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ORIGINAL PAPER

Diet of Adélie penguins (*Pygoscelis adeliae*) at Stranger Point (25 de Mayo/King George Island, Antarctica) over a 13-year period (2003–2015)

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Abstract Knowledge of the feeding ecology of a species at local level is fundamental to determine the relationship between the fluctuations in local marine resources and population dynamics of predators. In this study, we examined the diet of Adélie penguins (*Pygoscelis adeliae*) during the crèche stage at the Stranger Point colony, South Shetland Islands, Antarctica, over a 13-year period (2002/2003–2014/2015). Antarctic krill (*Euphausia superba*) was the dominant prey for Adélie penguins during the crèche period (contribution: 100% of occurrence and >99.7% by mass). The fish component in the diet represented a small proportion of the total prey (contribution: from 4 to 24% of occurrence but <0.15% by mass). A marked inter-annual variability in the mass of stomach contents, the krill size consumed and the proportion of juvenile krill was observed. Moreover, a possible recruitment event of krill was recorded. A negative relationship between the size of krill in the diet and breeding success was found, suggesting that population dynamics of krill also reflected changes in the local availability of this crustacean. This work is the first long-term study of dietary parameters of Adélie penguins for the Stranger Point colony.

Keywords *Pygoscelis adeliae* · Krill-dependent species · Prey availability · South Shetland Islands

Introduction

Knowledge of predator–prey relationships is essential to understand ecosystem structure and function, to assess the potential long-term changes in the abundance of predators and to model different future scenarios in their population dynamic (Nicol et al. 2008; Trivelpiece et al. 2011; Emmerson et al. 2015; Handley et al. 2016; Niemandt et al. 2016; Waluda et al. 2017). Antarctic krill (*Euphausia superba*) dominates the main flow of energy in food webs along the Western Antarctic Peninsula (Ducklow et al. 2006). However, krill is also the target of commercial exploitation from the Mar de la Flota/Bransfield Strait off the Antarctic Peninsula to the northwest of South Orkney Islands, and this activity overlaps with foraging areas of some krill-dependent predators, such as penguins, seals, and whales (Hinke et al. 2017; Weinstein et al. 2017).

The availability of prey depends on its abundance and accessibility (Emmerson et al. 2015) and changes in either of these aspects can affect the feeding ecology and reproductive performance of its predators (Lynnes et al. 2004; Nicol et al. 2008; Tierney et al. 2009; Waluda et al. 2017). Then, when a key predator responds predictably to shift in availability of its main prey, the diet of this predator can be used as an indicator of population state of this prey (e.g.

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Lynnes et al. 2004; Tierney et al. 2009; Saba et al. 2014; Waluda et al. 2017).

In Adélie penguin (*Pygoscelis adeliae*) breeding populations of the Scotia Arc, the Antarctic krill constitute their dominant prey (Volkman et al. 1980; Trivelpiece et al. 1983, 1987, 2011; Coria et al. 1995; Lynnes et al. 2004; Hinke et al. 2007; Juáres et al. 2016). During the breeding period, they become central place foragers due to the need to return regularly to their nests to complete incubating and brooding duties (Ainley 2002). In this period, the study of the diet composition, total meal mass and length of Antarctic krill found in the stomach contents, provides important information on the trophic ecology of the predator as well as evidence of changes in the availability, quality and quantity of food resource in the vicinity of its reproductive colony (Clarke et al. 2002; Fraser and Hofmann 2003; Lynnes et al. 2004; Nicol et al. 2008; Tierney et al. 2009; Rombolá et al. 2012; Saba et al. 2014; Emmerson et al. 2015). Thus, knowledge of feeding ecology of a species at each breeding site is essential to determine the relationship between the fluctuations in local marine resources and population dynamics of the predator (Scioscia et al. 2014).

The aims of this study were to examine the diet of Adélie penguins at the Stranger Point colony (25 de Mayo/King George Island) over a large temporal scale and to assess its inter-annual variability and its relationship with the index of breeding success. This work is the first long-term study of dietary parameters of Adélie penguins for the Stranger Point colony.

