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SPECIAL FEATURE The ornithological application of stable isotope analysis

Isotopic values of Antarctic Krill in relation to foraging habitat of penguins

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ORNITHOLOGICAL SCIENCE

Abstract Antarctic Krill *Euphausia superba* is a key component of the Antarctic coastal marine ecosystem. Investigations into stable isotopic values of krill in predation hotspots are important in facilitating our understanding of the feeding environments of krill in a local coastal ecosystem. In this study we investigated stable isotopic values and maturity and size composition of krill at a small spatial scale, by logging GPS tracks of five Chinstrap *Pygoscelis antarcticus* and seven Gentoo *P. papua* penguins, and analyzing their stomach contents. The study was conducted at a penguin colony on Barton Peninsula, King George Island, Antarctica. The main food item of both species was Antarctic Krill (>98% wet mass). One Chinstrap and four Gentoo penguin foraging trips were classified as "on-shelf" trips, and four Chinstrap and three Gentoo Penguin foraging trips were classified as "off-shelf" trips. Krill collected from off-shelf trips had higher δ^{15}N (4.22±0.28‰) values than those from on-shelf trips (3.78±0.29‰). The δ^{13}C of the krill samples did not differ between the two penguin species or between trip types. The proportion of juvenile krill taken was higher for Chinstrap (13.04±4.97%) than Gentoo penguins (3.33±2.43%). Our results suggest that the main food source of the krill in our sample originated as non benthic planktonic/suspended organic matter, and that krill in off-shelf habitat may occasionally consume higher trophic level prey compared to those in on-shelf habitats.

Key words GPS tracking, Off-shelf, On-shelf, Phytoplankton, Stomach flushing

The Antarctic Krill *Euphausia superba* (hereafter referred to as krill) is a key component of the Southern Ocean ecosystem because of it's high biomass and importance as prey for penguins, flying birds, marine mammals, fishes and benthic invertebrates (Atkinson et al. 2009). Krill occur in a wide range of marine habitats, from the epi-pelagic (the upper 200 m of the water column) to the abysso-pelagic (down to 3,500 m) zones, and from open water to beneath sea ice, and on the sea floor (Brierley et al. 2002; Siegel 2005; Schmidt et al. 2011). However, krill consumption by predators is concentrated in certain 'hotspots' such as along the continental shelf, along ice edges and ocean fronts, which occur at a scale of tens of kilometers (Atkinson et al. 2008). It is important to know the trophic condition of krill in hotspots such as these, as this condition is important in developing a fuller understanding of the relationship between krill and their feeding environment in the Antarctic coastal marine ecosystem.

In situ sampling of krill at hotspots has been difficult because of space and time constraints. Ship-based surveys have been a major approach to investigating krill distribution and/or composition; these have usually operated on large spatial scales or over limited timeframes (e.g., Lascara et al. 1999: >100s km, but see Cox et al. 2011: inflatable boat-based study with ~100s m scale along the Antarctic coast). Dietary analysis of krill predators provides a complementary approach (Croxall & Pilcher 1984; CCAMLR 2004), but diet samples themselves do not provide information on the locations where predators feed on krill at sea. Recently developed animal-borne GPS-

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depth loggers and camera/video loggers allow us to examine the foraging habitat of krill predators at a fine scale (<1 km: Kokubun et al. 2010; <1 min: Takahashi et al. 2008). With these techniques, we can use medium-sized penguins as "krill samplers" in the Antarctic coastal environment, including shallow waters (<50 m) where net sampling and/or acoustic surveys are usually difficult.

Meanwhile, carbon and nitrogen stable isotopic ratio (δ^{13}C and δ^{15}N) analyses have become a major approach for determining the source of food, such as the pelagic/benthic systems and trophic structure of marine organisms in the marine food web (Wada et al. 1987). The stable isotopic signatures of Antarctic Krill have been used as an indicator of seasonal/basin-scale variation in their food habits (Frazer 1996; Polito et al. 2013). Although some previous studies (Siegel 2005; Ichii et al. 2007) have demonstrated a relationship between local oceanographic environments and krill maturity and size composition, few studies have been made of the stable isotopic values of krill at a sufficiently small scale (<10s km) to correspond with predation hotspots. Small-scale studies of stable isotopic values of krill thus provide opportunities for new insights into the feeding environments of krill in the Antarctic coastal marine ecosystem. Specifically, we expected that krill foraging in on-shelf habitats would have higher δ^{13}C compared to those in off-shelf habitats, because on-shelf habitat is spatially close to the sea bottom, and benthic food sources (e.g., benthic diatoms) have higher δ^{13}C values compared to pelagic food sources (e.g. planktonic diatoms) (France 1995).

