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ORIGINAL PAPER

Size structure of Antarctic krill inferred from samples of Pygoscelid penguin diets and those collected by the commercial krill fishery

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Abstract

In the Antarctic Peninsula, during the chick-rearing period Adélie (*Pygoscelis adeliae*) and gentoo (*P. papua*) penguins feed primarily on Antarctic krill (*Euphausia superba*), which is also exploited by the commercial fishery. Krill length and proportion of juvenile krill consumed by these predators that breed at Stranger Point, South Shetland Islands (from 2007/2008 to 2015/2016), and those collected by the krill fishery in the Mar de la Flota/Bransfield Strait (from 2009/2010 to 2015/2016) were compared to evaluate the potential of each data source as an indicator of changes in the size composition and so, in the demographic structure of the krill population. Overall, the mean krill size taken by gentoo penguins was larger than that ingested by Adélie penguins, which consumed higher proportions of juvenile (≤ 35 mm) and one-year-old (≤ 25 mm) krill. Although the krill size caught by the fishery was statistically similar to that taken by both penguin species, there were differences in the frequency distributions of krill size among the three databases. Furthermore, when only adult krill (> 35 mm) was considered, the three sources of krill data showed a similar inter-annual variation in the availability of adult krill cohorts. Our findings suggest that each database analysed here can potentially provide different information (although complementary) about krill size composition. In addition, inter-annual fluctuations in the smaller size classes of krill likely reflect their first year of recruitment and, therefore, may be used as an indicator of shifts in local krill availability.

Keywords *Pygoscelis adeliae* · *Pygoscelis papua* · SISO database · *Euphausia superba*

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Introduction

The Antarctic krill (*Euphausia superba*), hereinafter "krill", is the principal prey for numerous top and meso-predators in the Antarctic marine food web (e.g. Santora et al. 2009; Trivelpiece et al. 2011; Siegel 2016; Hinke et al. 2017; Dimitrijević et al. 2018; Juáres et al. 2018), and is also the target of commercial exploitation which could compete with these predators (Hinke et al. 2017; Watters et al. 2020). South of the Antarctic Convergence, the commercial krill fishery is managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) taking into account the status of both target species and their dependent species. CCAMLR agreed to subdivide the Antarctic Peninsula region (i.e. Subarea 48.1) in Small-Scale Management Units (SSMUs; Fig. 1) which represent management units for the krill fishery (Hill et al. 2016). Furthermore, a CCAMLR Scheme of International Scientific Observation (SISO)—with observers on board vessels that supervise the fishing activity in each SSMU—provides a

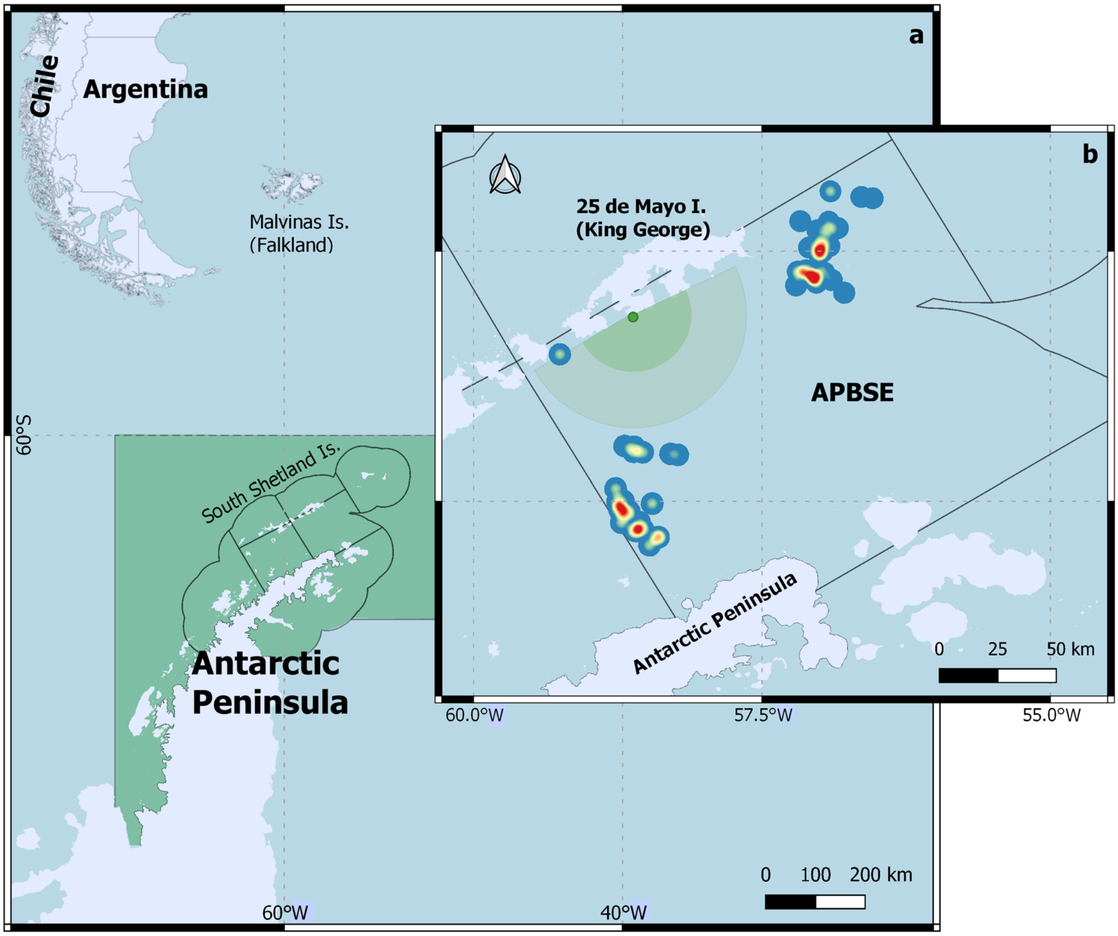

Fig. 1 **a** Subarea 48.1 (*green*) in the Antarctic Peninsula region. **b** Study area showing heatmap of the fishing distribution (i.e. of 49 hauls) from 2010 to 2016 weighted by the effort in terms of fishing hours in the Antarctic Peninsula Bransfield Strait East (APBSE) Small Scale Management Unit (SSMU, delimited by *continuous lines*); and buffers of 50 and 25 km from the colony representing the potential foraging range of Adélie and gentoo penguins, respectively breeding at Stranger Point/Cabo Funes (*green point*) on 25 de Mayo/King George Island, South Shetland Islands, Antarctica