Materials and methods

Study area

Fieldwork was conducted at Stranger Point/Cabo Funes (62°16′S, 58°37′W. 25 de Mayo/King George Island, South Shetland Islands, Antarctica; Fig. 1) during the crèche stage of the 2002/2003 (hereinafter 2003) to 2014/2015 (hereinafter 2015) seasons. This colony is located on the south side of the island facing the Mar de la Flota/Bransfield Strait and here, as in others colonies of the West Antarctica, a marked population decline has been recorded (Juáres et al. 2015). Over the study period, the mean number of breeding pairs occupying *c*. 50% of this colony was 1310 (±326.48; range 777–1979 nests; Juáres et al. 2015).

This research is part of a long-term monitoring program of Adélie penguins carried out by the Argentine Ecosystem Monitoring Program. The data were collected, whenever possible, according to the standard protocols defined by the Ecosystem Monitoring Program (CEMP) of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR 2004).

Stomach contents (CEMP parameter A8)

Stomach contents of Adélie penguins were collected annually except for the 2007 season, when the samples were lost in the fire of the icebreaker ARA "Almirante Irízar". Sampling was carried out in adults during the stage of crèche of chicks (mainly in January). Initially, each adult bird captured on the beach was assumed as breeder. Follow-up studies conducted in last seasons to confirm the breeding status of our candidate diet birds (i.e. following the bird to the nest after obtaining the sample) support this assumption. The diet samples were obtained by using the water-offloading technique (Wilson 1984; Gales 1987) and, after the removal of excess fluid, they were frozen (−20 °C).

At the laboratory, each sample was thawed, drained and weighed. Individual prey items were then separated and each of them was weighed and identified. The presence of each prey item was described in terms of frequency of occurrence (FO% = total number of samples containing the item/total number of samples analysed by 100) and percentage in mass (M% = total mass of the item/total mass of all samples by 100). To evaluate the individual variability in the contribution by mass of the main prey, we calculated the total mass of an item in one sample/total mass of that sample.

All entire Antarctic krill specimens from each sample have been measured annually, since 2004 (except for 2006 and 2007 seasons), from the anterior tip of the rostrum to the posterior tip of the telson using a digital caliper (0.01 mm error). Individuals with a size $\leq$ 35 mm were considered juveniles (CCAMLR 2004). Neither sex nor sexual maturity of these individuals was determined.

Statistical analyses

All data were examined for normality with the Shapiro–Wilk test and Levene's test for homogeneity of variances. Due to the lack of normality or homogeneity of variances, non-parametric tests were used. Kruskal–Wallis test (H) followed by multiple comparison tests was used to test the existence of inter-annual variation in the total meal mass. The size of krill consumed was compared among years using Kruskal–Wallis test (H) followed by multiple comparison tests to examine pair-wise differences. The length-frequency distribution of krill ingested in each breeding season was plotted in 12 size categories of 5 mm each (from 10 to $\geq$65 mm of length) in order to examine changes in the length-frequency distributions of krill in relation to its presumed annual growth (Fraser and Hofmann 2003; Saba et al. 2014).

We used Kendall's rank correlations coefficient (τ) to assess the relationship between pairs of dietary and