In this study, we aimed to investigate various characteristics of krill, including stable isotope ratios, the composition of maturity stages, and total length in relation to individual variation in penguin foraging habitat. We used GPS-depth loggers to track sympatric Chinstrap *Pygoscelis antarcticus* and Gentoo *P. papua* penguins as krill samplers. We investigated species-specific (penguin species) and habitat-specific (on-shelf and off-shelf trips) differences in the characteristics of the krill taken from the foraging habitat of the penguins.

MATERIALS AND METHODS

1) Study site

The field study was conducted on the Barton Peninsula, King George Island, Antarctica (62°14′16″S, 58°46′30″W), where 2,278 pairs of Chinstrap and 1,759 pairs of Gentoo penguins breed sympatrically (Antarctic Specially Protected Area no. 171: Narębski Point). The vicinity of the study colony is characterized by shallow waters less than 200 m deep, including glacial coves, neritic areas along the coast, and deep waters more than 200 m deep, including the central part of Maxwell Bay and the open water part of the northern Bransfield Strait (Fig. 1). We defined locations with a bottom depth of less than

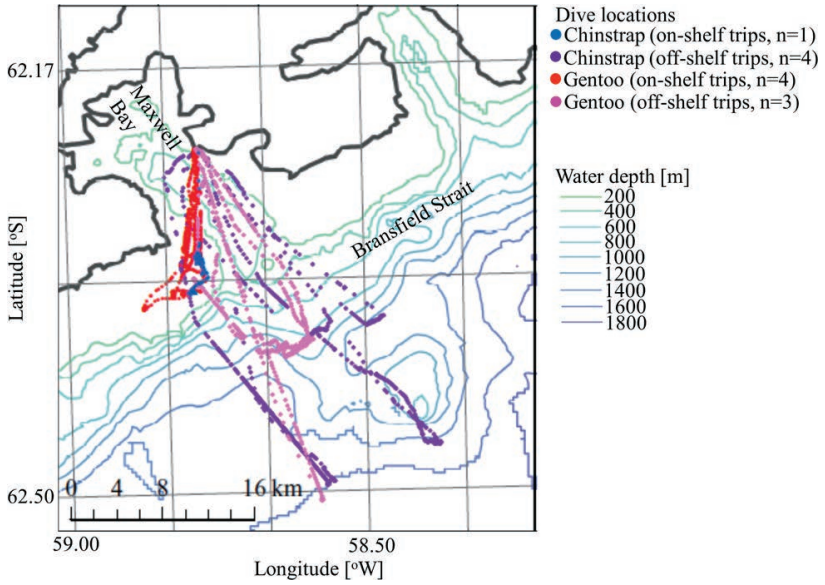

Fig. 1. Location of dives >5 m for on-shelf and off-shelf trips of chinstrap and gentoo penguins. The definitions of on-shelf and off-shelf trips are provided in MATERIALS AND METHODS.

200 m as "on-shelf", and locations with a bottom depth of more than 200 m as "off-shelf" according to the bathymetry, as previously defined by Ichii et al. (2007). Penguins occasionally make benthic dives in the on-shelf region (Takahashi et al. 2008; Kokubun et al. 2010). The study was conducted from 22 December 2009 to 23 January 2010, which covered the chick-guarding period of both penguin species. Sea ice was not observed in the study area during the study period.

