Contrasting specialist and generalist patterns facilitate foraging niche partitioning in sympatric populations of *Pygoscelis* penguins

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ABSTRACT: Specialization is a common mechanism of niche differentiation that can lead to ecological co-existence among species. However, species with specialized habitat or dietary requirements often exhibit a high degree of sensitivity to environmental change. Understanding patterns of specialization and niche segregation among Antarctic marine predators is of increased importance because of recent climate-driven reductions in a key prey species, Antarctic krill *Euphausia superba*. We examined the stomach contents and stable isotope values of sympatric chinstrap *Pygoscelis antarctica* and gentoo *P. papua* penguins across 5 breeding seasons at Cape Shirreff, Livingston Island, Antarctica. Our goal was to examine foraging niche segregation and the degree of specialization between species during the chick-rearing period. Dietary and isotopic foraging niches indicated consistent niche partitioning with higher krill consumption and greater use of offshore foraging habitats by chinstrap relative to gentoo penguins. While chinstrap penguin diets were dominated by krill with little variation, gentoo penguins exhibited broader dietary and isotopic niches with a higher degree of variation. There was little evidence that shifts in the availability of adult krill influenced penguin diets or foraging niches during our study, though the contrasting foraging strategies identified provide insight into the differing population trends observed between penguin species. The narrower foraging niche observed in declining chinstrap penguin populations indicates that they are likely highly sensitive to declines in the abundance of Antarctic krill. In contrast, the generalist niche exhibited by recently expanding gentoo penguin populations is likely better suited to the rapidly changing environmental conditions in the Antarctic Peninsula.

KEY WORDS: Stable isotope analysis · *Pygoscelis papua* · *Pygoscelis antarctica* · $\delta^{13}C$ · $\delta^{15}N$

INTRODUCTION

Hutchinson (1957, 1978) described the ecological niche as a multi-dimensional hypervolume that included axes relating to trophic position and habitat use. Since that time, niche theory has provided an important framework for ecological investigations of resource use, species interactions, community composition and evolution (Chase & Leibold 2003). Ecological theory predicts that competition for limited resources

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is most likely to occur between species with similar ecological requirements (Ricklifs & Miller 1999). However, when closely related species overlap, they often exhibit morphological or behavioral characteristics that lead to segregated niche hypervolumes (Hutchinson 1959, May & MacArthur 1972).

Specialization is a common mechanism of niche differentiation that can lead to species co-existence (Wilson & Yoshimura 1994). A specialist population is composed of individuals that utilize a narrow window of resources with little or no variation among individuals. While specialization can act to reduce interspecific resource overlap, there are ecological tradeoffs for specialist species. For example, species with specialized habitat or dietary requirements are likely to be highly sensitive to environmental changes (Davies et al. 2004, Wilson et al. 2008). In contrast, generalist species that have broad dietary and habitat niches are expected to be more resilient to disturbances and/or changes in resource and habitat availability (Devictor et al. 2008, Wilson et al. 2008). While often difficult to distinguish, generalist populations may be composed of generalist individuals all taking a wide range of food types (Type A generalists) or individuals each specializing in a different range of food types that combine to form a large population niche width (Type B generalists; Grant et al. 1976, Bearhop et al. 2004). Differences between sexes within generalist populations can also lead to large total population niches while limiting intraspecific competition (Phillips et al. 2011).

Penguins in the genus *Pygoscelis*, including chinstrap *P. antarctica* and gentoo *P. papua* penguins, co-occur and are the dominant avifauna in the Antarctic Peninsula region. These species utilize similar nesting habitats, have similar breeding schedules and both consume Antarctic krill *Euphausia superba*, which can dominate their diets (Trivelpiece et al. 1987, Miller et al. 2010). In addition, their foraging ranges are locally constrained during the chick-rearing period, as parents feed their chicks on a daily basis (Trivelpiece et al. 1987). While the potential for competition is therefore clearly evident, past studies using stomach contents and animal tracking suggest that differences in diet and foraging habitat during the breeding season can lead to niche partitioning in *Pygoscelis* penguins (Trivelpiece et al. 1987, Miller et al. 2010, Wilson 2010). Having a clear understanding of patterns of niche segregation among *Pygoscelis* penguins is of increased importance because of recent climate-driven reductions in Antarctic krill in the Antarctic Peninsula region (Atkinson et al. 2004, Ducklow et al. 2007). During this time, *Pygoscelis*

penguin population trends have differed, with dramatic declines in chinstrap penguin populations and stable or expanding gentoo penguin populations (Trivelpiece et al. 2011, Lynch et al. 2012). Therefore, a better understanding of differences in the diets and foraging strategies of these 2 species may help interpret these divergent population-level responses to recent declines in krill availability.

Stomach content analysis is one of the most common methods for dietary analysis and has been used in previous studies of the diet and foraging ecology of sympatric *Pygoscelis* penguins (Trivelpiece et al. 1987, Miller et al. 2010). However, stomach content data reflect a 'snapshot' of recent diet and can be highly variable while underestimating the importance of soft-bodied prey, such as fish and squid (Barrett et al. 2007). Stable isotope analysis provides a complementary approach for examining the diets and ecological niches of penguins, which avoids many of the biases inherent to stomach content analysis (Polito et al. 2011a). Nitrogen isotopic values (δ^{15}N) are commonly used to infer trophic level and diets, while carbon isotopic values (δ^{13}C) help trace trends in marine habitat use (inshore/benthic vs. offshore/pelagic; Cherel & Hobson 2007). In addition, combining isotopic approaches with stomach content analysis often allows for a greater ability to elucidate specialist and generalist strategies across species (Layman & Allgeier 2012).

In this study, we examine the stomach contents and stable isotope values of sympatrically breeding chinstrap and gentoo penguins across 5 breeding seasons. We build on previous studies of niche partitioning in these species (Trivelpiece et al. 1987, Miller et al. 2010) by incorporating stomach content analysis with stable isotope-based metrics of niche position, width and overlap to aid in identifying specialist and generalist foraging strategies in these 2 species. Specifically, the objectives of this study are to (1) identify the degree and consistency of dietary and habitat niche segregation between the 2 *Pygoscelis* penguin species during the chick-rearing period and (2) compare isotopic and dietary measures of penguin foraging niche width and specialization relative to changes in the availability of Antarctic krill.

MATERIALS AND METHODS

Study site and field sampling

Fieldwork was conducted from 2007 to 2011 at Cape Shirreff, Livingston Island, Antarctica (62° 28′ S,

60° 46′ W), at a single mixed colony of approximately 4500 pairs of chinstrap penguins and 800 pairs of gentoo penguins sympatrically breeding. We collected stomach content samples during the chick-rearing period (January to February) after chicks had reached the crèche stage (>2.5 wk of age) using the water-offloading lavage technique following the methods of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) ecosystem monitoring program standard methods (CCAMLR 1997) as modified by Polito et al. (2011a). We sampled breeding adults returning from foraging trips between 15:00 and 17:00 h local time at 5 to 7 d intervals, for a total of 10 to 15 gentoo penguins and 29 to 30 chinstrap penguins each year. Sampling was divided roughly equally across adults of both sexes as identified though morphometric techniques (Polito et al. 2012). For each stomach sample, we determined the percentage of krill, fish and other material by frequency occurrence and wet mass. For additional methodical detail on stomach sampling and analysis, see Polito et al. (2011a).

We used fish otoliths recovered from diet samples to identify prey fish to the lowest possible taxonomic level and 3 habitat groupings (benthic, pelagic and mesopelagic myctophids) using an internal reference collection and a published guide (Williams & McEldowney 1990). We calculated the frequency occurrence and the minimum number of individuals (MNI) of each fish taxa following standard methods (Polito et al. 2002). In addition, we used otolith measurements and published regression equations to calculate a total and percent of total reconstituted mass for each fish taxa identified (Polito et al. 2011a and references therein). In some samples, many similarly sized *Pleuragramma antarcticum* otoliths were recovered, and in such cases we measured a random subsample of 20 to 75 otoliths per diet sample and used mean values to extrapolate the total reconstituted mass.