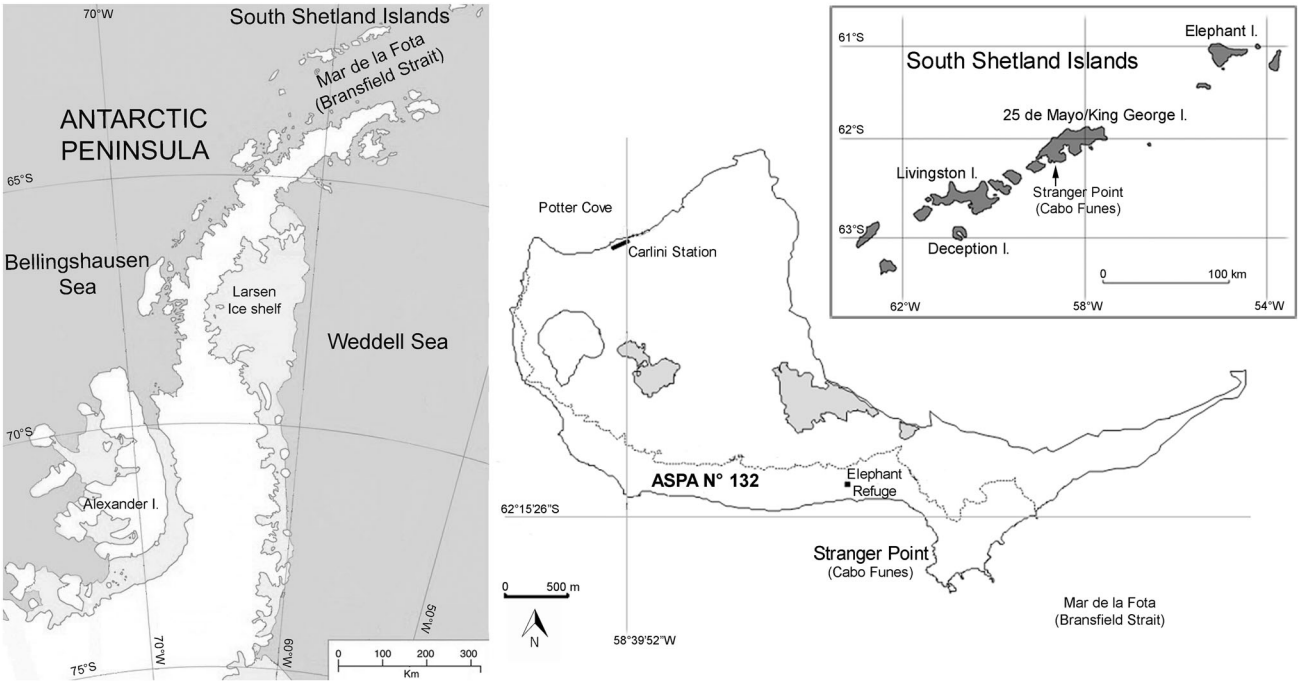

Fig. 1 Location of the Stranger Point/Cabo Funes colony within the Antarctic Specially Protected Area—ASPA No 132 ("Potter Peninsula") on 25 de Mayo/King George Island, South Shetland Islands, Antarctica

breeding variables. Annually, the number of breeding pairs and chicks crèched were counted in 16 breeding groups. Three counts were made for each breeding group and the average values were calculated (CCAMLR 2004). These counts were used to calculate the index of breeding success (IBS = the number of chicks in crèche/the number of occupied nests; Juáres et al. 2015).

Values are given as mean ± standard deviation (SD). We performed the data analysis using Statistica 7.0 software and the significance level was assumed at $p \leq 0.05$.

Results

Overall diet composition

Antarctic krill dominated the Adélie penguin diet over the study period ($n = 12$; Table 1). Krill was present in 100% of the samples, comprising in each season over 99.7% of the mass consumed. When assessing a possible individual variability in the diet composition, we observed that in all cases (i.e. 298 samples) the krill represented > 95% of each sample by mass.

Evidence of fish in the stomach contents was recorded in six of 12 seasons (Table 1). In those years, the frequency of occurrence of fish varied from 4 to 24% but contributed <0.15% to the diet by mass (Table 1). The only evidences of fish recorded in the samples analysed were scales and bone fragments, such as spines or vertebrae, but no otoliths were found. Other items (i.e. other euphausiids, amphipods, squid, algae, mollusc shells, unidentified material) represented <0.1% of the diet by mass in all cases.

Stomach content mass

The mass of the stomach contents collected from 2003 to 2015 showed a marked inter-annual variability (Kruskal–Wallis test, $H_{11,298} = 78.81$, $p < 0.0001$; Table 1).

The total meal mass recorded during the 2003, 2004 and 2013 seasons was similar to each other (multiple comparisons, ns) but significantly lower than the rest of the seasons (multiple comparisons, $p \leq 0.05$) except for 2010 and 2011, when meal mass showed intermediate values (multiple comparisons, ns).

Antarctic krill length

The mean krill size consumed by Adélie penguins varied significantly among years (Kruskal–Wallis test, $H_{9,6530} = 2184.48$, $p < 0.0001$), although a clear 4/5 year cycle was not evident (Fig. 2). During the 2004, 2005 and 2010 seasons, krill found in the diet were larger than in remaining years (multiple comparisons, $p \leq 0.05$), whereas the smallest krill were found in 2012 and 2014 (multiple comparisons, $p \leq 0.05$).