2) Foraging habitat of penguins

GPS-depth loggers (GPL380-DT, housed in a rectangular container measuring 58 mm long×28 mm wide×20 mm tall with a cylindrical battery section measuring 20 mm in diameter, 47 mm long, and with a mass of 92 g; Little Leonardo Inc., Tokyo, Japan) were deployed on six Chinstrap and seven Gentoo penguins to investigate the duration of foraging trips away from the colony, the maximum distance from the colony during the trips, as well as diving depth and location. The loggers were set to record location and diving depth once every second. We did not monitor the behavior of penguins with and without GPS-depth loggers, but Kokubun et al. (2010) found no significant effects of GPS-depth loggers (92 g) on either diving behavior or trip duration when compared with smaller (17 g) loggers. Stomach contents were collected (see "Krill Sampling and Analyses") from the same individuals just after they had completed a foraging trip. Diving depth, and the location of each dive deeper than 5 m, was investigated using the GPS-depth data (Kokubun et al. 2010). The last location recorded prior to a dive was regarded as the location of the dive. The average time between the last occasion when the GPS location was fixed and when the dive began was 8.97±5.90 s (ranging from 0 to 259 s). Given that *Pygoscelis* penguins swim at a mean speed of 2.1 ms^{-1} (Culik & Wilson 1994), the accuracy of the location of dives was within 20 m on average. If the data logger failed to record the location of a dive, the location was interpolated linearly using the nearest neighbor locations associated with the time when the dive occurred. Water depth where dives occurred was investigated with ArcView® using digitized bathymetric data. *Dives* were defined as "on-shelf dives" if the dive occurred in on-shelf area; otherwise they were defined as "off-shelf dives". Furthermore, dives were defined as "benthic dives" if the maximum dive depth exceeded the deepest 20% of the water column (Kokubun et al. 2010). *Trips* were defined as "on-shelf trips" if the proportion of on-shelf dives exceeded half of all dives made during the trip; otherwise trips were defined as "off-shelf trips", in consideration of the clear bimodal distribution in the proportion of on-shelf dives (Fig. 2).

3) Krill sampling and analyses

Stomach contents were collected using the standard stomach-flushing method (CCAMLR 2004) from the same individual penguins that were tracked by the GPS-depth loggers. We flushed the stomach contents using a funnel, a silicone gum tube and warm water (twice per individual). Stomach content samples were weighed to the nearest 1 g with an electronic balance, visually sorted and identified to the lowest possible taxonomic level. Twenty to 200 krill specimens

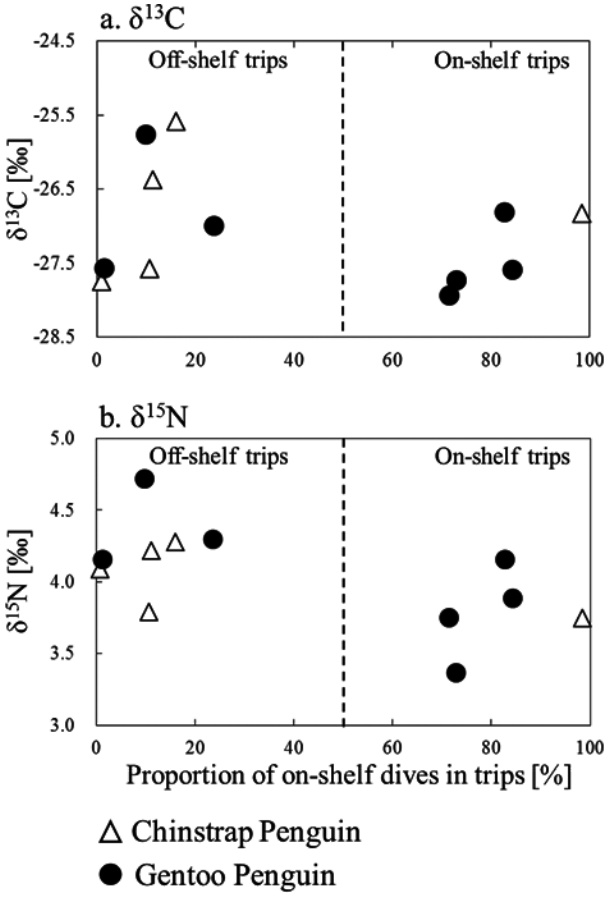

Fig. 2. Carbon (a: $\delta^{13}C$) and nitrogen (b: $\delta^{15}N$) stable isotopic ratio values of Antarctic Krill taken during on-shelf and off-shelf trips by Chinstrap and Gentoo penguins. The symbols listed below correspond to stable isotopic results for each penguin species. The vertical dotted line shows the 50% threshold in the proportion of on-shelf dives that separates on-shelf and off-shelf trips (see MATERIALS AND METHODS).