We used the percentage of adult Antarctic krill recovered from penguin diet samples and concurrent shipboard surveys to examine interannual variation in krill availability during the chick-rearing period. Previous studies indicate that this metric is a good proxy of krill availability to *Pygosceli*s penguins, as they capture prey items individually (Watanabe et al. 2014), and thus given the handling time needed to capture an adequate mass of juvenile krill, penguins will preferentially forage on larger, adult krill (Miller & Trivelpiece 2007, 2008). We measured the standard length of krill to the nearest millimeter, from the anterior side of the eye to the tip of the telson, and krill >35 mm were considered adults (Miller & Trivel-

piece 2007). From penguin stomach contents containing Antarctic krill, we measured a random sample of 50 krill per sample. Data from shipboard surveys were obtained using an Isaacs-Kidd midwater trawl towed obliquely from the surface to a maximum depth of 200 m during mid-January to early February of each year from sampling stations located directly north of Livingston Island, including the waters around Cape Shirreff. This grid covered a larger and more offshore area than may be typically used by foraging penguins but provided a relative index of the Antarctic krill available to breeding penguins in each year (Miller & Trivelpiece 2007). In net samples containing fewer than 100 krill, all individuals were measured, while in larger samples, 100 to 200 krill were measured per sample.

Stable isotope analysis

In early February of each year, we collected 3 breast feathers from a random sample of 20 to 30 fledgling-aged chicks from both species while they were preparing to leave their natal colonies for the sea at 7 to 10 wk of age (Polito & Trivelpiece 2008). Feathers from fledgling-aged chicks provide an integrated dietary history of the food parents provide chicks over much of the 7 to 10 wk provisioning period (Hobson & Clark 1992, Tierney et al. 2008, Polito et al. 2011a) and thus are well suited to examine population-level generalist vs. specialist patterns during this critical period of time. Sampled chicks were weighed with spring scales to the nearest 50 g. We cleaned feathers using a 2:1 chloroform: methanol rinse and then air-dried and cut them into small fragments with stainless steel scissors. We flash combusted (Thermo Finnigan and Costech ECS4010 elemental analyzers) approximately 0.5 mg of each sample loaded into tin cups to analyze for carbon and nitrogen isotopes ($\delta^{13}C$ and $\delta^{15}N$) through interfaced Thermo Finnigan Delta Plus XL and Delta V Plus continuous-flow stable isotope ratio mass spectrometers. Raw δ values were normalized on a 2-point scale using glutamic acid reference materials with low and high values (i.e. USGS-40: $\delta^{13}C = -26.4‰$, $\delta^{15}N = -4.5‰$; and USGS-41: $\delta^{13}C = 37.6‰$, $\delta^{15}N = 47.6‰$). Sample precision based on repeated sample and reference material was 0.1 and 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively.

Stable isotope ratios are expressed in δ notation in per mil units (‰), according to the following equation:

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000 \qquad (1)$$

where X is ^{13}C or ^{15}N, and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$. $R_{standard}$ values were based on the Vienna PeeDee Belemnite standard for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$.

Dietary and niche analysis using stomach contents

We analyzed stomach content data to test for differences across years, between species and between sexes of both species using generalized linear models (GLMs). We used a normal error distribution and identity link function for models, with percent composition (by wet mass) and reconstituted fish mass per sample as the response variables. Percent composition data were arcsine-transformed prior to analysis. We conducted post hoc analyses using a Bonferroni correction. We used GLMs with a binomial error distribution and logit link function for models with frequency occurrence of the main prey group (krill, fish and 'other' prey) as well as benthic, pelagic and mesopelagic fish otoliths recovered from stomach contents as the response variables. For models that used MNI of fish as the response variables, we used a Poisson error distribution with a logit link function. For GLMs with binomial and Poisson error distributions, we conducted post hoc analyses using a Bonferroni correction and reported chi-square and p-values from the likelihood ratio test statistics for Type 3 tests. Furthermore, we used chi-square tests to compare the distribution of the percent contribution by reconstituted mass of benthic, pelagic and mesopelagic fish across years, between species and between sexes of each species.

We calculated 2 dietary niche metrics by species, sex and year using percent composition data from stomach contents. We assessed similarity between species using Schoener's diet overlap index (Schoener 1968):

$$D = 1 - \tfrac{1}{2} \Sigma |p_{ij} - p_{ik}| \qquad (2)$$

where D is the index value, and p_{ij} and p_{ik} are the relative proportions of each food item i for species j and k, respectively. On this scale, 0 represents no overlap, and 1 represents complete overlap between species. Typically, values >0.6 are inferred to indicate significant dietary overlap (Schoener 1968). Next, we calculated the total niche width (TNW) based on Shannon-Weaver index information following Roughgarden (1979) using the program IndSpec 4.0 (Bolnick et al. 2002). We compared these 2 dietary niche metrics (D and TNW) across the 5 yr of our

study using Pearson correlation and tested for inter-specific and sexual differences using GLM.

Isotopic mixing model and comparison with stomach content data

We used the Stable Isotope Analysis in R (SIAR) Bayesian mixing model to quantify the chick-rearing diet composition of penguins based on their stable isotope values (Parnell et al. 2010). The SIAR model estimates probability distributions of multiple source contributions to a mixture while accounting for the observed variability in source and mixture isotopic signatures and dietary isotopic fractionation. A previous analysis based on a subset of our data found that the SIAR isotopic mixing model predictions provide a robust estimate of the relative amounts of fish and krill in penguin diets because of their large difference in $\delta^{15}N$ values (Polito et al. 2011a). In contrast, this same study found that isotopic mixing models had difficulty estimating the relative dietary contribution of different fish species to penguin diets because of a high degree of overlap in both $\delta^{13}C$ and $\delta^{15}N$ values. Therefore, we used SIAR to develop a 2-prey source (Antarctic krill vs. 'fish') and a single isotope ($\delta^{15}N$) mixing model to estimate diet composition for each species/year combination using the $\delta^{15}N$ values of chick feathers. Prior to these analyses, we tested for correlations between chick mass and feather stable isotope values (Pearson correlation: r = −0.14 to 0.15, p = 0.174 to 0.872) and confirmed that individual variation in feather isotope values were not a function of variation in growth or physiological condition but instead most likely reflect variation in dietary sources (Bearhop et al. 2004). We parameterized the model using the $\delta^{15}N$ value of Antarctic krill (3.3 ± 0.6) and the grand mean $\delta^{15}N$ value of 9 common prey fish (8.8 ± 0.8) concurrently collected from around the South Shetland Islands, as described in Polito et al. (2011a). We incorporated the $\delta^{15}N$ diet-to-feather discrimination factor from a captive feeding study of *Pygoscelis* penguins (3.5 ± 0.5; Polito et al. 2011b) in the model and ran 1 million iterations, thinned by 15, with an initial discard of the first 40 000, resulting in 64 000 posterior draws.

Similar to Polito et al. (2011a), we used model 95% credibility intervals to directly compare stomach content and stable isotope-based estimates of krill consumption (% of total diet). To facilitate these comparisons, we calculated Bayesian averages and 95% credibility intervals of the percentage of krill in stomach contents by species and year using Markov chain

Monte Carlo (MCMC) simulations via WinBUGS (Version 1.4). These MCMC simulations were implemented using the non-informative Dirichlet prior with an identical number of iterations, thins and discards as our Bayesian isotopic mixing model analysis.

Niche analyses using stable isotopes

To assess variation in isotopic niche (Newsome et al. 2007) position, width, partitioning and overlap during the chick-rearing period, we examined chick feather stable isotope values (δ^{13}C and δ^{15}N) using both multivariate and univariate techniques. We tested for significant differences in the isotopic niche position of species by computing the Euclidean distance (ED) between group centroids (δ^{13}C and δ^{15}N bivariate means) in each year following the methods of Turner et al. (2010). Isotopic niche positions were considered to be different if the ED between species examined was significantly greater than zero after comparison to null distributions generated by a residual permutation procedure. If niche positions were found to differ using this approach, we examined the results of univariate general linear models and Tukey-Kramer multiple comparison tests. This procedure allowed us to determine which niche axis (δ^{13}C and/or δ^{15}N) contributed to niche partitioning between species (Hammerschlag-Peyer et al. 2011). We supplemented these analyses by exploring interannual variation in niche width and overlaps using standard ellipse areas corrected for sample size (SEAc; Jackson et al. (2011). The SEAc are the equivalent of a bivariate standard deviation and are a measurement of isotopic dispersion, which can be interpreted as a measure of the core isotopic niche of a population.