The proportion of juvenile krill (i.e. ≤35 mm) consumed by Adélie penguins fluctuated among years (Fig. 3), being higher during 2012 (49.91%) and 2014 (52.92%)

Table 1 Diet composition of Adélie penguin (*Pygoscelis adeliae*) adults at Stranger Point during the crèche stage from 2002/2003 to 2014/2015 season (except for 2006/2007). The frequency of occurrence (FO%) and the percentage in mass (M%) of the main prey (Antarctic krill and fish); the mean (±SD) and the range of the total meal mass are shown

Season	*n*	FO (%)		M (%)		Stomach content mass (g)	Stomach contents range (g)
		Krill	Fish	Krill	Fish (%)		
2003	24	100	4.17	99.94	0.04	214.50 ± 95.57	48.80–469.10
2004	20	100	0	99.97	0	206.21 ± 90.35	79.10–475.00
2005	24	100	4.17	99.98	0.02	372.24 ± 147.67	87.90–637.80
2006	25	100	4.00	99.88	0.11	340.27 ± 120.86	147.46–567.97
2008	30	100	0	99.99	0	376.54 ± 150.73	111.96–683.26
2009	25	100	24.00	99.92	0.03	375.30 ± 152.99	146.01–736.70
2010	25	100	0	99.91	0	268.63 ± 132.54	62.60–569.00
2011	25	100	8.00	99.83	0.11	238.02 ± 81.22	71.20–390.69
2012	25	100	4.00	99.98	0.01	326.33 ± 80.56	169.80–471.23
2013	25	100	0	99.78	0	192.90 ± 87.01	73.86–380.67
2014	25	100	0	99.82	0	367.40 ± 142.07	98.19–674.51
2015	25	100	0	99.86	0	370.17 ± 152.31	140.65–733.81
Total	298	100	4.03	99.91	0.02	306.97 ± 140.68	48.80–736.70

Data detailed by breeding season and total values by analysing all samples together, regardless of seasons

n number of stomach contents analysed, *FO%* total number of samples containing the item/total number of samples analysed by 100, *M%* total mass of the item/total mass of all samples by 100

seasons. A higher percentage of krill with a size $\leq$ 25 mm (26.14%) was only recorded during the 2012 season (Fig. 3).

Associations between variables

The correlation coefficients (τ) and their significance (p) for each pair of variables compared (i.e. stomach content mass, krill length, presence and mass fish, breeding success) are shown in Table 2. Between pairs of dietary variables, the only significant relationship was found between the frequency of occurrence and percentage in mass of fish.

When considering the index of breeding success (Fig. 4), we observed a significant negative relationship between this and mean krill length (Kendall's rank correlation, $\tau = -0.47$, $n = 10$, $p = 0.04$; Table 2), indicating that the breeding success is higher when the krill length is smaller.

Discussion

The study of Adélie penguin diet at each breeding colony can help us to interpret the ecological role of the predator, to evaluate its potential relationship with its long-term population trends (Trivelpiece et al. 2011; Scioscia et al. 2014; Niemandt et al. 2016) and also to detect marine resources (prey and/or areas) that may need protection (Handley et al. 2016). Furthermore, fluctuations in the meal mass of Pygoscelid penguins can reveal changes in the local availability of their main prey (Clarke et al. 2002; Nicol et al. 2008; Tierney et al. 2009; Niemandt et al. 2016). In other cases, some higher-level predators can switch the diet composition and/or foraging behaviour to buffer the fluctuations in the availability (or size) of their main prey (Miller and Trivelpiece 2008; Nicol et al. 2008; Handley et al. 2016; Niemandt et al. 2016; Waluda et al. 2017).

On the other hand, as krill length can be used as a proxy indicator of its age, the krill sizes obtained from the stomach contents of penguins can reflect events of recruitment of krill (Fraser and Hofmann 2003; Lynnes et al. 2004; Saba et al. 2014) and might also indicate shifts in krill availability (e.g. Lynnes et al. 2004; Rombolá et al. 2012). In poor recruitment years, large krill is dominant but less abundant and frequently observed in offshore waters (e.g. Fraser and Hofmann 2003; Lynnes et al. 2004; Reiss et al. 2008). Thus, when krill is less available penguins spend more time searching for food. For example, longest foraging trips were recorded in Adélie penguins when the large krill dominated their diet (Fraser and Hofmann 2003).