fundamental source of biological data to assess the potential impact of commercial fishing on krill predators, and the status and population dynamics of target species (Tarling et al. 2016; Hinke et al. 2017; CCAMLR Secretariat 2019). The Mar de la Flota/Bransfield Strait region, located between the South Shetland Islands and the Antarctic Peninsula, is a spawning and nursery area of krill (e.g. Siegel 2016; Perry et al. 2019) as well as a productive krill fishing ground (Siegel 2016; Hinke et al. 2017; Santa Cruz et al. 2018; Krüger 2019). Moreover, the environmental variability driven by climate warming, what is critically important in this region, also affects the population dynamics of krill. The increases in temperature and consequent sea-ice loss impact negatively on the numerical densities, distribution, survival, and recruitment of krill (Atkinson et al. 2019).

Along the Antarctic Peninsula, Adélie (*Pygoscelis adeliae*) and gentoo (*P. papua*) penguins feed mainly on krill during the chick-rearing period (Volkman et al. 1980; Hinke et al. 2007; Trivelpiece et al. 2011; Juáres et al. 2018; Pickett et al. 2018; among others). Although both species feed in open-waters, spatio-temporal differences in their foraging behaviors have been recorded. Gentoo penguins generally forage earlier (during the morning), nearshore and/or at deeper depths, compared to their congeners (e.g. Wilson 2010; Juáres 2013; Cimino et al. 2016; Hinke et al. 2017; Pickett et al. 2018). However, both species are constrained to a central place-foraging strategy due to the need to return regularly to their nests to provision the offspring, i.e. breeders depend on adequate food availability within a restricted foraging range near the colony (Hinke et al. 2017).

Krill reproductive success, recruitment, abundance and hence, its availability for predators are highly variable in space and time. Variability in the krill availability is also a consequence of its swarming behaviour, vertical and horizontal migration, and spatial segregation according to life stage and age (Reiss et al. 2008; Santora et al. 2009; Siegel

2016; Richerson et al. 2017). During austral spring and summer, those fluctuations in krill population dynamics can have a significant impact on the abundance, distribution and ultimately the feeding ecology and breeding performance of krill-dependent predators (Nicol et al. 2008; Santora et al. 2009; Trivelpiece et al. 2011; Cimino et al. 2016). Conversely, the diet of krill predators may reflect changes in the abundance and size composition of krill (Fraser and Hofmann 2003; Hinke et al. 2007; Miller and Trivelpiece 2007; Saba et al. 2014; Juáres et al. 2018; Pickett et al. 2018; CCAMLR Secretariat 2019). For example, since the krill length can be used as a proxy indicator of its age, the krill size taken by predators allows tracking temporal changes in the size-structure of the krill population, which reflect events of recruitment and hence, the local krill availability (Fraser and Hofmann 2003; Lynnes et al. 2004; Miller and Trivelpiece 2007; Saba et al. 2014; Juáres et al. 2018; Pickett et al. 2018; CCAMLR Secretariat 2019).

In order to achieve effective conservation management, CCAMLR requires to improve our understanding on the population dynamics of krill and its predators by obtaining the information from different sources, such as the krill fishing vessels, scientific net surveys and predator monitoring programs (Hill et al. 2016; Tarling et al. 2016; Watkins et al. 2016; CCAMLR Secretariat 2019; Meyer et al. 2020). The Mar de la Flota/Bransfield Strait is an area of ecological and commercial importance, which makes it an area of interest for its conservation (Hinke et al. 2017; Santa Cruz et al. 2018; Perry et al. 2019). Thus, this study aimed to provide a comparative analysis of the krill length obtained from three different datasets, i.e. the krill found in the diet samples of two krill-dependent predators at the Stranger Point/Cabo Funes colony in the South Shetland Islands (Adélie and gentoo penguins), and those collected by the commercial krill fishery in the Mar de la Flota/Bransfield Strait region (APBSE SSMU). So, by investigating the interannual variability in the krill size composition we can assess the potential of each datasets as an indicator of changes in the availability of this crustacean, in order to improve our understanding on the ecological role of predators at Stranger Point, and thus providing relevant knowledge for effective fisheries management.

Materials and methods

Study area

The Pygoscelid penguin diet was studied at Stranger Point/Cabo Funes (62°16′S, 58°37′W. 25 de Mayo/King George Island, South Shetland Islands, Antarctica; Fig. 1) from the 2007/2008 (hereinafter 2008) to the 2015/2016 (hereinafter 2016) breeding seasons. The dietary data of Adélie penguins from 2008 to 2015 breeding seasons was previously published by Juáres et al. (2018).

This research is part of a long-term monitoring of Adélie and gentoo penguins conducted by the Argentine Ecosystem Monitoring Program of the Argentine Antarctic Institute. Data were collected, whenever possible, according to the standard protocols defined by the Ecosystem Monitoring Program (CEMP) of the CCAMLR (CCAMLR 2014).

Stomach contents (CEMP parameter A8)

During the crèche stage of chicks, a total of 230 and 210 complete stomach contents were collected from Adélie and gentoo penguins, respectively, using the water-offloading technique (Wilson 1984; Gales 1987). The methodology employed in the field and the laboratory analysis has previously been described in Juáres et al. (2018).

The diet composition was described in terms of frequency of occurrence (*FO%* = total number of samples containing the item/total number of samples analysed multiplied by 100) and percentage in mass (*M%* = total mass of the item/total mass of all samples multiplied by 100) of the two main prey taken by penguins (i.e. Antarctic krill and all fish species).

The length of all intact krill specimens collected from each sample has been measured annually from the tip of the rostrum to the tip of the telson by using a digital calliper (0.01 mm error). Individuals with a size ≤ 35 mm were considered juveniles and, within of this category, individuals with a length ≤ 25 mm were considered 1-year-old krill (e.g. Reiss et al. 2008).