Because measures of central tendency can disguise ecologically important variation within species and individual-level specialization (Layman & Allgeier 2012), we calculated 3 additional metrics of niche width and overlap. First, we calculated the mean distance to centroid (MDC) for each species and year (Turner et al. 2010). MDC is a proxy for the degree of trophic diversity among individuals of a species and is calculated using the distances of each individual from the mean of all individuals (Layman et al. 2007). Using an analysis of nested linear models and residual permutation procedures, the absolute value of MDC differences was evaluated between species in each year, with absolute values greater than zero indicating a significant difference in niche width (Turner et al. 2010). When pairwise comparisons

indicated significant differences in MDC and thus niche width, we used Bartlett's tests to examine the homogeneity of variance of δ^{13}C and δ^{15}N values between species in each year to determine which isotopic niche axis drove the observed differences in niche width (Hammerschlag-Peyer et al. 2011). Next, we calculated total isotopic niche area (TA) as the area of the smallest convex hull that contains all individuals of a group in a δ^{13}C and δ^{15}N bi-plot (Layman et al. 2007). TA can be thought of as a measure of the total niche width of a population, as it does not exclude individual niches from the characterization of the population niche (Layman & Allgeier 2012). Last, we calculated the proportion of individual isotopic values for both species in each year that were encompassed by the other species' convex hull as a measure of the isotopic niche overlap (TAO; Hammerschlag-Peyer et al. 2011). As a previous study found that these metrics (MDC, TA, TAO) can be sensitive to variation in sample size, we used Pearson correlation to confirm that variation in these 3 metrics was not biased by variation in sample size within and between species (r = 0.01 to 0.30, p = 0.391 to 0.985). Following this preliminary analysis, we used paired t-test and Pearson correlations to assess interspecific trends in isotopic niche metrics across the 5 yr of our study. Next, we used correlation analysis to determine if the variation in TAO between species was driven by fluctuations in niche width and/or the proportion of krill consumed by both species as derived from our SIAR model. Finally, for both species, we compared estimates of total niche width from stomach content (TNW) and niche width indices from stable isotope analysis (SEAc, MDC and TA) using correlation analysis.

Comparisons with krill availability

We used Pearson correlations to test for relationship across years between the proportion of adult krill recovered from stomach contents and those from concurrent net trawls. We used similar correlation approaches to compare these 2 proxies of krill availability to interannual variation in mean penguin diet composition and foraging niche metrics derived from stomach content and stable isotope analysis.

All statistics were computed in SAS (Version 9.3), and mixing model and niche-metric analyses were performed using the program R (Version 2.15.3). Prior to analysis, we examined all datasets and their residuals to confirm that they conformed to the distributions and statistical assumptions applied, and the

significance of all tests were assumed at the 0.05 level. Data are presented ± standard deviation (SD) unless otherwise noted.

RESULTS

Stomach contents

Chinstrap penguin stomach samples had a higher percent contribution of krill relative to gentoo penguin samples ($F_{1,211}$ = 93.11, p < 0.001; Fig. 1), but the proportion of krill consumed by chinstrap penguins did not differ across years ($F_{4,211}$ = 1.40, p = 0.214) or have a significant species × year interaction ($F_{4,211}$ =

1.06, p = 0.376). Gentoo penguin samples contained a significantly higher percentage by mass of fish relative to chinstrap penguin samples ($F_{1,211}$ = 51.86, p < 0.001; Fig. 1) but did not differ across years ($F_{4,211}$ = 1.35, p = 0.248) or have a significant species × year interaction ($F_{4,211}$ = 1.32, p = 0.259). The percent contribution to stomach samples of other prey species, including cephalopods, amphipods and other euphausiid species, did not differ by penguin species ($F_{4,211}$ = 0.15, p = 0.695) or across years ($F_{4,211}$ = 1.27, p = 0.278) and did not have a significant species × year interaction ($F_{4,211}$ = 0.08, p = 0.987; Fig. 1). In addition, we found no differences in contribution of krill, fish and other prey items between sexes for either of the penguin species (chinstrap: $F_{1,149}$ = 1.02
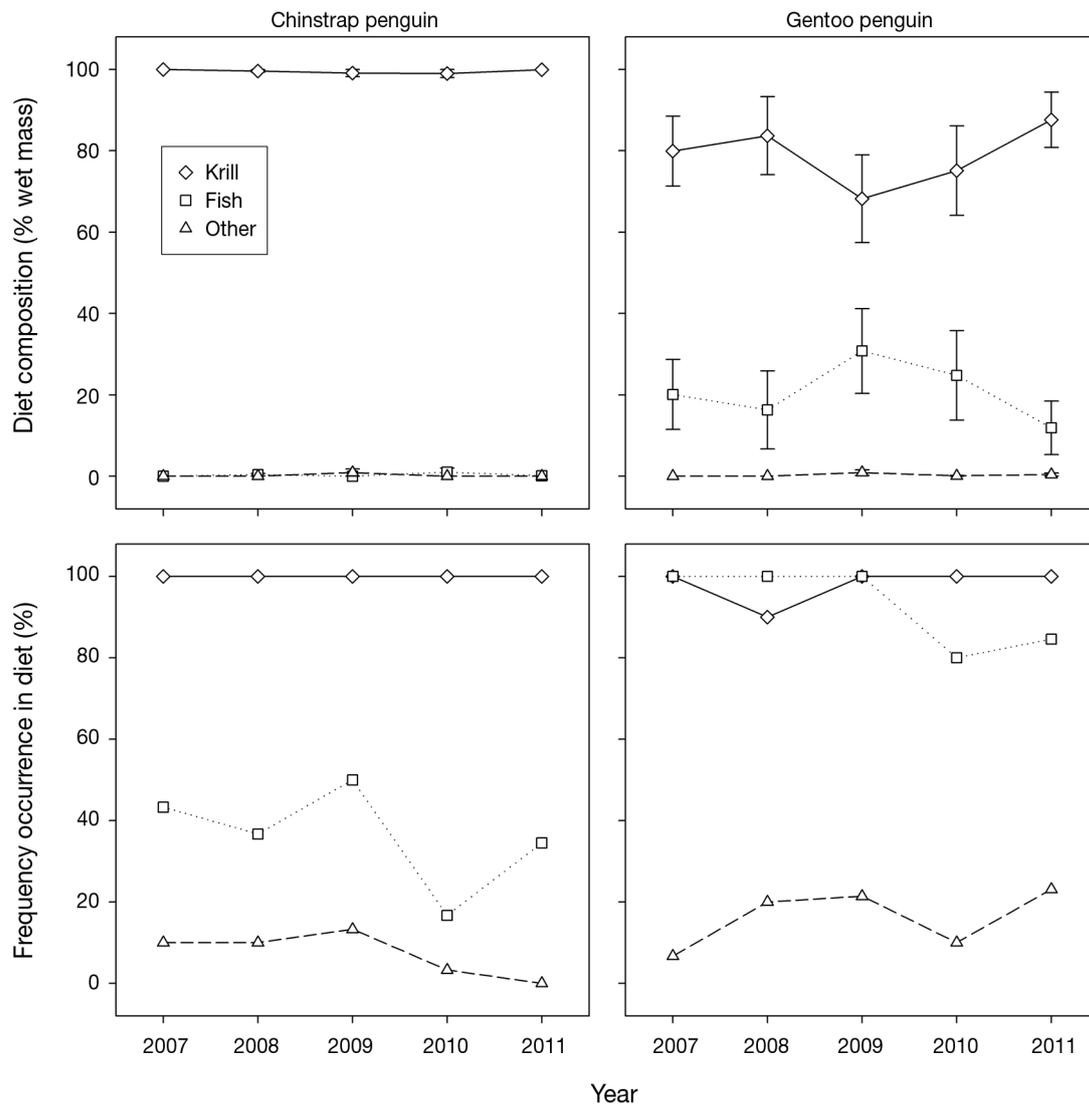
Fig. 1. Composition and occurrence of common prey groups recovered from adult penguin stomach contents during the crèche period at Cape Shirreff, Livingston Island, Antarctica. Krill indicates Antarctic krill *Euphausia superba*, and other prey include cephalopods, hyperiid amphipods and small euphausiids (primarily *Thysanoessa macrura*). Values are mean ± SE

Table 1. Composition and occurrence of common prey groups and the minimum number of individual fish and reconstituted fish mass recovered from chick-rearing adult penguin stomach contents during the crèche period at Cape Shirreff, Livingston Island, Antarctica, from 2007 to 2011. Other prey include cephalopods, hyperiid amphipods and small euphausiids (primarily *Thysanoessa macrura*). Values are mean ± SE, with the frequency of occurrence (% FO) of common prey species and the total minimum number of individual (MNI) fish and reconstituted fish mass (g) presented in parentheses