Diet composition

Diet composition of Adélie penguins at Stranger Point during the chick-provisioning stage was dominated by Antarctic krill in all years and only a small fraction of the

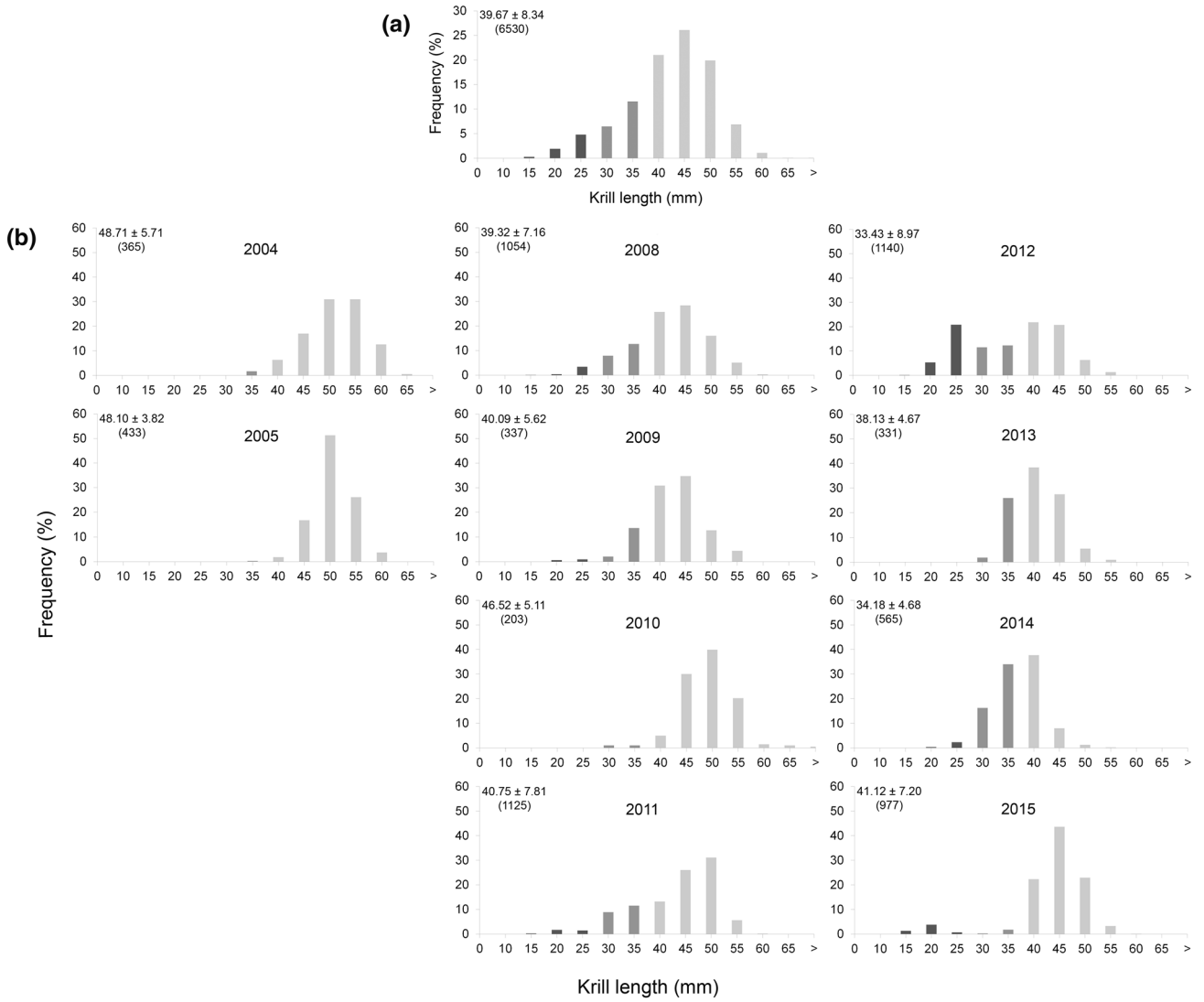

Fig. 2 Length-frequency distribution of Antarctic krill (*Euphausia superba*) from diet samples of Adélie penguins (*Pygoscelis adeliae*) at Stranger Point, during crèche stage, over all seasons (**a**) and each season (**b**) from 2003/2004 to 2014/2015 (except for 2005/2006 and 2006/2007). The *grey scale* represents three subcategories: size $\leq$ 25 mm (*dark grey*), size between >25 and $\leq$35 mm (*intermediate grey*) and size > 35 mm (*light grey*). Mean $\pm$ SD and *n* of krill size are shown in the *upper left corner*