CCAMLR Scheme of International Scientific Observation (SISO)

SISO database was obtained from the CCAMLR's Secretariat (www.ccamlr.org/). For our study, we filtered the commercial krill fishery information based on a spatio-temporal criterion to ensure a more robust comparison with the penguins' datasets (i.e. a greater spatio-temporal coincidence among the three data sources). Thus, our subset of data contained the individual length measurements of krill of January and February from 2010 to 2016, spatially limited within the Antarctic Peninsula Bransfield Strait East (APBSE) SSMU. So, the SISO database comprised a total of 49 hauls made from nine fishing vessels where 8812 krill individuals were measured.

To visualize the proximity between the locations of the commercial krill fishery and the maximum potential area exploited by penguins breeding at Stranger Point, a spatial processing of this information was carried out in QGIS 3.10. A heatmap of the fishing distribution (i.e. of 49 hauls) was generated using Kernel Density Estimation with a radius of 5 km, pixel size of 50 × 50, kernel shape Quartic and weighted by the fishing effort in terms of fishing hours higher than zero (Krüger 2019). In addition, following the conservation objectives established in the Marine Protected Area proposal for the Subarea 48.1, we added a buffer zone of 50 km and another one of 25 km from the colony for representing the potential foraging range of Adélie and gentoo penguins, respectively (Fig. 1) (Santos and Capurro 2017). The topography map of the Antarctic Peninsula was sourced from the Antarctic Digital Database (https://www.scar.org/data-products/antarctic-digital-database/), and the limits of the SSMU were obtained from the CCAMLR (https://data.ccamlr.org/search/type/dataset).

Statistical analyses

Generalized linear mixed-effects models (GLMM) were used to test the effect of the source of krill data and years on the size of krill, which was the response variable. Two separate models were fitted: (i) including all krill size recorded, and (ii) with only adult krill (i.e. krill > 35 mm). Models that included the predictors source of krill data (categorical variable with three classes: Adélie penguins, gentoo penguins and SISO data) and years (categorical variable with seven classes: from 2010 to 2016 when comparing the three sources) as fixed effects were tested. Since several items were measured from the same individual or haul the random effect of factor identity (ID of each individual or haul) was included, and random intercepts that model between-ID variation were employed. The response variable was modelled assuming a Gaussian distribution of errors and identity link function. An automatic backward step-wise approach was applied for model selection using the command "drop1", removing the non-significant terms. Modelling was performed with R software v.3.6.0 (R Core Team 2018) in RStudio software v.1.1.463 (RStudio Team 2018), using the "lmer" function from the *lme4* package (Bates et al. 2015). Residual plots were examined for model validation following the protocol described by Zuur et al. (2009), by inspecting residuals versus fitted values, and plots residuals versus each explanatory variable included and not included in the model, using the package *lattice* (Sarkar 2008). Post hoc Tukey tests were calculated to detect differences between treatments by using the function "emmeans" of the *emmeans* package (Russell 2019). Furthermore, correlations between the mean krill length (of all krill and only adult krill) recorded in each data source were assessed using Pearson's product-moment correlation coefficient with the "cor.test" function.

The length–frequency distribution of krill ingested and caught in each season was plotted in 12 size categories of 5 mm each (from 10 to ≥ 65 mm of length) in order to visually inspect changes in the size structure of krill population in relation to its presumed annual growth (Fraser and Hofmann 2003; Saba et al. 2014). We compared the distributions of krill lengths between datasets each season using a Kolmogorov–Smirnov two-sample test ("ks.test" function). Furthermore, the proportion of juvenile and adult krill was compared among the three data sources using a Chi-square test with Yates' continuity correction ("chisq.test" function). For both tests, we used the Bonferroni method to adjust the *p*-values ("p.adjust" function) in order to neutralize the possibility of type-I error due to multiple comparisons.

Results are reported as mean ± standard error (SE). Significance level was assumed at $\alpha = 0.05$.

Results

Diet composition of penguins

Antarctic krill dominated the diet of chick-provisioning Adélie (> 99% of the diet by mass) and gentoo (> 92% by mass) penguins in all breeding seasons (Table 1). Fish was a secondary prey that occurs more frequently in gentoo than Adélie penguins, although with low contribution by mass in both species (0–0.11% in Adélie penguins and 0–7.02% in gentoo penguins; Table 1). Other items (i.e. other euphausiids, amphipods, squid, algae, mollusc shells, unidentified material) represented < 0.1% of the diet by mass in all cases.

Antarctic krill length

The krill size fluctuated significantly by the source–season interaction (GLMM: $p < 0.0001$). Although the mean krill size consumed by gentoo penguins was always larger than that ingested by their congener (Table 2), significant differences were found in five out of the nine seasons compared (Tukey test, 2009: $z = -3.66$, $p = 0.03$; 2011: $z = -4.10$, $p = 0.007$; 2012: $z = -7.71$, $p = < 0.0001$; 2014: $z = -8.78$, $p = < 0.0001$, and 2015: $z = -3.61$, $p = 0.04$; Table 3). Furthermore, there was a significant difference in the prey size between gentoo penguins and the commercial fishery samples in one out of the seven seasons compared (Tukey test, 2014: $z = 4.16$, $p = 0.006$; Table 3), and in two seasons out of seven there was a significant difference between Adélie penguins and the commercial fishery samples (Tukey test, 2012: $z = -4.05$, $p = 0.009$, and 2014: $z = -5.51$, $p = < 0.0001$; Table 3). Only during 2014, the average krill size was significantly different among the three datasets, being larger in gentoo penguins, then in the SISO data, and ultimately in Adélie penguins.

When only adult krill was considered, the differences among datasets were smaller (Table 3). Moreover, mean krill lengths of all datasets were positively correlated (Fig. 2b).