retaining their original form were sub-sampled and inspected under a microscope to determine their sex and stage of maturity (Makarov & Denys 1981). Krill carapace lengths were measured after removal, and the total length of each krill was estimated using sex- and maturity stage-specific equations for the relationship between carapace length and body length (Hill 1990). Fish species were identified following Gon and Heemstra (1990).

Krill were randomly sub-sampled and freeze dried for about 48 hours in preparation for stable isotope analysis (δ^{13}C and δ^{15}N). Lipids were not extracted from the krill samples. The samples were analyzed using a system that coupled an elemental analyzer (EuroVector 3000 Series) with a continuous-flow isotope ratio mass spectrometer (CF-IRMS; Isoprime, GV Instruments, U.K.). Stable isotope abundance is expressed in delta (δ) notation as the deviation from the conventional standard Pee Dee Belemnite (PDB) for carbon and air N_2 for nitrogen in parts per thousand (‰), according to the equation: $\delta X=([R_{sample}/R_{standard}]-1)\times 10^3$, where X is ^{13}C or ^{15}N and R is the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio, respectively (Fry & Sherr 1984). Sucrose (ANU $C_{12}H_{22}O_{11}$; NIST, Gaithersburg, MD) and ammonium sulfate ($[NH_4]_2SO_4$; NIST) were used for the internal ^{13}C and ^{15}N calibration, respectively, and were analyzed twice after every six samples. The analytical reproducibility, based on the standard deviations of at least three analyses for each sample, was approximately ±0.1‰ for δ^{13}C and ±0.3‰ for δ^{15}N.

The δ^{13}C, the δ^{15}N, the proportion of adult females and juveniles, and the total lengths of Antarctic Krill, were compared between the two penguin species and between trip types.

4) Statistics

The data were analyzed using a generalized linear model (GLM) or a generalized linear mixed model (GLMM) to investigate the effects of penguin species and/or trip types. GLMs were used for analyzing data that were sampled only once for each individual, such as trip duration, maximum trip distance from the colony, stable isotope, the proportion of on-shelf and off-shelf dives or benthic dives, and the proportion of adult female and juvenile krill. A binomial error distribution was used to analyze the proportion data, and a Gaussian error distribution was used after examining the normality (Shapiro-Wilk normality test, $P>0.05$) for the GLM analyses. GLMMs were used for analyzing data sampled repeatedly from the same individual, such as diving depth and total length of krill. A Gamma error distribution was used in the models given the skewed nature of the dependent variables, and bird identity was set as a random effect in the models. We used the "lme4" package in the R® 2.7.0 software (R Development Core Team 2008). Data are presented as mean values±S.D.

RESULTS

1) Foraging habitat of penguins

Six Chinstrap and seven Gentoo penguins fitted with GPS-depth loggers were recaptured as they arrived back at their colony from foraging trips (in each case within one day of release), the loggers were retrieved, and stomach contents were collected. The stable isotope analysis of the stomach contents of one Chinstrap Penguin failed. As a consequence, five trips made by Chinstrap and seven trips made by Gentoo penguins (combination of GPS tracks, diving depth and stomach contents with stable isotope analyses) were available for the subsequent analyses. The percentage of actual GPS locations of dives to deeper than 5 m located during the trips averaged 50.41±17.54% for Chinstrap and 43.97±26.65 % for Gentoo penguins. Other locations of dives to deeper than 5 m were linearly interpolated from nearest neighbor locations (see Materials and Methods). The average times and distances to the nearest neighbor GPS locations from the interpolated locations were: 39.70±27.62 min (ranging from 0.02 to 212.93 min) and 1.97±1.75 km (ranging from 0.00 to 14.29 km).