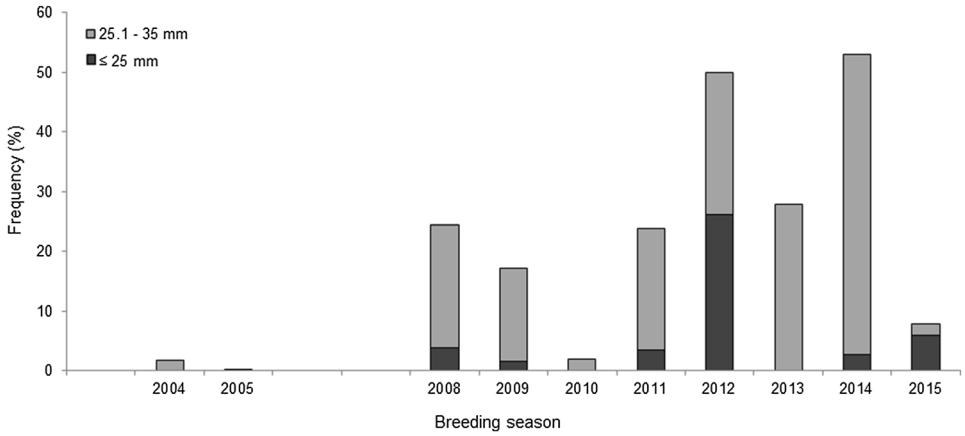

Fig. 3 Percentage of Antarctic krill (*Euphausia superba*) juveniles consumed by Adélie penguins (*Pygoscelis adeliae*) at Stranger Point, during crèche stage from 2003/2004 to 2014/2015 (except for 2005/2006 and 2006/2007). The juveniles were separated into two categories according to their size: those with a size $\leq$ 25 mm (*dark grey*) and those with sizes between >25 and $\leq$35 mm (*light grey*)

Table 2 Kendall's rank correlations between pairs of dietary and breeding variables recorded in Adélie penguins (*Pygoscelis adeliae*) at Stranger Point; Kendall's tau (τ) and p (in brackets) values. The signs + and − show the type of association

	Stomach content mass (mean)	Antarctic krill length (mean)	FO% fish	M% fish
Stomach content mass (mean)				
Antarctic krill length (mean)	−0.07 (0.43)			
	$n = 10$			
FO% fish	+0.12 (0.58)[a]	−0.05 (0.50)		
	$n = 12$	$n = 10$		
M% fish	+0.02 (0.94)[a]	0.00 (1.00)	**+0.78 (0.0004)**	
	$n = 12$	$n = 10$	$n = 12$	
IBS	−0.02 (0.94)	**−0.47 (0.04)**	+0.41 (0.08)	+0.43 (0.07)
	$n = 11$	$n = 10$	$n = 11$	$n = 11$

Statistically significant values in bold

FO% frequency of occurrence, *M%* percentage in mass, *IBS* index of breeding success (in Juáres et al. 2015)

[a] Same results were obtained when comparing these variables (FO% and M% of fish) with M% of Antarctic krill (Kendall's rank correlation, FO% fish vs. M% krill: $\tau = 0.12$, $n = 12$, $p = 0.58$. M% fish vs. M% krill: $\tau = 0.02$, $n = 12$, $p = 0.94$)

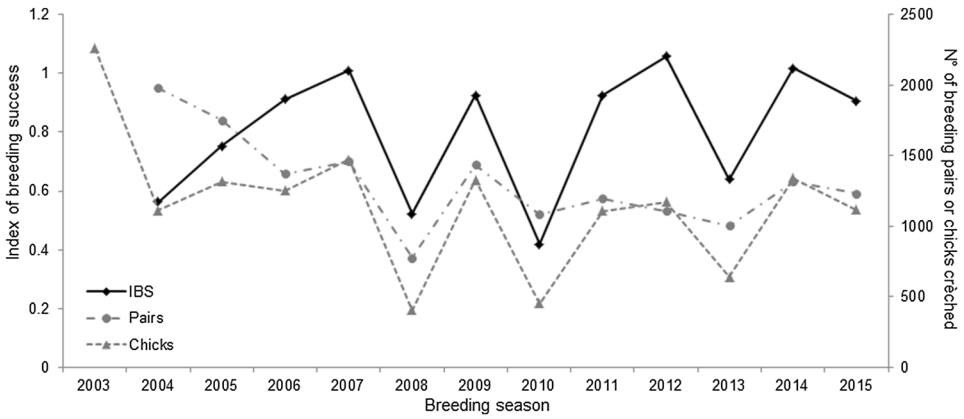

Fig. 4 Fluctuation in the index of breeding success (*IBS* the number of chicks in crèche/the number of occupied nests) of Adélie penguins (*Pygoscelis adeliae*) at Stranger Point from 2003/2004 to 2014/2015 (modified from Juáres et al. 2015). The graph also shows the number of breeding pairs (from 2003/2004) and the chicks in crèche (from 2002/2003)