Significant differences among sources in the length–frequency distributions of krill were evidenced

Table 1 Diet composition of Adélie and gentoo penguin adults at Stranger Point during the crèche stage from the 2008 to the 2016 season

Season	Adélie penguins					Gentoo penguins				
	n	Antarctic krill		Fish		*n*	Antarctic krill		Fish	
		FO (%)	*M* (%)	FO (%)	*M* (%)		FO (%)	*M* (%)	FO (%)	*M* (%)
2008	30	100	99.99	0	0	25	100	99.90	28.00	0.09
2009	25	100	99.92	24.00	0.03	25	100	99.25	40.00	0.75
2010	25	100	99.91	0	0	11	100	98.46	45.45	1.53
2011	25	100	99.83	8.00	0.11	24	100	98.50	25.00	1.49
2012	25	100	99.98	4.00	0.004	25	100	92.84	24.00	7.02
2013	25	100	99.78	0	0	25	100	99.53	20.00	0.46
2014	25	100	99.82	0	0	25	100	100	0	0
2015	25	100	99.86	0	0	25	100	99.65	12.00	0.35
2016	25	100	99.90	20.00	0.08	25	100	99.56	36.00	0.44

The Adélie penguin data from 2008 to 2015 was previously published by Juáres et al. (2018)

n number of stomach contents analysed (i.e. number of penguins sampled); *FO%* frequency of occurrence percentage; and *M%* percentage in mass

(Kolmogorov–Smirnov two-sample test, $p < 0.05$ after applying the Bonferroni correction; Table 4), except between the size distributions of krill recorded from the gentoo diet and fishery samples in 2010 and 2016 (Kolmogorov–Smirnov two-sample test, 2010: $D = 0.13$, $p = 1$ and 2016: $D = 0.07$, $p = 1$ after Bonferroni correction; Table 4). Although without a clear pattern evident, the bimodal distribution in the krill size was more frequently recorded in Adélie penguins (Fig. 3), with a first smaller peak of small krill (generally ≤ 25 mm) and a second largest peak of large size classes (generally ≥ 40 mm). Instead, both in gentoo penguins and SISO data a single dominant modal length was observed (except 2010 in SISO data; Fig. 3), generally ≥ 45 mm, reflecting a dominance of older age classes of krill.

Antarctic krill juveniles

The higher proportion of juvenile krill (i.e. ≤ 35 mm) found in Adélie diet samples was observed during 2012 and 2014 (49.9% and 52.9%, respectively; Fig. 4), while a high percentage of smaller-sized krill (i.e. ≤ 25 mm) was evidenced in 2012 (26.1%; Fig. 4). Instead, the proportion of juvenile krill taken by gentoo penguins and collected by the commercial fishery was higher in 2013 (13.9% and 31.4%, respectively; Fig. 4), but the presence of smaller-sized krill never reached 2% (Fig. 4).

The proportion of juvenile krill ingested by both penguin species differed significantly (Yates corrected chi-square test: $p \leq 0.05$ after applying the Bonferroni correction; Table 5) being higher in the Adélie penguin, except during 2010 (Yates corrected chi-square test: $\chi^2 = 10.8$, *Bonferroni-adjusted* $p = 1$; Table 5 and Fig. 4) when this species consumed a high percentage of large krill. Otherwise, the presence of juvenile krill was not totally consistent when comparing the SISO and the penguins' datasets (Table 5 and Fig. 4). The high proportion of juveniles recorded during 2013 in the SISO dataset was similar to Adélie penguins (Yates corrected chi-square test: $\chi^2 = 1.44$, *Bonferroni-adjusted* $p = 1$), but it was significantly higher than gentoo penguins (Yates corrected chi-square test: $\chi^2 = 42.38$, *Bonferroni-adjusted* $p = < 0.0001$; Table 5 and Fig. 4).

Discussion

In this study we compared the krill lengths found in the diet of Adélie and gentoo penguin breeding at Stranger Point, and in catches of the commercial fishery in the Mar de la Flota/Bransfield Strait region (APBSE SSMU; Fig. 1) in order to evaluate the potential of each dataset as an indicator of inter-annual changes in the size structure of the krill population. Krill was the dominant prey in the diet of both Pygoscelid penguins breeding at Stranger Point (Table 1). Nevertheless, a high inter-annual variability in the krill lengths consumed by both penguin species and caught by the fishery was observed over the study period (Table 2; Fig. 3). Overall, three important findings emerged from our analysis. First, krill taken by gentoo penguins was larger than those ingested by their congeners, between 2.47 and 10.30 mm longer (Table 2), which suggests that the differences between species were biologically meaningful because they were larger than our measurement error. Instead, the mean krill size caught by the fishery was statistically similar to that taken by both penguin species in most years. Second, the differences between databases in the size composition of krill were reflected in their length–frequency distributions, where the smallest age classes of krill were better represented in Adélie penguins despite the fact that older age krill classes were dominant in the three sampling methods

Table 2 Mean (± SE) and range of Antarctic krill length, and sample size (*n*) of individual krill consumed by Adélie and gentoo penguins at Stranger Point from 2008 to 2016 season, and collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016

All krill

Season	Adélie penguins				Gentoo penguins				SISO data			
	Date (Month–Day)	Antarctic krill			Date (Month–Day)	Antarctic krill			Date (Month–Day)	Antarctic krill		
		n	Mean ± SE	Range		*n*	Mean ± SE	Range		*n (h)*	Mean ± SE	Range
2008	Jan 7–23	1054	39.32 ± 0.22	13.53–58.70	Jan 26–Feb 21	1020	44.02 ± 0.17	27.06–58.85				
2009	Dec 27–Jan 19	337	40.09 ± 0.31	16.33–54.10	Dec 28–Jan 19	555	44.81 ± 0.20	31.88–57.26				
2010	Jan 11–18	203	46.52 ± 0.36	28.67–66.59	Jan 25–Feb 12	122	48.99 ± 0.32	38.92–57.53	Feb 23	200 (1)	48.11 ± 0.35	32.00–57.00
2011	Jan 13–21	1125	40.75 ± 0.23	14.85–57.70	Jan 19–Feb 2	950	44.74 ± 0.18	24.46–56.49	Jan 12	212 (1)	48.56 ± 0.38	28.00–59.00
2012	Jan 2–22	1140	33.43 ± 0.27	13.94–53.10	Jan 9–27	636	43.73 ± 0.23	22.17–60.50	Jan 2–3	800 (5)	42.82 ± 0.16	21.00–57.00
2013	Jan 16–Feb 6	331	38.13 ± 0.26	27.16–53.20	Jan 22–Feb 11	359	40.84 ± 0.28	29.25–60.19	Jan 28–31	1400 (7)	37.65 ± 0.12	24.21–53.16
2014	Jan 4–22	565	34.18 ± 0.20	17.81–50.07	Jan 8–28	229	44.44 ± 0.31	33.45–61.06	Jan 1–14	5100 (26)	40.19 ± 0.05	18.70–55.00
2015	Jan 3–24	977	41.12 ± 0.23	10.95–58.24	Jan 20–Feb 10	1013	45.06 ± 0.12	31.79–57.06	Jan 12–Feb 10	700 (6)	41.28 ± 0.18	22.00–53.00
2016	Dec 30–Jan 8	298	40.99 ± 0.46	16.00–60.31	Jan 11–14	440	45.49 ± 0.22	28.36–59.95	Jan 6–15	400 (3)	45.25 ± 0.24	24.00–56.00