Neither foraging trip duration nor maximum trip distance from the colony differed between the two penguin species (Table 1, trip duration: GLM with Wald test, $t=-0.8$, $P=0.448$; maximum trip distance: GLM with Wald test, $t=-1.3$, $P=0.212$). Diving depth did not differ between the penguin species (Table 1: GLMM with LRT, $\chi^2=0.1$, $P=0.725$; see also Fig. 1). Gentoo Penguins made proportionally more on-shelf dives than did Chinstrap Penguins (Table 1: GLM with Wald test, $z=8.8$, $P<0.001$), they also made a higher proportion of benthic dives than Chinstrap Penguins (Table 1: GLM with Wald test, $z=8.0$, $P<0.001$).

One Chinstrap and four Gentoo penguin trips were categorized as "on-shelf", and four Chinstrap and three Gentoo penguin trips were categorized as "off-shelf" (Figs. 1 and 2). Diving depth was unrelated to trip type (Table 1: GLMM with LRT, $\chi^2=1.2$, $P=0.269$).

Table 1. Comparison of trip and dive parameters between chinstrap and gentoo penguins, and on-shelf and off-shelf trips (means±S.D.).

	Chinstrap	Gentoo	On-shelf trips	Off-shelf trips
N	5 trips	7 trips	5 trips	7 trips
Trip and dive parameters				
Trip duration (h)	12.19± 4.90	10.58± 2.04	8.89± 0.51	12.94±3.64
Trip distance (km)	23.68± 8.60	17.36± 7.76	12.42± 2.02	25.40±6.65
Proportion of on-shelf dives (%)	27.42±40.09	47.62±34.98	79.70±11.79	10.28±7.60
Proportion of benthic dives (%)	1.87± 3.70	15.36±18.16	22.62±16.87	0.54±0.86
Diving depth (m)	39.09± 7.34	37.31±10.85	32.22±10.01	40.37±8.24

Only dives >5 m were used for the analyses.

Table 2. Comparison of krill characters between chinstrap and gentoo penguins, and on-shelf and off-shelf trips (means±S.D.).

	Chinstrap	Gentoo	On-shelf trips	Off-shelf trips	
N	5 trips	7 trips	5 trips	7 trips	
Krill characters					
δ^{13}C of the krill sample	−26.82± 0.89	−27.19± 0.75	−27.37±0.53	−26.80± 0.90	
δ^{15}N of the krill sample	4.03± 0.24	4.05± 0.43	3.78±0.29	4.22± 0.28	
Proportion of female adult krill (%)	29.22±10.19	41.78±10.13	42.36±9.03	32.40±12.08	
Proportion of juvenile krill (%)	13.04± 4.97	3.33± 2.43	5.03±5.49	9.05± 6.34	
Body length of krill (mm)	45.47± 1.56	46.66± 0.61	46.58±0.69	45.87± 1.45	
Statistical analyses	Between penguin species		Between trip types		
	Statistic	P value	Statistic	P value	Model used
δ^{13}C of the krill sample	t=−0.788	0.449	t=−1.269	0.233	GLM (g) & W
δ^{15}N of the krill sample	t=0.115	0.910	t=−2.662	0.024*	GLM (g) & W
Proportion of female adult krill (%)	z=1.766	0.077	z=1.675	0.094	GLM (B) & W
Proportion of juvenile krill (%)	z=−3.770	<0.001*	z=−0.065	0.948	GLM (B) & W
Body length of krill (mm)	χ^2=0.056	0.812	χ^2=0.005	0.943	GLMM (G) & LRT

Statistical terms are abbreviated: *GLM* generalized linear model, *GLMM* generalized linear mixed model, W Wald test, LRT likelihood ratio test.
In GLMs and GLMMs, "g", "G" and "B" mean that the Gaussian, gamma and binomial distribution were used (see MATERIALS AND METHODS).
Asterisks mean that significant differences were observed.

The main prey of both penguin species was Antarctic Krill (wet mass, 99.80±0.21% for Chinstrap and 99.44±1.08% for Gentoo). A total of four partially digested Antarctic Silverfish *Pleurogramma antarcticum* were found in the stomach contents of two Chinstrap and two Gentoo penguins (one fish per individual). Because of the high proportion of Antarctic Krill in the penguin diet, we focused only on this species in further dietary analyses.