Sex	n	Percent diet composition by wet mass (% FO)			Fish content per stomach sample based on otoliths (total)	
		Antarctic krill *Euphausia superba*	Fish	Other	MNI	Reconstituted mass (g)
Chinstrap penguin						
Male	74	100.0 ± 0.0 (100.0)	0.0 ± 0.0 (35.1)	0.0 ± 0.0 (6.8)	1.1 ± 0.3 (79)	11.5 ± 5.5 (854)
Female	75	99.1 ± 0.5 (100.0)	0.5 ± 0.3 (37.3)	0.3 ± 0.3 (8.0)	2.4 ± 0.9 (180)	20.6 ± 8.1 (1545)
All	149	99.5 ± 0.3 (100.0)	0.3 ± 0.2 (36.2)	0.2 ± 0.2 (7.4)	1.7 ± 0.5 (259)	16.1 ± 4.9 (2399)
Gentoo penguin						
Male	30	76.4 ± 6.2 (100.0)	22.9 ± 6.0 (96.7)	0.6 ± 0.4 (23.3)	50.2 ± 15.5 (1507)	150.3 ± 36.0 (4508)
Female	32	80.9 ± 5.7 (96.9)	19.1 ± 5.7 (90.6)	0.0 ± 0.0 (9.4)	94.2 ± 35.0 (3013)	198.9 ± 56.1 (6365)
All	62	78.76 ± 4.2 (98.4)	20.9 ± 4.1 (93.5)	0.3 ± 0.2 (16.1)	72.9 ± 19.6 (4520)	175.38 ± 33.7 (10873)

to 2.60, p = 0.106 to 0.312; gentoo: $F_{1,62}$ = 0.10 to 2.93, p = 0.085 to 0.748; Table 1).

Krill were evident in all chinstrap penguin samples and in all but one female gentoo penguin sample (Fig. 1, Table 1). Fish remains (e.g. bones, scales, otoliths) were evident in all gentoo penguin samples and in 16.7 to 50.0% of chinstrap penguin samples, even when there was no detectable wet mass of fish (Fig. 1). The frequency occurrence of fish in chinstrap penguin samples did not differ across years ($\chi^2_{4,149}$ = 8.67, p = 0.070; Fig. 1) or sexes ($\chi^2_{1,149}$ = 0.08, p = 0.780; Table 1). The frequency occurrence of other prey species was slightly higher in gentoo penguins relative to chinstrap penguins ($\chi^2_{1,211}$ = 4.75, p = 0.029) but did not differ across years ($\chi^2_{4,211}$ = 5.28, p = 0.260) or have a significant species × year interaction ($\chi^2_{4,211}$ = 5.99, p = 0.120). The frequency occurrence of other prey species did not differ by sex for either chinstrap penguins ($\chi^2_{1,149}$ = 0.08, p = 0.772) or gentoo penguins ($\chi^2_{1,62}$ = 2.27, p = 0.132; Table 1).

A total of 4787 otoliths were recovered from stomach samples, with 99.8% of otoliths identifiable to one of 14 fish species (Table 2). Chinstrap penguin diets had consistently lower MNI ($\chi^2_{1,211}$ = 1579.67, p < 0.001) and reconstituted fish mass ($\chi^2_{1,211}$ = 51.25, p < 0.001) than gentoo penguin diets, with

both variables having significant year (MNI: $\chi^2_{1,211}$ = 312.26, p < 0.001; fish mass: $\chi^2_{1,211}$ = 19.99, p < 0.001) and species × year (MNI: $\chi^2_{1,211}$ = 481.85, p < 0.001; fish mass: $\chi^2_{1,211}$ = 22.80, p < 0.001) interactions. Females, relative to males, had a greater number of MNI for both chinstrap penguins ($\chi^2_{1,149}$ = 39.11, p < 0.001) and gentoo penguins ($\chi^2_{1,62}$ = 419.01, p < 0.001; Table 1). However, this pattern was not significant or consistent when examined across individual years (Appendix, Fig. A1). Reconstituted fish mass did not differ between sexes for either chinstrap penguins ($\chi^2_{1,147}$ = 0.85, p = 0.356) or gentoo penguins

Table 2. Minimum number of individuals (MNI), frequency of occurrence (% FO) and percent of reconstituted mass (% mass) of fish species identified from otolith recovered from adult penguin stomach contents during the crèche period at Cape Shirreff, Livingston Island, Antarctica, from 2007 to 2011

Fish species	Chinstrap penguin			Gentoo penguin		
	MNI	% FO	% mass	MNI	% FO	% mass
Mesopelagic						
Electrona antarctica	136	8.7	29.6	3	4.8	0.1
E. carlsbergi	0	0.0	0.0	4	4.8	0.2
Gymnoscopelus nicholsi	17	3.4	19.9	12	6.5	3.7
Protomyctophum bolini	2	1.3	0.0	5	3.2	0.1
Pelagic						
Notolepis coatsi	29	6.0	31.5	0	0.0	0.0
Pleuragramma antarcticum	60	15.4	7.7	4241	53.2	49.6
Benthic						
Chaenodraco wilsoni	0	0.0	0.0	1	1.6	0.2
Champsocephalus gunnari	0	0.0	0.0	27	22.6	10.4
Harpagifer antarcticus	1	0.7	0.3	0	0.0	0.0
Lepidonotothen larseni	0	0.0	0.0	2	3.2	0.1
L. nudifrons	7	2.0	3.0	21	9.7	0.8
L. squamifrons	4	2.7	7.0	143	33.9	6.8
Notothenia rossii	1	0.7	2.9	36	4.8	22.5
Trematomus newnesi	6	3.4	4.4	19	19.4	5.5
Unknown fish species	0	0.0	–	10	12.9	–

($\chi^2_{1,147}$ = 0.52, p = 0.472; Table 1). The frequency occurrence and reconstituted mass of pelagic, meso-pelagic and benthic fishes in penguin diets differed between species ($\chi^2_{1,211}$ = 18.31 to 1021.1, all p < 0.001) and across years ($\chi^2_{1,211}$ = 52.74 to 2216.3, all p < 0.001), though no significant species × year interactions were observed ($\chi^2_{1,211}$ = 1.82 to 3.21, all p > 0.524). There were no differences between sexes in these same parameters (chinstrap: $\chi^2_{1,149}$ = 0.06 to 1.16, all p > 0.281; gentoo; $\chi^2_{1,62}$ = 0.01 to 0.59, all p < 0.442). Gentoo penguins had a higher occurrence of fish from all habitats relative to chinstrap penguins in each year (Fig. 2). One pelagic species (*Notolepis coatsi*) and 2 mesopelagic species (*Electrona antarctica* and *Gymnoscopelus nicholsi*) dominated the fish component of chinstrap penguin diet by mass (Table 2), with the relative importance of pelagic and mesopelagic fish varying over the 5 yr of our study (Fig. 2). In contrast, the fish component of gentoo

penguin diet by mass was comprised predominantly of a combination of pelagic (*Pleuragramma antarcticum*) and benthic (*Notothenia rossii*, *Champsocephalus gunnari* and *Lepidonotothen squamifrons*) fish species (Table 2), with the relative importance of these 2 groups differing over time (Fig. 2).