Adult krill (> 35 mm)

Season	Adélie penguins			Gentoo penguins			SISO data		
	Antarctic krill			Antarctic krill			Antarctic krill		
	n	Mean ± SE	% adult	*n*	Mean ± SE	% adult	*n*	Mean ± SE	% adult
2008	796	42.49 ± 0.16	75.52	980	44.50 ± 0.16	96.08			
2009	279	41.81 ± 0.25	82.79	544	45.04 ± 0.19	98.02			
2010	199	46.85 ± 0.33	98.03	122	48.99 ± 0.32	100	189	48.92 ± 0.28	94.50
2011	857	44.39 ± 0.14	76.18	888	45.65 ± 0.14	93.47	204	49.23 ± 0.32	96.23
2012	571	41.19 ± 0.16	50.09	593	44.65 ± 0.20	93.24	779	43.13 ± 0.14	97.38
2013	239	40.24 ± 0.24	72.21	309	42.17 ± 0.25	86.07	961	39.64 ± 0.13	68.64
2014	266	37.98 ± 0.16	47.08	226	44.58 ± 0.31	98.69	4830	40.68 ± 0.04	94.71
2015	901	42.81 ± 0.13	92.22	1004	45.16 ± 0.12	99.11	619	42.48 ± 0.13	88.43
2016	242	44.20 ± 0.27	81.21	433	45.69 ± 0.21	98.41	393	45.59 ± 0.20	98.25

Statistical descriptions of all krill and adult krill recorded in each dataset across years are detailed

Date time period in which the samples were collected; *n* number of krill individuals measured; (*h*) number of hauls analysed; % *adult* percentage of adult krill

Table 3 Comparison of Antarctic krill length consumed by Adélie and gentoo penguins at Stranger Point from 2008 to 2016, and collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016

Season	Source	All krill		Adult krill (> 35 mm)	
		GLMM	Tukey test	GLMM	Tukey test
		z-statistic	*p*-value	*z*-statistic	*p*-value
2008[a]	Adélie–Gentoo	−3.48	0.051	−2.56	0.4852
2009[a]	Adélie–Gentoo	−3.66	**0.028**	−4.28	**0.0025**
2010	Adélie–Gentoo	−1.33	0.9993	−1.91	0.9447
	Adélie–SISO	−0.45	1.0000	−1.06	1.0000
	Gentoo–SISO	0.12	1.0000	−0.16	1.0000
2011	Adélie–Gentoo	−4.10	**0.0073**	−2.60	0.5336
	Adélie–SISO	−2.16	0.8425	−2.59	0.5410
	Gentoo–SISO	−0.99	1.0000	−1.81	0.9679
2012	Adélie–Gentoo	−7.71	**< 0.0001**	−6.80	**< 0.0001**
	Adélie–SISO	-4.05	**0.0087**	−2.94	0.2836
	Gentoo–SISO	0.63	1.0000	1.42	0.9982
2013	Adélie–Gentoo	−2.21	0. 8156	−3.00	0.2460
	Adélie–SISO	0.42	1.0000	1.10	1.0000
	Gentoo–SISO	2.01	0.9149	3.45	0.0735
2014	Adélie–Gentoo	−8.78	**< 0.0001**	−9.86	**< 0.0001**
	Adélie–SISO	−5.51	**< 0.0001**	−4.30	**0.0031**
	Gentoo–SISO	4.16	**0.0055**	6.83	**< 0.0001**
2015	Adélie–Gentoo	−3.61	**0.0438**	−3.93	**0.0142**
	Adélie–SISO	0.06	1.0000	0.79	1.0000
	Gentoo–SISO	2.37	0.7114	3.37	0.0927
2016	Adélie–Gentoo	−3.38	0.0895	−2.47	0.6347
	Adélie–SISO	−1.43	0.9982	−0.97	1.0000
	Gentoo–SISO	0.29	1.0000	0.38	1.0000

Statistics reported for the generalized linear mixed-effects models (GLMM) and *p*-values of Tukey test comparing the size of all krill and adult krill among each data source across years are detailed

Significant *p*-values are bolded

[a] Results of the same model when we compared only krill size ingested by Adélie and gentoo penguins

(Fig. 3). Third, when juvenile krill was excluded, the means of adult krill length (i.e. > 35 mm) of the three databases were positively associated which suggest that likely the three data sources tracked similar inter-annual trends in the adult krill population.

The higher frequency of occurrence of one-year-old krill (i.e. ≤ 25 mm) taken by Adélie penguins in January 2012 (> 25%; Fig. 4), might evidence an event of krill recruitment in Mar de la Flota/Bransfield Strait nearby Stranger Point in that period. This result is in line with those reported by Saba et al. (2014) and Bernard et al. (2017) for the western Antarctic Peninsula, who observed a good recruitment year of krill during the summer 2011–2012. By contrast, 1-year-old krill was almost absent from gentoo diet samples and krill fishery nets (Fig. 4). Nevertheless, while SISO data could not show the first recruitment year of krill, they could reflect the second recruitment year, as evidenced by the high proportion of krill sizes between 25 and 35 mm in 2013 (Fig. 4). The overall same pattern was found in gentoo diet samples. However, the samples of commercial krill fishery could provide a more comprehensive data to investigate the recruitment of juvenile krill than those from gentoo penguins.