2) Characteristics of antarctic krill

The δ^{13}C of the krill samples did not differ between penguin species or trip types (Table 2; Fig. 2a). The δ^{15}N of krill did not differ between penguin species, but krill collected from off-shelf trips had higher δ^{15}N values than those from on-shelf trips (Table 2; Fig. 2b).

There was no significant difference in the proportion of adult female krill taken, between penguin species or trip types (Table 2). Chinstrap Penguins took a higher proportion of juvenile krill than did Gentoo Penguins (Table 2). The size of krill taken did not differ between the penguin species or the trip types (Table 2).

DISCUSSION

This study investigated the characteristics of Antarctic Krill at a small spatial scale (tens of kilometers) by combining GPS tracking data and stomach contents analyses of krill-feeding penguins. In regard to the stable isotope values, on the one hand the δ^{13}C of the krill did not differ between trip types (Table 2), contrary to the expectation that krill from on-shelf trips would have higher δ^{13}C compared with off-shelf trips. On the other hand, krill from off-shelf trips had higher δ^{15}N values than those from on-shelf trips (Table 2). Despite the small sample size (five Chinstrap and seven Gentoo, or five on-shelf and seven off-shelf trips), our results may be helpful for inferring feeding environments of krill in predation hotspots.

First, the δ^{13}C result may suggest that krill collected from on-shelf foraging trips did not necessarily feed on benthic food sources. δ^{13}C is an index implying that marine food sources originate from benthic or pelagic environments (France 1995). Wada et al. (1987) and Corbisier et al. (2004) showed that δ^{13}C of Antarctic Krill (without lipid extraction) have similar or even lower values (~1 to 2 ‰) than their food sources. Krill in this study (−27.32±0.53‰ for on-shelf and −26.80±0.90‰ for off-shelf) had similar δ^{13}C values to small pelagic phytoplankton or particulate organic matter (POM), and considerably lower than micro-phytobenthos (δ^{13}C values available from previous studies were −25.6±1.9‰ for small phytoplankton <62 μm; −16.7±2.1‰ for micro-phytobenthos, −28.7‰ for large phytoplankton or zooplankton >150 μm, and −26.6±1.3‰ for POM, in the same region during the austral summer season; Corbisier et al. 2004; Eun-Jung Choy personal communication). These results suggest that the main food source of krill in this study probably originated as planktonic/suspended organic matter (e.g. nano- to pico-sized phytoplankton, not benthic phytoplankton) for both on-shelf and off-shelf habitats, although benthic diatoms are occasionally found in the water column as a result of re-suspension following tidal and/or storm mixing (Kang et al. 2002). Krill occasionally feed on benthic diatoms (Ligowski 2000) in the same region.

Second, the difference in δ^{15}N values between trip types may suggest a slightly different food composition of krill between on-shelf and off-shelf habitats. The δ^{15}N is expected to increase by 3.3‰ if one trophic level increases in the Antarctic marine environment (Wada et al. 1987). Therefore, the small difference in the krill δ^{15}N between the penguin trip types (0.44‰ higher on average for the on-shelf trips compared with the off-shelf trips) suggests that the trophic level of the krill food source did not differ distinctly between on-shelf and off-shelf habitats in this study. Nevertheless, there is a possibility that the dietary composition of krill differed between on-shelf and off-shelf habitats, as adult krill consume not only phytoplankton, but also higher trophic prey such as copepods (Schmidt et al. 2011; Polito et al. 2013). Copepods are transported from the Bransfield Strait and are commonly found off King George Is. near the study site (Walkusz et al. 2004). It is possible that the krill in the off-shelf habitat occasionally fed on closely distributed copepods, resulting in the slightly higher δ^{15}N value compared to that in the on-shelf habitat. Other factors may also potentially affect the δ^{15}N value, such as the origin of the organic matter (terrestrial or oceanic: Wada & Hattori 1991) and the degree of degradation of the organic matter (Wada & Hattori 1991; Koppelmann & Weikert 2003). We were unable to evaluate the effects of these factors because of our small sample sizes and/or lack of actual krill diet data. In addition, in a previous study Schmidt et al. (2003) reported low isotopic turnover rates (i.e. <1% per day) of Antarctic Krill, which may have resulted in the relatively small differences in the δ^{15}N of krill between on-shelf and off-shelf habitats due to krill movement. An estimation of the preferred sample size for sufficient statistical power ([1-probability of type II error] >0.8) was 8 to 10 individuals for each species or each trip type, given the same difference in mean δ^{15}N value between groups standardized by standard deviation. Clearly, more data sets are required for elucidating the effects of on-shelf and off-shelf trips with greater confidence.

