delta^{15}\text{N}$  values we observed best support the hypothesis that adult Antarctic krill in the South Shetland Islands expanded their dietary niche to include higher trophic food sources.

Our study also substantiates increasing evidence that  $\delta^{13}\text{C}$  values of marine organisms are influenced by temporal and spatial variation in primary production (Schell 2000; Hirons et al. 2001; Hilton et al. 2006). Our krill  $\delta^{13}\text{C}$  values were positively related to chl-a concentration, a proxy for primary production, at each sampling site. Similarly, Schell et al. (1998) found spatial variation in  $\delta^{13}\text{C}$  values of zooplankton across the Bering, Chukchi, and Beaufort Seas that were due to differences in oceanographic conditions and phytoplankton growth rates, thereby forcing isotopic discrimination at the base of each food web. Furthermore, Jaeger and Cherel (2011) found that seasonal variation in feather  $\delta^{13}\text{C}$  values of six southern ocean penguin species and chl-a concentration were positively correlated. Because many of the penguin species examined by Jaeger and Cherel (2011) are crustacean predators, our two studies suggest a causal link between the productivity of the pelagic ecosystem and  $\delta^{13}\text{C}$  values of Antarctic krill and their predators.

We found no evidence of correlations between krill  $\delta^{13}\text{C}$  values and depth or temperature at sampling stations, despite the predicted relationships identified by previous

studies (Hinga et al. 1994; France 1995). The lack of relationship with these parameters may be a function of scale. While the maximum bottom depths observed at several sampling stations are within the vertical migration range of krill (Schmidt et al. 2011), they were deeper than the distributional limits of most benthic algae (~40 m; Gómez et al. 2009) limiting their potential impacts to baseline  $\delta^{13}\text{C}$  values. In addition, the range of temperatures observed in our study area is small (−0.2–2.4 °C) relative to previous experimental and field studies (0–26 °C) that have found temperature-related effects on  $\delta^{13}\text{C}$  values of pelagic phytoplankton (Rau et al. 1991; Hinga et al. 1994). In contrast, there is evidence to suggest that at larger spatial scales, both krill and ecosystem baseline  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values can vary widely in the Southern Ocean and are influenced by factors such as changes in phytoplankton communities and increases in the  $\delta^{15}\text{N}$  values of the nitrate pool by phytoplankton uptake (Table 4; Lara et al. 2010).

Our study highlights an ontogenetic dietary niche expansion in Antarctic krill during the austral summer around the South Shetlands Islands with narrower dietary niches in juveniles relative to adults. Evidence from empirical and modeling studies suggest organisms that undergo ontogenetic niche shifts are often hypersensitive to changes in resource availability due to specialized, stage-specific niches (Rudolf and Lafferty 2011). Therefore, it is possible that differences in the trophic niches of juvenile and adult Antarctic krill may be shaping their species-level responses to recent warming trends along the Antarctic Peninsula and South Shetlands Islands (Vaughan et al. 2003). Over the last 30 years, there have been significant declines in Antarctic krill biomass around the South Shetland Islands that are correlated with reductions in the abundance of juvenile krill cohorts (Atkinson et al. 2004; Reiss et al. 2008; Trivelpiece et al. 2011). Recent changes in ocean temperatures, salinity, and sea ice-cover are thought to have shifted phytoplankton community compositions toward smaller species and reduced diatom biomass available to krill around the South Shetland Islands and Antarctic Peninsula (Gille 2002; Moline et al. 2004; Stammerjohn et al. 2008; Montes-Hugo et al. 2009). Both adult and juvenile Antarctic krill selectively graze on diatoms in preference to smaller phytoplankton (Maciejewska 1993; Opalinski et al. 1997; Haberman et al. 2003). For adult krill, the ability to consume zooplankton may buffer them from shifts in the phytoplankton community that might negatively affect larval or juvenile krill that rely predominately on phytoplankton. Future work would benefit from examining the isotopic niches of juvenile and adult krill in this region during the austral winter to determine how ontogenetic niche differences may shape the responses of Antarctic krill to recent environmental changes.

**Acknowledgments** This research was funded by U.S. National Science Foundation (NSF) Office of Polar Programs (OPP) grant ANT-0739575 and the US AMLR program. We thank A. Cossio, K. Dietrich, R. Driscoll, M. Goebel, C. Hewes, V. Loeb, A. VanCise, J. Walsh and the AMLR physical and biological oceanography and zooplankton teams for assistance with the collection of oceanographic data and krill samples. J. Seminoff, K. Durenberger, D. Besic, and J. Blum assisted with lipid extractions, stable isotope, and statistical analyses. J. Hinke, M. Goebel and two anonymous reviewers provided helpful comments on an earlier version of this manuscript.

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