diet was composed of fish. These results are in agreement with those reported by Coria et al. (1995) in a previous study carried out in the same colony during the 1988 breeding season (contribution of krill: 100% of occurrence and 98 ± 1.6% by mass). Although we recorded a lower frequency of occurrence of fish (24 vs. 83%), in both studies, the contribution of fish by mass was insignificant (<1.5%). These results suggest that the Adélie penguin diet at Stranger Point was krill-dominated, at least in the last 27 years. In this early study, Coria et al. found *Pleuragramma antarcticum* (Nototheniidae) as the most frequently observed fish species, followed by *Electrona antarctica* (Myctophidae) and unidentified species of the family Channichthyidae. These fish species were also recorded in the diet of other predators of the same location, such as gentoo penguins (*Pygoscelis papua*; Juáres 2013), southern elephant seals (*Mirounga leonina*; Carlini et al. 2005) and Antarctic fur seals (*Arctocephalus gazella*; Daneri et al. 2008), suggesting that these species are available as prey for adults of Adélie penguin at Stranger Point.

Overall, our results are also in line with those previously published in breeding colonies located in the Scotia Arc (Volkman et al. 1980; Trivelpiece et al. 1983, 1987; Lynnes et al. 2004; Hinke et al. 2007). In these studies, the diet has been analysed from stomach contents collected by gastric lavage, except in Volkman et al. (1980) who analysed complete stomachs of animals sacrificed. In all these cases, krill accounted for >98% of the diet by mass.

Since fish are digested faster than krill and that small otoliths can be digested completely or excreted (see Karnovsky et al. 2012 and their references), the analysis of stomach contents might underestimate the real contribution of that soft-bodied prey to the specific requirements of the adult breeders of Adélie penguin, i.e. for self-maintenance and not for chick provisioning. This hypothesis is in line with that proposed by Quillfeldt et al. (2005) and Juáres et al. (2016) who analysed the diet of chicks and adults of

Adélie penguins at Stranger Point, respectively, with the stable isotope method. These results suggested that chick diets would be krill-dominated while the pelagic fish would be best represented in adult diets (24%, range 8.6–37%; Juáres et al. 2016).

Although higher contribution of fish was recorded during two seasons (2006 and 2011), this was insignificant respect to the mass of krill consumed (<1%). This finding was similar to that reported by Volkman et al. (1980) by analysing complete stomachs of animals sacrificed. Besides, during our study, there was no association between the frequency of occurrence of fish (or its percentage in mass) and the index of breeding success. Thus, we consider that the presence of fish in the diet of Adélie penguins at Stranger Point as reflected by the analysis of stomach contents did not reveal a change in the local krill availability, similar to that reported by Tierney et al. (2009).

Stomach content mass

In our long-term study, we recorded both a total mean and some annual means of meal mass similar to that reported by Volkman et al. (1980) for the 1978 season (350 g), although different methodologies were used in both studies (gastric lavage and complete contents, respectively). Nevertheless, the mean meal mass reported by Coria et al. (1995) from the same location during 1988 (554 ± 210 g, range 127–1197 g) was higher that any annual mean mass recorded in our study (Table 1).