Inter-specific and/or inter-annual differences in the maturity and size composition of krill have been described in previous studies of the diets of Antarctic penguins (Reid et al. 1996; Miller & Trivelpiece 2007). In these cases, it was not clear whether or not the differences in krill characteristics were attributed to inter-specific differences in foraging habitat or species-specific prey preferences. Information regarding individual foraging tracks and stable isotopic values of dietary samples, would help to clarify whether inter-specific or habitat-specific effects are related to differences in the characteristics of prey species. An inter-specific difference was observed in the proportion of juvenile krill taken by two penguin species (Table 2), as suggested in a previous study (Miller

& Trivelpiece 2007). Krill samples in the stomach contents of birds from the same colony in an earlier season (2006–2007) also showed that Chinstrap Penguins tended to predate juvenile krill more frequently than did Gentoo Penguins (10.53±16.36% for Chinstrap and 2.34±3.56% for Gentoo; Nobuo Kokubun unpublished). Such species-specific preferences should be considered carefully when interpreting krill data derived from different penguin species.

In conclusion, isotopic values of Antarctic Krill were investigated using GPS tracking and stomach content analysis of Chinstrap and Gentoo penguins. Based on δ^{13}C values, the main food of Antarctic Krill was presumed to be derived from planktonic/suspended organic matter (not benthic prey). Also, based on δ^{15}N values, Antarctic Krill taken from off-shelf habitats was presumed to consume higher trophic level prey, compared with those from on-shelf habitats.

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REFERENCES

Atkinson A, Siegel V, Pakhomov EA, Rothery P, Loeb V, Ross RM et al. (2008) Oceanic circumpolar habitats for Antarctic krill. Mar Ecol Prog Ser 362: 1–23.

Atkinson A, Siegel V, Pakhomov EA, Jessopp MJ & Loeb V (2009) A re-appraisal of the total biomass and annual production of Antarctic krill. Deep Sea Res I 56: 727–740.

Brierley AS, Fernandes PG, Brandon MA, Armstrong F, Millard NW, McPhail SD et al. (2002) Antarctic krill under sea ice: elevated abundance in a narrow band just south of the ice edge. Science 295: 1890–1892.

CCAMLR (2004) *CCAMLR Ecosystem Monitoring Program: standard methods*. CCAMLR, Hobart.

Corbisier TN, Petti MAV, Skowronski RSP & Brito TAS (2004) Trophic relationships in the nearshore zone of Martel Inlet (King George Island, Antarctica): δ13C stable-isotope analysis. Polar Biol 27: 75–82.

Cox MJ, Borchers DL, Demer DA, Cutter GR & Brierley AS (2011) Estimating the density of Antarctic krill (*Euphausia superba*) from multi-beam echo-sounder observations using distance sampling methods. Appl Statist 60: 301–316.

Croxall JP & Pilcher MN (1984) Characteristics of krill *Euphausia superba* eaten by Antarctic fur seals *Arctocephalus gazella* at South Georgia. Br Antarct Surv Bull 63: 117–125.

Culik BM & Wilson RP (1994) Underwater swimming at low energetic cost by Pygoscelid penguins. J Exp Biol 197: 65–78.

France RL (1995) Carbon-13 enrichment in benthic compared to planktonic algae: foodweb implications. Mar Ecol Prog Ser 124: 307–312.

Frazer TK (1996) Stable isotope composition (δ^{13}C and δ^{15}N) of larval krill, *Euphausia superba,* and two of its potential food sources in winter. J Plankton Res 18: 1413–1426.

Fry B & Sherr EB (1984) δ^{13}C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contrib Mar Sci 27: 13–47.