Dietary niche metrics

Diet composition based on wet mass overlapped significantly between gentoo and chinstrap penguins in all years (i.e. *D* > 0.6; Table 3). Even so, the dietary niche width (TNW) of gentoo penguins was significantly larger than that of chinstrap penguins ($F_{1,20}$ = 58.29, p < 0.001; Fig. 3) but did not differ between sexes ($F_{1,20}$ = 0.01, p = 0.981) or exhibit a significant interaction between these 2 terms ($F_{1,20}$ = 0.49, p = 0.492). Measurements of TNW in gentoo penguins
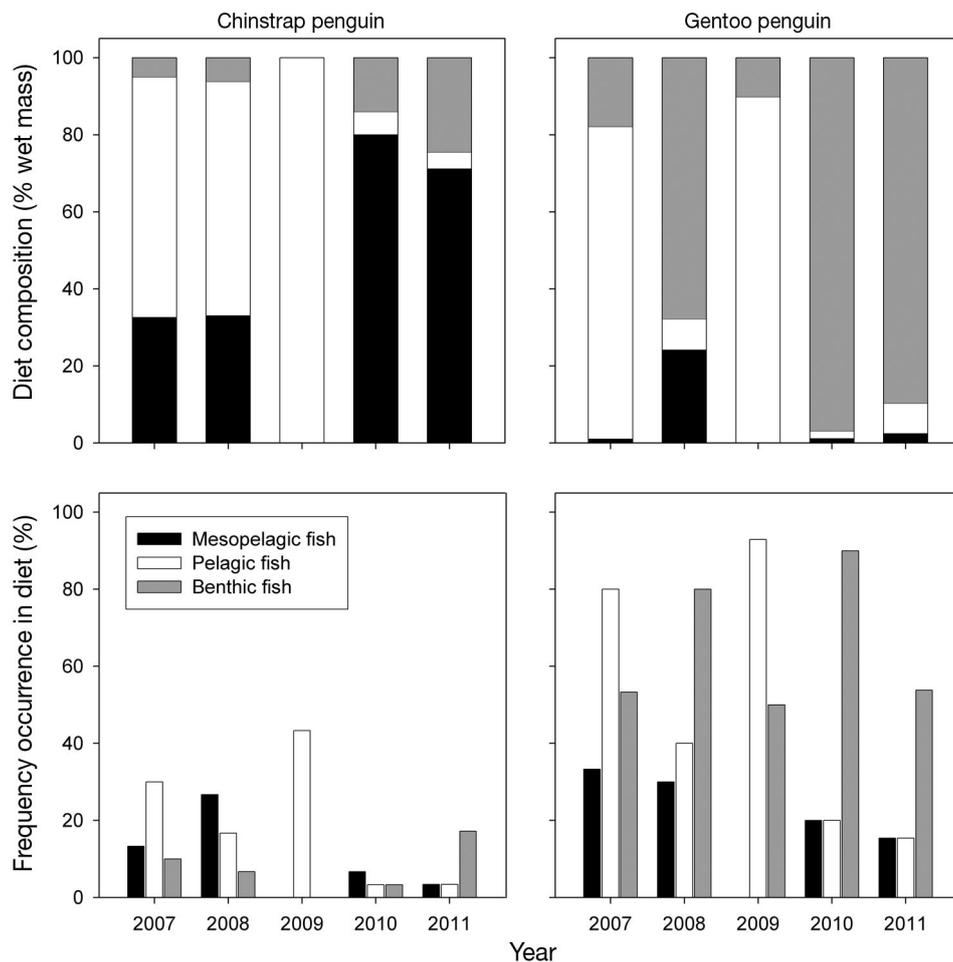
Fig. 2. Frequency occurrence and proportion of reconstituted mass of mesopelagic, pelagic and benthic fish species based on otoliths recovered from adult penguin stomach contents during the crèche period at Cape Shirreff, Livingston Island, Antarctica

also varied across years (Table 3) and was strongly correlated with D (Pearson correlation: r = −0.99, p < 0.001), suggesting that variation in dietary niche of gentoo penguins influenced their dietary overlap with chinstrap penguins. In contrast, measures of TNW did not differ greatly in chinstrap penguins

Table 3. Dietary and isotopic niche indices of *Pygoscelis* penguins during the crèche period at Cape Shirreff, Livingston Island, Antarctica, from 2007 to 2011. Dietary niche indices include Schoener's diet overlap index (D; Schoener 1968) and total niche width (TNW; Roughgarden 1979). Isotopic niche indices include standard ellipse area corrected for sample size (SEAc; Jackson et al. 2011), mean distance to centroid (MDC; Turner et al. 2010), total isotopic niche area (TA; Layman et al. 2007) and isotopic niche overlap at the individual level (TAO; Hammerschlag-Peyer et al. 2011)

| Year | Dietary niche | | Isotopic niche | | | |
	Overlap (D)	Width (TNW)	SEAc (‰)	MDC (‰)	TA (‰)	TAO (%)
Chinstrap penguin						
2007	0.80	0.00	0.2	0.3	0.7	20.0
2008	0.84	0.03	0.3	0.4	0.6	15.0
2009	0.69	0.05	0.3	0.4	0.7	0.0
2010	0.76	0.06	0.3	0.4	0.8	15.0
2011	0.88	0.01	0.1	0.2	0.3	0.0
Gentoo penguin						
2007	0.80	0.50	0.3	0.6	1.3	16.7
2008	0.84	0.45	0.4	0.6	0.9	25.0
2009	0.69	0.67	0.6	0.7	1.6	0.0
2010	0.76	0.57	0.5	0.5	1.1	25.0
2011	0.88	0.39	0.3	0.5	0.9	0.0
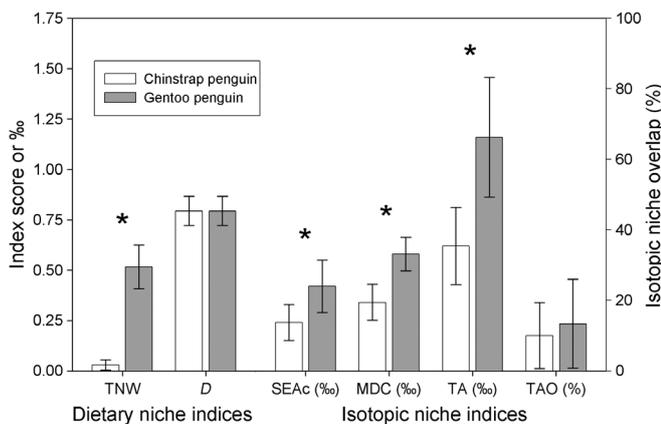
Fig. 3. Dietary and isotopic niche indices (mean ± SD) of *Pygoscelis* penguins during the crèche period at Cape Shirreff, Livingston Island, Antarctica. Dietary niche indices: total niche width (TNW) and Schoener's diet overlap index (D). Isotopic niche indices: standard ellipse areas corrected for sample size (SEAc), mean distance to centroid (MDC), total isotopic niche area (TA) and isotopic niche overlap at the individual level (TAO). Asterisks denote significant differences between species

over the 5 yr of our study (Table 3), and correlations between D and TNW (r = −0.67, p = 0.217) were not significant in chinstrap penguins.

Isotopic dietary predictions

Similar to a previous study (Polito et al. 2011a), isotopic mixing models predicted a higher mean contribution of fish in the chick diets of both penguin species in comparison to diet composition estimates derived from the stomach contents of chick-rearing adults (Fig. 4). This was especially significant for chinstrap penguins, as 95% credibility intervals (CI) did not overlap between methods in 3 out of 5 years. In addition, the SIAR model predicted that chinstrap penguin chicks were fed a small proportion of fish in all years (11.1 to 22.0%), validating the occurrence of otoliths in the stomachs of chick-rearing adult chinstrap penguins even when there was little to no detectable wet mass of fish (Fig. 1, Table 1). While 95% CI from stomach content analysis and SIAR model predictions of gentoo penguin chick diets overlap in all years, estimates from stomach contents were 3 to 5 times more variable relative to SIAR model predictions (Fig. 4). Given the lower variability, it was possible to detect variation in gentoo chick diets across years using SIAR model predictions. In 2009, gentoo penguin chicks were fed significantly less krill relative to 2007, 2008 and 2010 (Fig. 4). Furthermore, similar to trends observed in stomach content analysis, the SIAR model predicted that gentoo penguin chicks were fed a significantly larger proportion of fish relative to chinstrap penguin chicks in all years with no overlap of model 95% CI (Fig. 4).