The low abundance of smallest sized krill (i.e. ≤ 25 mm) in the fishery data might be related to the trawl nets selectivity (Atkinson et al. 2012; Siegel 2016), due to the size and opening angle of the mesh used by the fishing vessels the smallest size classes are likely underrepresented (Krag et al. 2014; Tarling et al. 2016). In addition to the net size, the fast speed of the fishery vessels also could explain the less avoidance by larger krill, which are good swimmers (Tarling et al. 2016). Meanwhile, the presence of large krill in the gentoo penguin diet compared to their congeners can be attributed to their larger body size; it can be associated with higher energy expenditure in gentoo penguins feeding chicks; it could also indicate a variability in the distribution and/or abundance of local krill (e.g. krill aggregations by size or age class), and/or it could evidence a segregation in the areas exploited by these penguin species due to differences in their foraging behaviours (i.e. segregation temporal, horizontal and/or vertical) (Volkman et al. 1980; Miller and Trivelpiece 2007; Wilson 2010; Juáres 2013; Cimino et al. 2016; Dimitrijević et al. 2018; Pickett et al. 2018). In this sense, Adélie penguins could exploit surface krill swarms at the offshore waters while gentoo penguins could exploit deeper krill swarms at the nearshore waters (Wilson 2010; Cimino et al. 2016; Hinke et al. 2017; Pickett et al. 2018; among others). So, the deeper dives performed by gentoo penguins could explain the larger krill consumed by them (e.g. Quetin and Ross 1984; Ichii et al. 2020). Thus, future studies combining information on feeding behaviour and breeding performance of penguins, simultaneously with surveys of krill and oceanographic conditions in waters adjacent to Stranger Point are required to evaluate the potential causes of the inter-specific difference recorded.

Excluding the krill juveniles, the differences among databases in the size of adult krill (i.e. > 35 mm) were reduced. Furthermore, the mean krill lengths from the three data sources were positively associated (Fig. 2b), indicating that the three data sources tracked a similar pattern of inter-annual changes in the local availability of adult krill

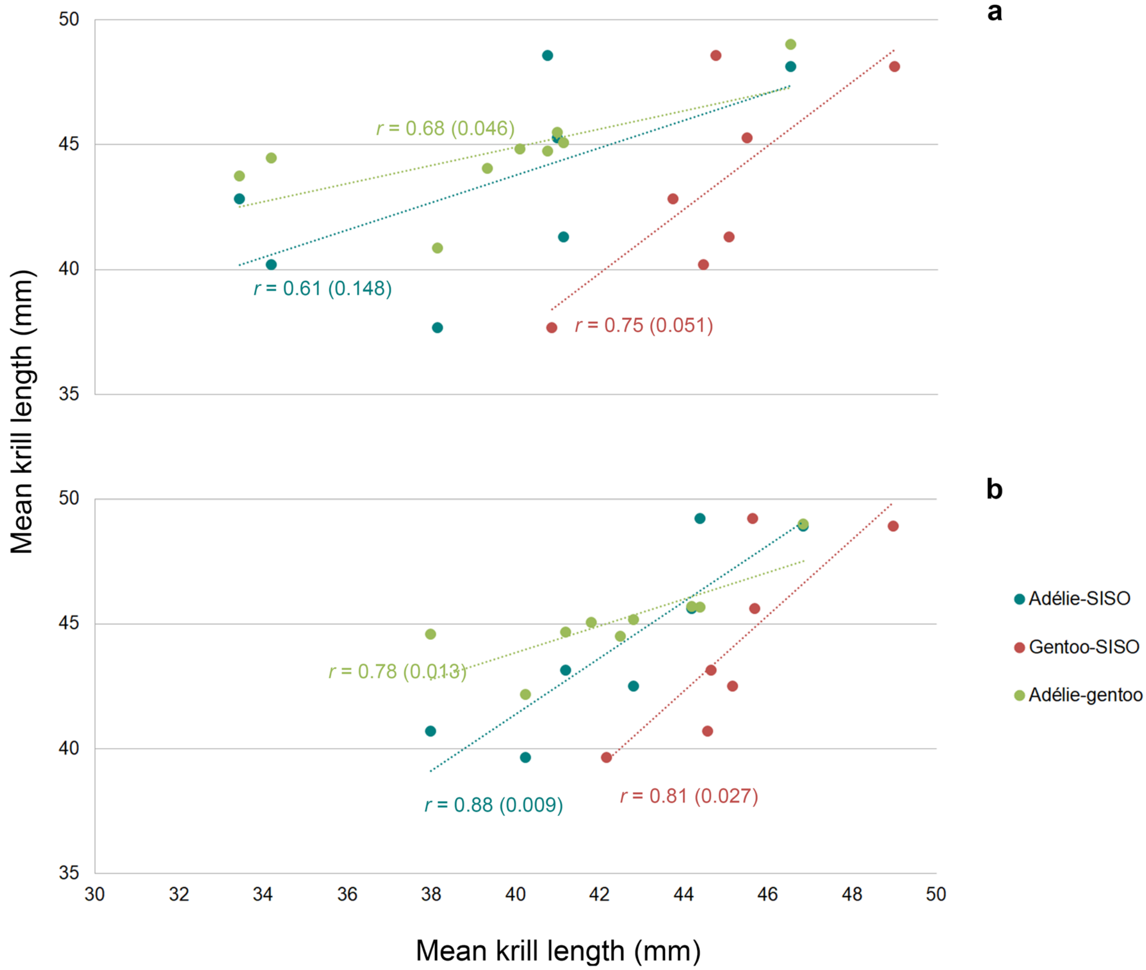

Fig. 2 Pearson's correlations among the mean lengths of Antarctic krill consumed by Adélie and gentoo penguins at Stranger Point from 2008 to 2016, and those collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016; Pearson's product–moment correlation coefficient (*rho*) and *p*-values (in brackets). **a** All krill sizes. **b** Only adult krill (i.e. krill length > 35 mm)

Table 4 Test statistic (*D*) and *p*-value of the Kolmogorov–Smirnov two-sample test comparing the length–frequency distributions of Antarctic krill consumed by Adélie and gentoo penguins at Stranger Point at Stranger Point from 2008 to 2016, and collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016