During our study period, the mass of the stomach contents varied significantly among years. Given that the meal masses were significantly lower during 2003, 2004 and 2013 compared to the rest of the seasons, a reduction in krill availability within the area potentially exploited by the penguins could be assumed for these seasons (Clarke et al. 2002; Nicol et al. 2008; Tierney et al. 2009; Niemandt et al. 2016). Evidences of a reduction of krill availability in the surroundings of Stranger Point have been reported for 2003 and 2004 (Rombolá et al. 2010; Richerson et al. 2017). Despite this, no association was found between the stomach content mass and the index of breeding success. Emmerson et al. (2015) hypothesised that there are different thresholds of prey availability, and only during extremely good or poor conditions the predators' response is observed. Thus, the feeding strategies of penguins such as an increase in the duration of foraging trips or changes in the diving behaviour could help mask the prey variability (e.g. Fraser and Hofmann 2003; Lynnes et al. 2004). Given the discordance in krill abundance and the high spatio-temporal variability reported in different studies (e.g. Reiss et al. 2008; Saba et al. 2014; Richerson et al. 2017), we do not support the idea that the mass stomach contents may be a good indicator of food availability.

Antarctic krill length

The krill size consumed by Adélie penguins in the Stranger Point colony varied appreciably among years. The proportion of krill juveniles in the diet was higher during 2012 and 2014 (unavailable data for 2006 and 2007 season), with a higher frequency of one-year-old krill (i.e. length ≤ 25 mm) only during 2012 (>25%). This class of krill individuals of the smallest size was absent from the samples during four seasons (Fig. 3). Based on our results, and without a clear pattern in the krill length distribution (similar to that reported by Clarke et al. 2002 and Rombolá et al. 2012), we could interpret that at least one year of high recruitment of krill occurred in the waters surrounding Stranger Point (i.e. 2012). This event of recruitment is consistent with the findings reported by Saba et al. for 2012 (2014; see Fig. 1). Although large krill individuals were more frequent for all seasons (representing about 70% of krill taken by Adélie penguins; Fig. 2a), during 2012 and 2014 we recorded a similar percentage of both small and large krill individuals (Fig. 2b). Our results support the hypothesis of Lynnes et al. (2004) that when small krill individuals are available, predators even forage predominantly on them.

Although several factors can affect the breeding performance, when analysing the relationship between diet and breeding success we can assess the possible predator response to changes in its ecosystem (e.g. Hinke et al. 2007; Waluda et al. 2017). Unlike findings of Clarke et al. (2002) and Miller and Trivelpiece (2008), but similar to those reported by Lynnes et al. (2004) and others, our results indicate that foraging on larger krill was correlated with lower breeding success. Foraging on large krill might have resulted in higher cost for Adélie breeders if those krill were located farther from shore. Alternatively, prey may have been more abundant overall in years of high recruitment leading to greater breeding success for Adélie penguins. This conclusion is consistent with the pattern of overall krill distribution (e.g. Fraser and Hofmann 2003; Lynnes et al. 2004; Reiss et al. 2008). So, similarly to previous studies, our results suggest that the krill size found in the stomach contents of Adélie penguins at Stranger Point could be a better indicator of local food availability than the meal mass or diet composition.

Our results underline also the need to know the Antarctic krill abundance (and its spatial and temporal variability) in the vicinity of the study area (i.e. within the feeding range of penguins). This information is essential to assess the degree to which each dietary variable reflects the food resource availability near the breeding colony, since

clear inconsistencies with others studies were observed. Moreover, these results highlight the need for future studies to establish the relationship between the diet and feeding strategies (i.e. duration of foraging trips, diving behaviour and foraging areas) and thus, improve our understanding of the trophic ecology of Adélie penguins at Stranger Point and its influence on their reproductive performance.

This long-term study shows that Adélie penguins at Stranger Point are krill specialists. If the abundance of this prey declines, this can adversely affects species with a narrow feeding niche, which in turn can impact on their population trends (Trivelpiece et al. 2011; Niemandt et al. 2016). Nevertheless, other drivers of Adélie penguin trends should not be underestimated, such as the sea ice conditions during winter (e.g. Fraser et al. 1992; Hinke et al. 2007, 2014; Carlini et al. 2009) and the local weather conditions during summer (e.g. Fraser et al. 2013; Juáres et al. 2015). Hinke et al. (2017) and Weinstein et al. (2017) have demonstrated that there is a spatio-temporal overlap between krill fishery and krill-dependent predators in the Scotia Sea, suggesting a competition between them for the resource. Management strategies require expanding our knowledge on the trophic ecology of predators in a larger number of breeding sites. As the Adélie penguin diet at Stranger Point has only been described in a few seasons (Coria et al. 1995; Juáres 2013; Juáres et al. 2016), the main relevance of this study was to assess the long-term diet composition of Adélie penguins in an area where effects of climate warming and fishing pressure are expected to increase.

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