Isotopic niche metrics

The mean isotopic niche position of chinstrap and gentoo penguin chicks at Cape Shirreff differed significantly in all years (ED = 0.9 to 2.5‰, all p < 0.001; Fig. 5). This was because gentoo penguins had significantly higher $\delta^{15}N$ values in all years ($F_{4,219}$ = 391.27, p < 0.001) and higher $\delta^{13}C$ values in 2006 to 2007 and 2008 to 2009 ($F_{4,180}$ = 68.91, p < 0.001; Table 4). Core isotopic niche area (SEAc) did not overlap between species in any year (Fig. 5) and was larger in gentoo relative to chinstrap penguins across and within years (Fig. 3, Table 3). Niche width, as measured by MDC, was also larger in gentoo relative to chinstrap penguins across (Fig. 3) and within all years of our study (p < 0.01; Table 3). These differ-
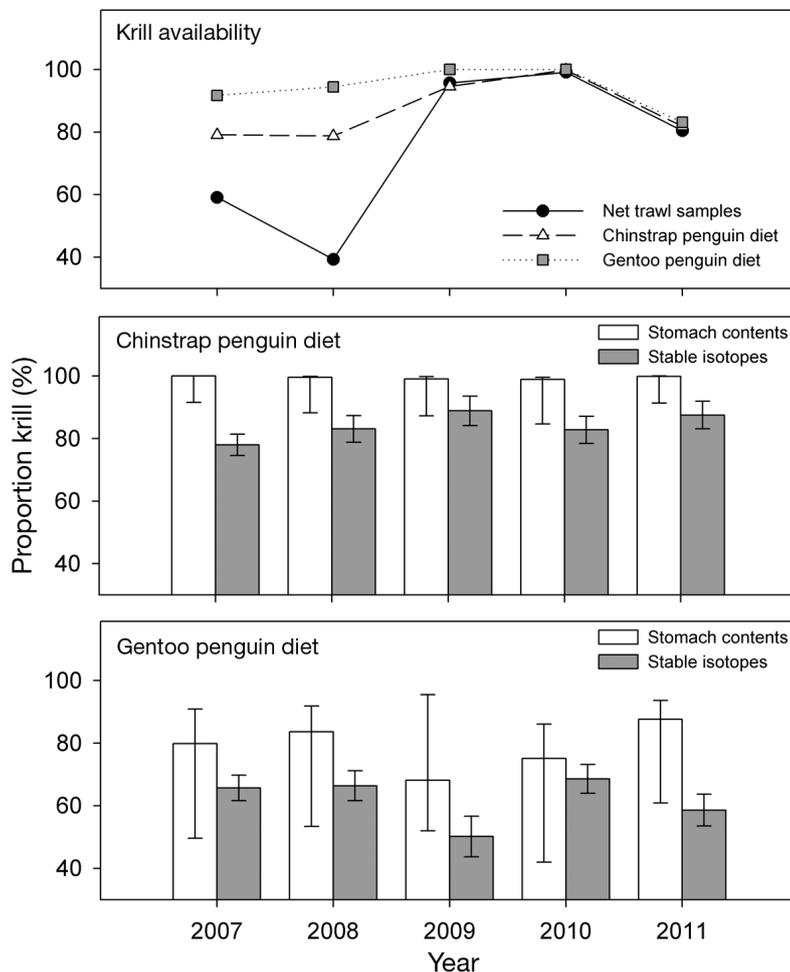
Fig. 4. Availability (%) of adult krill to penguins based on concurrent stomach content and net trawl samples relative to the proportion of krill estimated in chinstrap and gentoo penguin chicks' diets at Cape Shirreff, Livingston Island, Antarctica, using stomach content analysis and stable isotope-based mixing models. Diet estimates are mean ± 95% credibility intervals

mated by our SIAR model (gentoo: r = 0.90, p = 0.037; chinstrap: r = −0.96, p = 0.011). Years when gentoo penguins consumed more krill and/or chinstrap penguins consumed less krill led to greater isotopic niche overlap in both species (Appendix, Fig. A2).

Comparisons with krill availability

There was a significant and positive correlation found across years between the proportion of adult krill found in penguin stomach contents and concurrent net trawls for chinstrap penguins (Pearson correlation: r = 0.88, p = 0.050) but not gentoo penguins (r = 0.56, p = 0.322; Fig. 4). When testing for relationships between penguin and net-based proxies of adult krill availability and stomach content-based measures of chick diet composition (% krill) and foraging niche metrics (TNW and D), only 2 significant relationships were observed (all others p < 0.058). In years when there were more adult krill found in penguin stomach contents, chinstrap penguin chicks were fed slightly less krill overall (r = −0.92, p = 0.028) and thus had slightly larger TNW (r = 0.88, p = 0.048). Even so, as the proportion of krill (by wet mass) found in chinstrap penguin chick diet varied by no more than 1% across years (99 to 100%; Fig. 1), the above correlations are not biologically significant. When compar-

ences were primarily due to the more variable $\delta^{15}N$ values exhibited by gentoo penguins at Cape Shirreff in all years, as variability in $\delta^{13}C$ values only differed in 2010 (Fig. 5, Table 4). Similarly, total niche area (TA) was significantly larger in gentoo relative to chinstrap penguins in all years (Figs. 3 & 5). TAO ranged from 0 to 20% in chinstrap penguins and 0 to 25% in gentoo penguins and did not differ between species across the 5 yr of our study (Table 3).

TAO was the only isotopic niche metric that was correlated between species across the 5 yr of our study (Pearson correlation: r = 0.88, p = 0.048; all other comparisons p > 0.126). Variation in TAO was not related to our 3 isotopic niche width metrics for either species (all comparisons p > 0.094) but was strongly correlated with interannual variation in the proportion of krill consumed by each species as esti-

Table 4. Feather carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values of penguin chicks at Cape Shirreff, Livingston Island, Antarctica, from 2007 to 2011. Stable isotope values are mean ± SD

Year	n	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Chinstrap penguin			
2007	30	−23.8 ± 0.3	8.2 ± 0.3
2008	20	−24.7 ± 0.3	7.8 ± 0.3
2009	20	−25.2 ± 0.3	7.5 ± 0.3
2010	20	−24.5 ± 0.5	7.9 ± 0.2
2011	20	−22.0 ± 0.2	7.6 ± 0.2
Gentoo penguin			
2007	30	−23.2 ± 0.3	8.9 ± 0.7
2008	20	−24.6 ± 0.3	8.9 ± 0.6
2009	21	−24.3 ± 0.3	9.8 ± 0.8
2010	20	−24.4 ± 0.3	8.7 ± 0.5
2011	20	−22.1 ± 0.2	9.3 ± 0.6
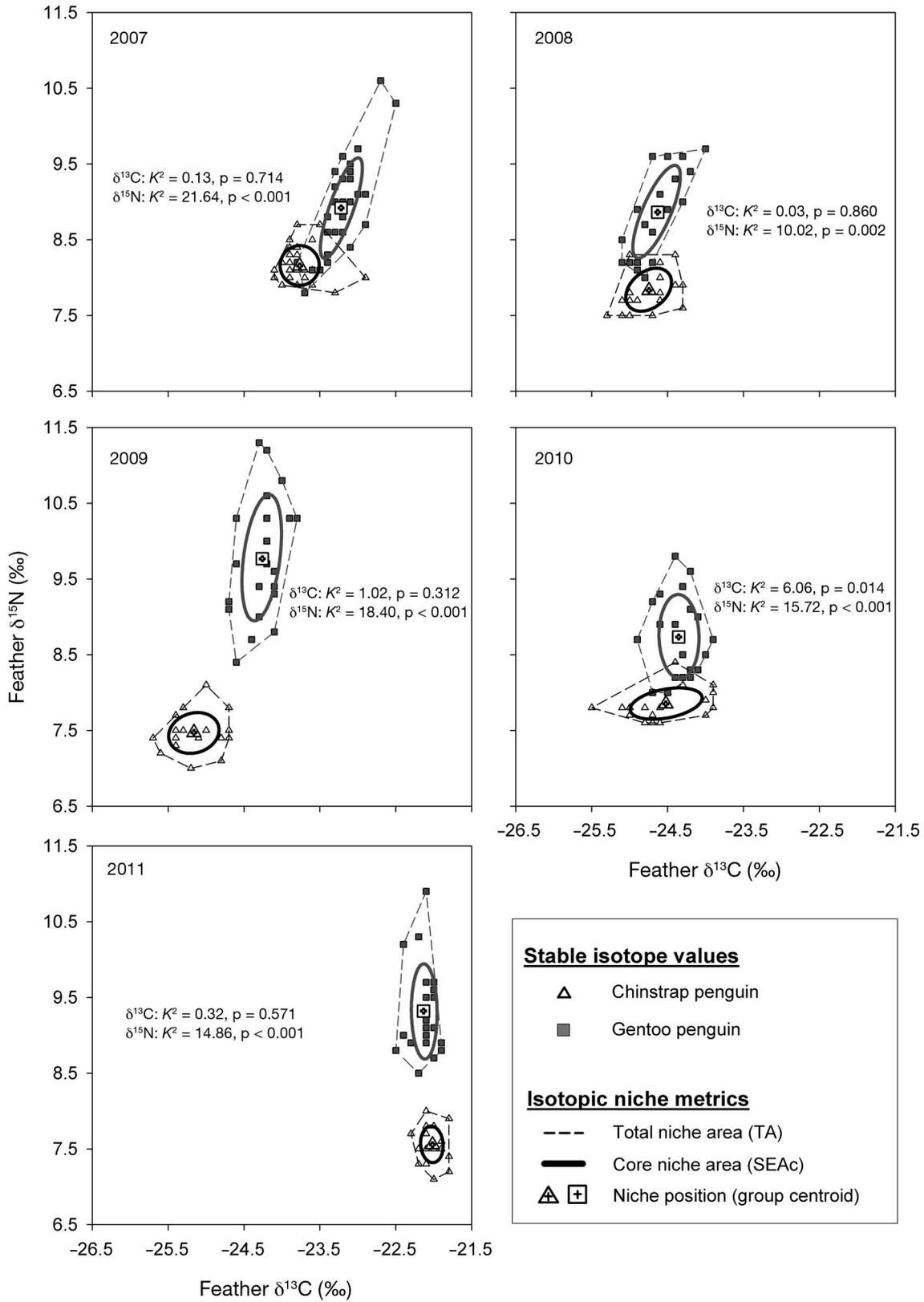
Fig. 5. Feather stable isotope values ($\delta^{13}C$ and $\delta^{15}N$), isotopic niche position and total and core isotopic niche area of chinstrap and gentoo penguin chicks at Cape Shirreff, Livingston Island, Antarctica. Statistics represent Bartlett's tests of homogeneity of variance between species on feather stable isotope values

ing penguin and net-based proxies of adult krill availability with stable isotope-based measures of chick diet composition (% krill) and foraging niche metrics (SEAc, MCD and TAO), no relationships across year were found in either chinstrap or gentoo penguins (all p > 0.241). These results suggest that penguin diets and foraging niches were not responsive to interannual fluctuation in the availability of adult krill during the course of our study.