Season	Adélie vs. gentoo data		Adélie vs. SISO data		Gentoo vs. SISO data	
	D	*p*-value	*D*	*p*-value	*D*	*p*-value
2008	0.30	**< 0.0001**				
2009	0.39	**< 0.0001**				
2010	0.32	**< 0.0001**	0.34	**< 0.0001**	0.13	1
2011	0.21	**< 0.0001**	0.50	**< 0.0001**	0.39	**< 0.0001**
2012	0.48	**< 0.0001**	0.50	**< 0.0001**	0.15	**< 0.0001**
2013	0.25	**< 0.0001**	0.13	**0.003**	0.35	**< 0.0001**
2014	0.78	**< 0.0001**	0.62	**< 0.0001**	0.44	**< 0.0001**
2015	0.28	**< 0.0001**	0.13	**< 0.0001**	0.38	**< 0.0001**
2016	0.23	**< 0.0001**	0.28	**< 0.0001**	0.07	1

The *p*-values are adjusted for multiple comparison using the Bonferroni method. Significant *p*-values are bolded

D maximum difference between cumulative length–frequency distributions of two sources

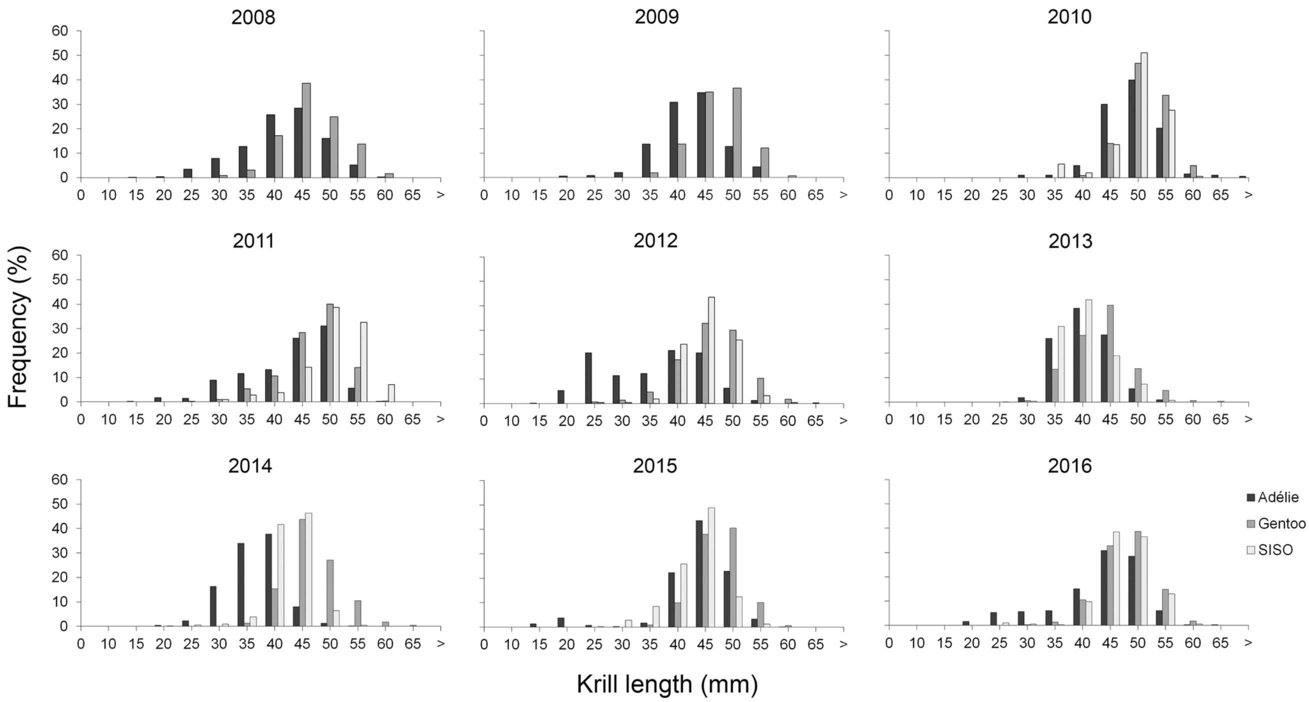

Fig. 3 Length–frequency distributions of Antarctic krill ingested by Adélie and gentoo penguins at Stranger Point from 2008 to 2016, and collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016. The Adélie penguin data from 2008 to 2015 was previously published by Juáres et al. (2018)