Gon OZ & Heemstra PC (eds) (1990) *Fishes of the southern ocean*. J. L. B. Smith Institute of Ichthyology, Grahamstown.

Hill HJ (1990) A new method for the measurement of Antarctic Krill *Euphausia superba* Dana from predator food samples. Polar Biol 10: 317–320.

Ichii T, Bengtson JL, Boveng PL, Takao Y, Jansen JK, Hiruki-Raring LM et al. (2007) Provisioning strategies of Antarctic fur seals and chinstrap penguins produce different responses to distribution of common prey and habitat. Mar Ecol Prog Ser 344: 277–297.

Kang JS, Kang SH, Lee JH & Lee SH (2002) Seasonal variation of microalgal assemblages at a fixed station in King George Island, Antarctica, 1996. Mar Ecol Prog Ser 229: 19–32.

Kokubun N, Takahashi A, Mori Y, Watanabe S & Shin H-C (2010) Comparison of diving behavior and foraging habitat use between chinstrap and gentoo penguins breeding in the South Shetland Islands, Antarctica. Mar Biol 157: 811–825.

Koppelmann R & Weikert H (2003) Vertical distribution of mesozooplankton and its δ^{15}N signature at a deep-sea site in the Levantine Sea (eastern Mediterranean) in April 1999. J Geophys Res 108 (C9): 8118.

Lascara CM, Hofmann EE, Ross RM & Quetin LB (1999) Seasonal variability in the distribution of Antarctic krill, *Euphausia superba*, west of the Antarctic

Peninsula. Deep Sea Res I 46: 951–984.
Ligowski R (2000) Benthic feeding by krill, *Euphausia superba* Dana, in coastal waters off West Antarctica and in admiralty Bay, South Shetland Islands. Polar Biol 23: 619–625.
Makarov RR & Denys CJI (1981) *Stages of sexual maturity of Euphausia suberba. BIOMASS Handbook 1.1*. Scientific Committee on Antarctic Research (SCAR), Cambridge.
Miller AK & Trivelpiece WZ (2007) Cycles of *Euphausia superba* recruitment evident in the diet of Pygoscelid penguins and net trawls in the South Shetland Islands, Antarctica. Polar Biol 30: 1615–1623.
Polito MJ, Reiss CS, Trivelpiece WZ, William P. Patterson WP & Emslie SD (2013) Stable isotopes identify an ontogenetic niche expansion in Antarctic krill (*Euphausia superba*) from the South Shetland Islands, Antarctica. Mar Biol 160: 1311–1323.
R Development Core Team (2008) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.
Reid K, Trathan PN, Croxall JP & Hill HJ (1996) Krill caught by predators and nets: differences between species and techniques. Mar Ecol Prog Ser 140: 13–20.
Schmidt K, Atkinson A, Stübing D, McClelland JW, Montoya JP & M Voss (2003) Trophic relationships among Southern Ocean copepods and krill: Some uses and limitations of a stable isotope approach. Limnol Oceangr 48: 277–289.
Schmidt K, Atkinson A, Steigenberger S, Fielding S, Lindsay MCL, Pond DW et al. (2011) Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. Limnol Oceangr 56: 1411–1428.
Siegel V (2005) Distribution and population dynamics of *Euphausia superba*: Summary of recent findings. Polar Biol 29: 1–22.
Takahashi A, Kokubun N, Mori Y & Shin HC (2008) Krill-feeding behaviour of gentoo penguins as shown by animal-borne camera loggers. Polar Biol 31: 1291–1294.
Wada E, Terazaki M, Kabaya Y & Nemoto T (1987) δ^{15}N and δ^{13}C abundance in the Antarctic Ocean with emphasis on the biogeochemical structure of the food web. Deep Sea Res 34: 829–841.
Wada E & Hattori A (1991) *Nitrogen in the sea: forms, abundances, and rate processes*. CRC Press, Boca Ranton.
Walkusz W, Kwaśniewski S, Dmoch K, Hop H, Żmijewska MI, Bielecka L et al. (2004) Characteristics of the Arctic and Antarctic mesozooplankton in the neritic zone during summer. Polish Polar Res 25: 275–291.