DISCUSSION

Patterns of interspecific niche partitioning

Ecological theory predicts that when closely related species overlap, they often exhibit morphological or behavioral characteristics that lead to niche segregation and thus co-existence (Hutchinson 1959). In support of this principle, we found constant and significant differences in the dietary and isotopic niches of chick-rearing chinstrap and gentoo penguins over the 5 yr of our study at Cape Shirreff, Livingston Island, Antarctica. Niche partitioning between these 2 sympatric species was a function of the generally lower trophic position (e.g. higher krill consumption) and a greater use of pelagic and mesopelagic foraging habitats by chinstrap penguins relative to gentoo penguins. Confirming the results of previous studies, fish and other high-trophic prey were a more frequent and abundant component of gentoo penguin stomach contents relative to chinstrap penguins (Volkman et al. 1980, Miller et al. 2010, Polito et al. 2011a). Our results build on these previous studies and find broad agreement between stomach content data and the stable isotope-based dietary mixing model, which estimated that gentoo penguin chicks were fed a higher proportion of fish relative to chinstrap penguin chicks in all years.

Stomach contents also reflected a clear difference in habitat use between these 2 species. While both penguin species consumed pelagic fish, mesopelagic fish were found relatively more frequently in chinstrap penguin stomach contents, indicating their predilection for offshore foraging (Miller & Trivelpiece 2008). In contrast, the relatively higher occurrence of benthic fish in gentoo penguin diets are likely reflective of nearshore foraging (Miller et al. 2009). Stable isotope data also provide some support for differences in foraging habitats between these 2 species. Consumer $\delta^{13}C$ values in marine systems are often used to infer inshore vs. offshore habitat use because of differences in fractionation during photo-

synthesis between benthic macroalgae and pelagic phytoplankton (France 1995, Cherel & Hobson 2007). For example, gentoo penguin chick feathers had higher $\delta^{13}C$ values relative to chinstrap penguins in 2 years (2006 to 2007 and 2008 to 2009), which were also marked by a high occurrence of benthic fish in stomach contents of chick-rearing gentoo penguins (Fig. 2, Table 3). Combined, the results from both stomach content and stable isotope analysis agree with recent tracking studies at Cape Shirreff and other sites that found that gentoo penguins often forage closer to shore than chinstrap penguins (Kokubun et al. 2010, Miller et al. 2010).

These results indicate a general pattern of trophic and habitat niche segregation between chick-rearing chinstrap and gentoo penguins. While these segregated niches may have evolved because of competition, they also may reflect niche conservatism based on independently evolved species-specific differences (Trivelpiece et al. 1987). Whatever the evolutionary mechanism driving differences in penguin foraging niches, data from both stomach contents and stable isotope analysis suggest that a variable degree of niche overlap can still occur. Schoener's (1968) diet overlap index for chick-rearing adult stomach contents was significant in all years, and while core isotopic niches of chicks (SEAc) did not overlap, total isotopic niches (TA) did overlap by as much as 25% in some years. Interannual variation in both dietary and isotopic niche overlap was driven primarily by the proportion of krill consumed by penguins. Gentoo penguins consuming more krill and/or chinstrap penguins consuming less krill lead to greater niche overlap in both species. While these shifts in diets contributed to a partial niche overlap, it is likely that any competitive overlap in these 2 species at Cape Shirreff is mediated by differences in their niche breadth, population sizes and choice of non-krill prey. For example, the broader dietary and isotopic niche found in gentoo penguins may help to mitigate competitive interactions when partial niche overlap occurs with a sympatric species (Wilson & Yoshimura 1994), while the relatively smaller population of gentoo penguins may offset any negative effects of partial niche overlap for chinstrap penguins (Miller et al. 2010). In addition, differences in the type of fish consumed by chinstrap and gentoo penguins (e.g. mesopelagic vs. benthic) may also offset niche overlap when krill consumption is reduced. Temporal differences in foraging behaviors, prey mobility and abundance are also predicted to influence foraging niche partitioning and mediate competitive overlap in *Pygoscelis* penguins (Wilson 2010). Interestingly, we

found little evidence indicating that shift in the availability of adult krill across years influenced penguin diet composition or the degree of dietary or isotopic niche overlap between species.

Interspecific differences in niche width

Both dietary and isotopic measures of niche width differed between chinstrap and gentoo penguins during the crèche period at Cape Shirreff. Stomach content data from this study and others suggest that chinstrap penguin diets at Cape Shirreff are dominated almost exclusively by Antarctic krill (Miller et al. 2010, Polito et al. 2011a), leading to a narrow dietary niche with little to no individual and interannual variation. The only caveat to this finding was the slightly higher proportion of otoliths in female chinstrap penguin stomach samples relative to males. Even so, any sexual differences in diet during chick rearing are likely to be small, as this and previous studies found that diet estimates based on percent composition or frequency occurrence of prey items did not differ between sexes (Miller et al. 2010).

Stable isotope-based estimates of diets and niche width further confirmed that chick-rearing chinstrap penguins utilized a narrow range of prey species (primarily krill) and foraging habitats. As stable isotope analyses reflect an integrated measure of diets and habitat (Polito et al. 2011a) when combined with stomach content data, it provides strong evidence that chinstrap penguins at Cape Shirreff can be considered a specialist population during the chick-rearing period. For example, the small and relatively consistent core and total isotopic niche widths observed in chinstrap penguins across years suggest that individuals within this population utilized similar dietary resources and foraging habitats and respond to interannual changes in environmental conditions in a similar manner. In addition, the low degree of individual variation in chinstrap penguins may be a reflection of reduced intraspecific competition via an adaptation to forage on locally abundant Antarctic krill swarms offshore and along the continental shelf slope (Trivelpiece et. 1987). Finally, we found that during our study, chick-rearing chinstrap penguins continued to target krill even in years when adult krill were less available, and it may have been more efficient to switch to an alternate prey source (Miller & Trivelpiece 2008). Unfortunately, there are no independent data available to assess variation in the availability of alternative prey such as mesopelagic fish during our study period.

In contrast, measures of dietary niche width based on stomach contents in gentoo penguins were broader and more variable than those observed in chinstrap penguins from our study. For example, TNW was on average an order of magnitude higher in gentoo penguins relative to chinstrap penguins in each of the 5 years of our study. Isotopic measures also indicated that gentoo penguins had broader and more flexible core and total isotopic niche areas relative to chinstrap penguins. Combined, these independent measures suggest that at the population level, chick-rearing gentoo penguins at Cape Shirreff occupy a generalist niche. This agrees with previous studies of gentoo penguins around the South Shetland Islands and other regions, which suggest that gentoo penguins often have more diverse and flexible diets (Lescroël & Bost 2005, Miller & Trivelpiece 2008, Polito et al. 2011a) and use a broader habitat range than other *Pygoscelis* penguins (Miller et al. 2010). Interestingly, variation in gentoo penguin diets and foraging niches in our study was not correlated with interannual shifts in the availability of adult krill. Given their diverse diets, it is likely that gentoo penguin diet and foraging niches are also influenced by the availability of other prey species such as fish. Furthermore, given the shorter foraging range of gentoo penguins, this and other studies indicate that their foraging choices may be a reflection of small-scale changes in prey availability (Miller & Trivelpiece 2008, Miller et al. 2010).