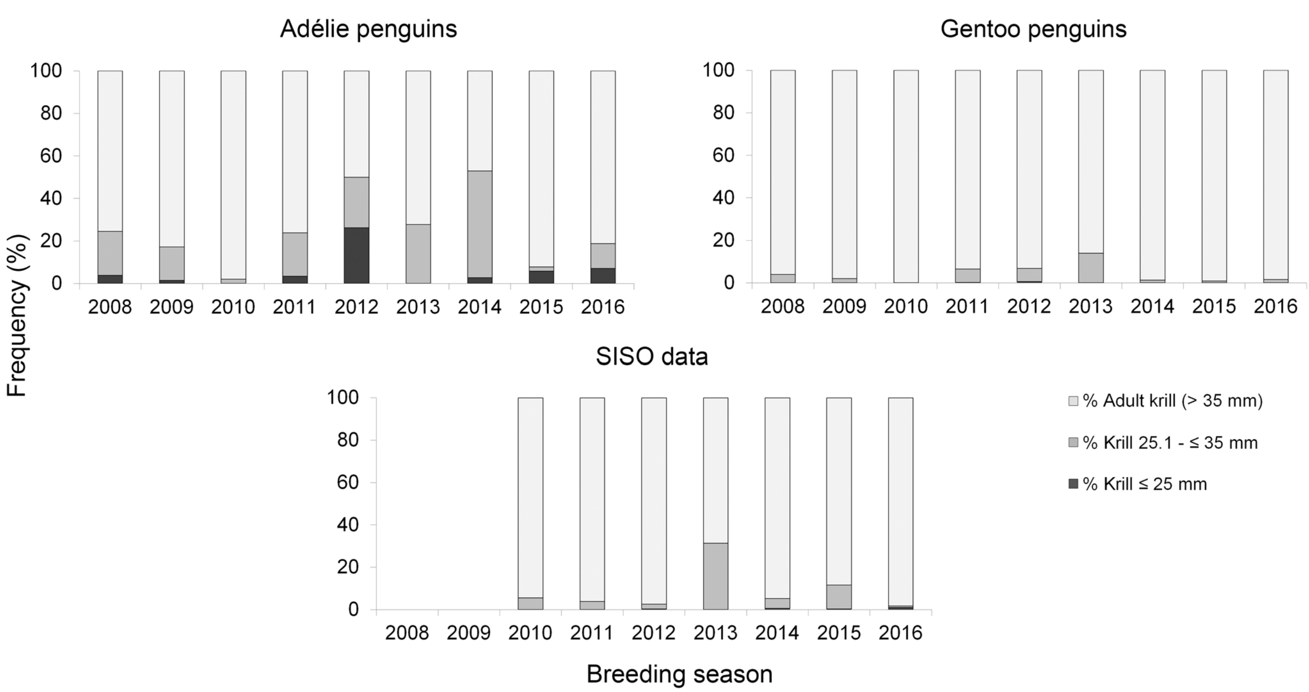

Fig. 4 Percentage of juvenile and adult Antarctic krill consumed by Adélie and gentoo penguins at Stranger Point from 2008 to 2016, and collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016. The juvenile individuals were separated into two categories according to their size: those with a size ≤ 25 mm (*dark grey*) and those with sizes between > 25 and ≤ 35 mm (*light grey*). The Adélie penguin data from 2008 to 2015 was previously published by Juáres et al. (2018)

Table 5 Results of the Chi-square test with Yates' continuity correction comparing the proportion of juveniles and adults (i.e. ≤ 35 mm vs. > 35 mm) of Antarctic krill consumed by Adélie and gentoo penguins at Stranger Point from 2008 to 2016, and collected by the Scheme of Scientific Observation (SISO) on board fishing vessels from 2010 to 2016

Season	Adélie vs. gentoo data		Adélie vs. SISO data		Gentoo vs. SISO data	
	Chi-square (dg = 1)	*p*-value	Chi-square (dg = 1)	*p*-value	Chi-square (dg = 1)	*p*-value
2008	176.36	**< 0.0001**				
2009	66.02	**< 0.0001**				
2010	1.08	1	2.59	0.75	5.38	0.17
2011	113.92	**< 0.0001**	42.55	**< 0.0001**	1.86	1
2012	334.67	**< 0.0001**	494.47	**< 0.0001**	13.28	**0.002**
2013	19.42	**0.0001**	1.44	1	42.38	**< 0.0001**
2014	181.98	**< 0.0001**	1271.70	**< 0.0001**	6.36	0.82
2015	56.08	**< 0.0001**	6.47	0.77	92.77	**< 0.0001**
2016	65.14	**< 0.0001**	58.35	**< 0.0001**	< 0.0001	1

The *p*-values are adjusted for multiple comparison using the Bonferroni method. Significant *p*-values are bolded

dg degree of freedom

cohorts or in the older krill age classes. Although Adélie and gentoo penguins are able to consume a similar krill size range (Table 2; Fig. 3), the inter-specific differences between them were primarily due to the higher proportion of small-sized krill consumed by Adélie penguins compared to their congeners (Fig. 4), similar to those observed by Volkman et al. (1980).

This study may suffer of different potential drawbacks: (1) both sources of information (i.e. penguin data and SISO data), which has different limitations or biases (Miller and Trivelpiece 2007; Atkinson et al. 2012; Tarling et al. 2016; CCAMLR Secretariat 2019; Perry et al. 2019; Ichii et al. 2020), might represent different fractions of krill populations given that fishing vessels select the krill swarms to fish (e.g. Tarling et al. 2016; Ichii et al. 2020) while predators could consume a non-random portion of the krill population due to constrains derived from their foraging capabilities (e.g. Miller and Trivelpiece 2007; Atkinson et al. 2012); (2) differences in the sampling effort within and among seasons and so, in sample sizes compared, which might be solved—at least partially—by an increase of the number of seasons analysed (e.g. CCAMLR Secretariat 2019); and (3) given that krill distribution is variable in space and time (Siegel 2016), limited spatial and temporal overlap in the sampling (for example in 2010; Table 2) can introduce a bias into our conclusions, leading to apparent changes in the population dynamics of krill (Atkinson et al. 2012; Hill et al. 2016, but see Watkins et al. 1992). Despite these potential limitations, we argue that each database analysed here can potentially provide different information (although complementary, see Fig. 3) about krill size composition, and that the Adélie penguin diet could be a useful bioindicator of shifts in the krill population structure in waters surrounding the Stranger Point colony, reflecting events of recruitment more closely than the fishery data or gentoo penguins. Nevertheless, with the combined use of the three sources of krill data it is possible to obtain an overview of all size classes of krill available to predators (i.e. even the largest sizes, Fig. 3) and so, increase the information available to CCAMLR in order to assess the potential impacts of fishing activity on krill dependent species (Watkins et al. 2016; CCAMLR Secretariat 2019).

Finally, although the ecological datasets obtained from long-term monitoring studies of predators can provide relevant information on the krill population, it should be noted the importance to (1) know the sex and maturity stage of krill individuals taken by penguins to have a complete understanding of the population dynamics of krill, and (2) evaluate the use of non-invasive methods to study the krill sizes consumed by penguins, such as stomach contents of dead individuals (e.g. Dimitrijević et al. 2018) or spontaneous regurgitated (i.e. "krill spill") from adults feeding their chicks (Grilly et al. 2018).

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Data availability The penguin datasets analysed during the current study are available from the corresponding author on reasonable request. The krill fishery dataset that supports the findings of this study is available from the CCAMLR's Secretariat but restrictions apply to the availability of these data, which were used under license for the current study, and so are not publicly available.

Code availability Not applicable.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interests. The krill fishery data was provided by the CCAMLR's Secretariat (Hobart, Tasmania) and has been published in accordance with the rules adopted by the Twenty-Second Meeting of the Commission (CCAMLR-XXII, paragraphs 12.1 to 12.6; https://www.ccamlr.org/en/document/publications/rules-access-and-use-ccamlr-data).

Ethical approval All procedures involving Adélie and gentoo penguins were conducted under appropriate international, national and/or institutional guidelines for the care and use of animals. All necessary approvals were obtained. Each year, sampling was completed under the permit granted by the Dirección Nacional del Antártico (Environmental Management Office).

Consent to participate Not applicable.

Consent for publication Consistent with CCAMLR Rules for data Access and Use.

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