Broader dietary niches in gentoo penguin populations might in part be due to sexual differences in foraging behaviors and diet, with larger males diving deeper and consuming a higher proportion of fish than females (Volkman et al. 1980, Bearhop et al. 2006, Miller et al. 2010). In addition, a recent analysis of the pre-breeding diets of gentoo penguins at Biscoe Point along the western Antarctic Peninsula indicate that females foraged at a slightly lower trophic level than males in 2 out of 3 years (Gorman et al. 2014). In contrast, we did not observe sexual differences in diets based on percent composition or frequency occurrence of prey items or when comparing measures of dietary niche width. The only evidence of sexual differences observed in our study was the higher number of otoliths in female penguins' stomach samples, though this was not consistent in all years. This suggests that factors such as differences in foraging habitat across sites and interannual or spatial variation in resource availability may mediate the degree and consistency of sexual variation in gentoo penguin diets, similar to results found in other seabirds (Miller et al. 2010, Phillips et al. 2011).

Generalist strategies in gentoo penguins

Both stomach content and stable isotope analysis indicate that during the chick-rearing period, gentoo penguins at Cape Shirreff represent a generalist population. However, determining if this generalist population is composed of individuals all taking a wide range of food types (Type A generalists) or individuals each specializing in a different range of food types (Type B generalists) is a more complex undertaking. Studies in other species have addressed this question by using direct or isotopic methods to serially sample the diet composition of individuals over time (Woo et al. 2008, Hückstädt et al. 2012).

Unfortunately, we are unable to conclusively determine the generalist strategy used by gentoo penguins during the chick-rearing period at Cape Shirreff, as we could not repeatedly sample individuals' diets over time. Even so, comparing isotopic niche metrics derived from chick feather stable isotope values between species may help to provide some indirect insights into the generalist strategy used by gentoo penguins in our study. For example, while chick feather $\delta^{13}C$ values were generally equally variable across species, $\delta^{15}N$ values were 2 to 3 times more variable in gentoo penguin chicks than in chinstrap penguin chicks. Furthermore, isotopic metrics indicated broader niches (SEAc and TA) and a greater degree of trophic diversity (MDC) among individual gentoo penguin chicks. This higher degree of intra-population variation in gentoo penguin stable isotope values and niche metrics relative to chinstrap penguins indicate that they may exhibit some degree of individual specialization when it comes to the trophic level of diet (i.e. Type B generalist strategy). If gentoo penguins were using a strict Type A generalist strategy during the chick-rearing period, we might expect that chick feather stable isotope values and niche metrics would exhibit the same degree of variation as that observed in the specialist chinstrap penguins (Bearhop et al. 2004).

One caveat to the above interpretation is that chick feathers are a reflection of the average dietary inputs from 2 individual parents and are not a direct measure of individual foraging specialization per se. This is likely to reduce the degree of interindividual variation in the stable isotope values of chicks, relative to a similar population of adults, and thus the stable isotope values of chick feathers are at best a proxy of the minimum degree of individual or pair foraging specialization that occurs in chick-rearing adults. Given these potential biases, future isotopic analyses of adult tissues that serially record dietary history over time (Hückstädt et al. 2012) or tissues from the same individual that differ in their temporal integration of dietary signatures (e.g. short vs. long; Bearhop et al. 2006, Matich et al. 2011) will be essential to assess the degree of individual foraging specialization in *Pygoscelis* penguins during and outside of the breeding season.

Pygoscelis penguin ecological niches and recent declines in Antarctic krill

Differences in foraging strategies and the width of dietary and habitat niches between chinstrap and gentoo penguins provide insights into population trends in the Antarctic Peninsula over the past 30 yr. While populations of chinstrap penguins in this region have declined dramatically, gentoo penguin populations have been stable or expanding (Trivelpiece et al. 2011, Lynch et al. 2012). Of the 2 species, our study suggests that gentoo penguins are generalists and have a broader and more plastic niche relative to chinstrap penguins. This may provide them greater resilience to the effects of recent climate-driven changes in the Antarctic marine ecosystem (Ducklow et al. 2007, Stammerjohn et al. 2008). A greater diversity of diet, proclivity for foraging on fish and use of nearshore benthic habitats all allow gentoo penguins to be less sensitive to the availability of Antarctic krill (Miller et al. 2009). Gentoo penguins may also benefit from competitive release as other *Pygoscelis* species decline (Miller et al. 2010, Trivelpiece et al. 2011) and as reductions in spring sea ice allows greater accessibility to ice-free coastlines for colony establishment near their southern range limit (Lynch et al. 2012). Other factors, such as a greater flexibility in the timing of breeding and longer parental investment during chick rearing, likely benefit gentoo penguins relative to other *Pygoscelis* species (Polito & Trivelpiece 2008, Hinke et al. 2012).

In contrast, several features of the niches of chinstrap penguins may help address why their populations are declining in the Antarctic Peninsula. Chinstrap penguins in our study consumed predominantly Antarctic krill, had narrower trophic niches with less individual niche variation and foraged primarily in offshore habitats where Antarctic krill are a readily available prey source (Ichii et al. 1998). Together, these factors agree with recent population-level trends indicating that chinstrap penguins are highly sensitive to environmental changes that impact the abundance of Antarctic krill (Trivelpiece et al. 2011), especially if these same environmental conditions have

also likely reduced the availability of alternative prey such as pelagic or mesopelagic fish (Torres et al. 2012). Furthermore, our study shows that when chinstrap penguins forage less on krill, they may risk greater niche overlap with sympatrically breeding gentoo penguins. Therefore, while all *Pygoscelis* penguins are likely to adjust their dietary and habitat niches in response to environmental conditions to some degree, the flexible generalist niche exhibited by gentoo penguins appears to be better suited to the rapidly changing climatic and oceanographic conditions now occurring in the Antarctic Peninsula.

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Appendix
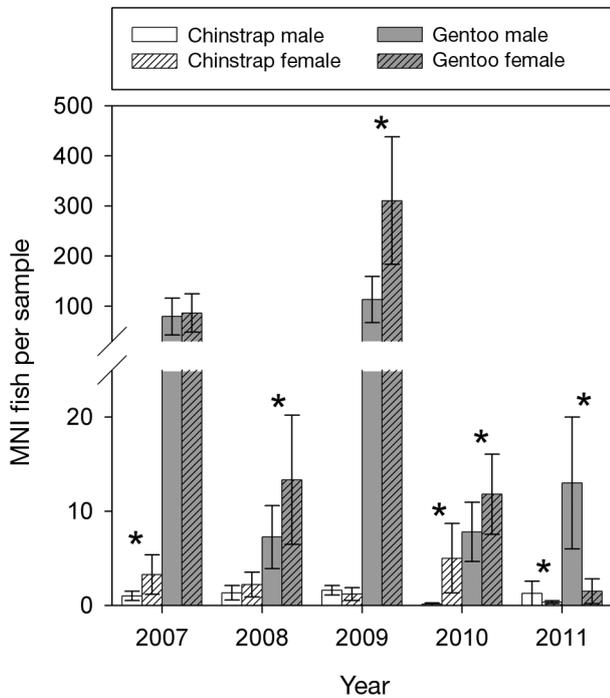
Fig. A1. Minimum number of individual (MNI) fish based on otoliths recovered from adult male and female penguin stomach contents during the crèche period at Cape Shirreff, Livingston Island, Antarctica, from 2007 to 2011. Values are presented mean ± SE. Asterisks denote significant differences between sexes at the 0.05 level
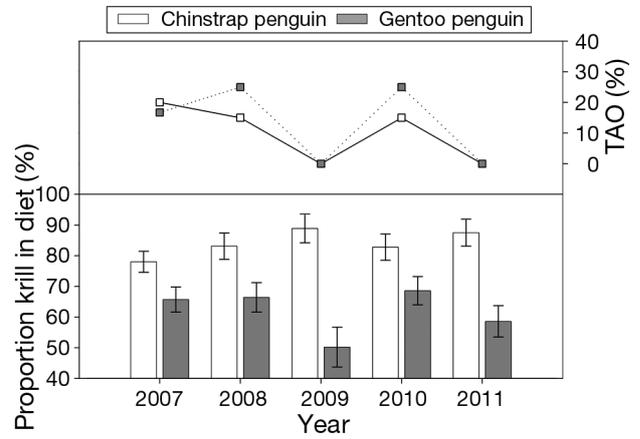
Fig. A2. Relationship between total isotopic niche overlap at the individual level (TAO; Hammerschlag-Peyer et al. 2011) and proportion of krill in diets as estimated by stable isotope analysis of penguin chicks at Cape Shirreff, Livingston Island, Antarctica, from 2007 to 2011