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ORIGINAL PAPER

Temporal variation in the diet of gentoo penguins at the Falkland Islands

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Abstract Knowledge of diet is critical in interpreting the ecological roles of marine top predators and provides information towards their conservation and management. The Falkland Islands hold the largest number of breeding gentoo penguins. Yet knowledge of gentoo penguin diet at the Falklands is limited to either broad taxonomic divisions of prey items or dietary samples collected only on a single day. This study is the first to investigate gentoo penguin diet at Cow Bay, Falklands, to the species level, over repeated sampling intervals during the breeding period. Through stomach content analysis, we determined diet over a large temporal scale (2002/2003/2004–2011/2012/2013) and between the guard and crèche periods of chick rearing. The principle prey item by reconstituted mass was rock cod fish *Patagonotothen* spp., for all periods (47–78 %) except that of the 2012/2013 crèche period (19 %) when Falkland herring *Sprattus fugensis* made up the bulk of the diet (52 %). Of the cephalopods recovered, Patagonian squid *Doryteuthis gahi* was prominent (1–24 %), while crustaceans contributed negligibly to gentoo penguin diet. Our findings revealed that gentoo penguins breeding at the Falkland Islands were primarily demersal foragers with an ability for pelagic feeding. Diet choice appears to reflect prey availability.

Keywords *Spheniscidae* · *Pygoscelis* · Foraging ecology · Feeding technique

Introduction

Understanding predator–prey relationships provides valuable information for elucidating ecosystem structure and function (Gon and Heemstra 1990; Cury et al. 2011). In seabirds, knowledge of diet facilitates an understanding of at-sea behaviour and reliance on marine habitats (Deagle et al. 2007; Iverson et al. 2007; Karnovsky et al. 2012). During the breeding period, seabirds are constrained in the total available habitat they may exploit by the need to return regularly to share incubating duties or to provision chicks (Alonzo et al. 2003; Ropert-Coudert et al. 2006; Masello et al. 2010). Thus, understanding seabird diet during chick rearing, a period of increased nutritional demand, can help determine factors influencing population numbers (Davoren and Montevecchi 2003) and identify particular prey or foraging areas that need protection (Hooker and Gerber 2004; Louzao et al. 2006; Karnovsky et al. 2012).

This study focuses on the diet of breeding gentoo penguins *Pygoscelis papua* at the Falkland Islands through analysis of stomach contents. The Falklands have the largest population of breeding gentoo penguins, accounting for 34 % of the world's population (Baylis et al. 2013a).

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Previous studies assessed composition between broad taxonomic groups of prey items for gentoo penguins across the islands (Putz et al. 2001; Clausen and Putz 2002) or inferred diet from stable isotope analysis for a single breeding colony on the west, New Island (Weiss et al. 2009; Masello et al. 2010). A study conducted at five breeding colonies on the west of the Islands and a single colony in the south, found that gentoo penguins appeared to be selective in feeding during simultaneous diet observation and at-sea surveys of prey availability (Clausen et al. 2005). However, these studies did not explore temporal trends in diet at the taxonomic level of species, nor short-term variability in the diet within the guard and crèche periods of chick rearing (Putz et al. 2001; Clausen and Putz 2002; Clausen et al. 2005). Given variability in diet between breeding colonies, a detailed investigation of diet and dietary shifts during chick guard and crèche periods for gentoo penguins at the Falklands is timely. Such information is important for understanding the potential for short-term variability in diet and identifying potential threats towards the gentoo population, such as overlap of prey species with fisheries. Therefore, the aim of the study was to (1) describe in detail the diet of gentoo penguins breeding at Cow Bay in the Falklands, (2) for the first time investigate whether diet may differ during the chick guard and crèche periods at the Falklands, and (3) investigate whether inter-annual shifts in diet occur.

Materials and methods

Sample collection

This study was conducted at Cow Bay (51°26′3.5″S, 57°52′39.2″W, Fig. 1), which lies in the north-east of the Falklands archipelago with approximately 1821 breeding pairs of gentoo penguins, calculated in 2012 during the annual surveys by the Falkland Islands Seabird Monitoring Program (Baylis et al. 2013a). Following the 5-yearly 2010 island-wide census, it was the 26th largest of 75 breeding colonies monitored that year (Baylis et al. 2013a). Diet samples were collected during the guard and crèche periods of the austral summers 2011/2012 ($n_{\text{Guard}} = 28$, $n_{\text{Crèche}} = 10$) and 2012/2013 ($n_{\text{Guard}} = 10$, $n_{\text{Crèche}} = 11$). The guard and crèche periods were defined as those when partners take turns to brood and guard chicks at the nest, and when chicks are left alone with other chicks in crèches, respectively (Polito and Trivelpiece 2008; Lescroël et al. 2009). Eight to ten birds were sampled on three occasions (22–24/11/2011; 5–9/12/2011; 19–21/12/2012) during the guard period of 2011/12, five birds each on two occasions (15/12/2012; 17/12/2012) in the guard period of 2012/13, and five to six birds daily over 2 days (17–18/01/2012 and 11–12/01/2013) during the crèche periods of these seasons. Data were available for ten diet samples collected at the same colony during the guard periods of the 2002/2003 and 2003/2004 seasons.

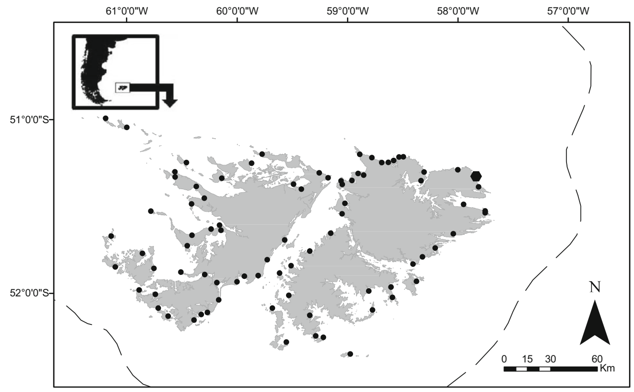

Fig. 1 Gentoo penguin colonies monitored in 5-yearly island-wide census (*dots*) and study colony, Cow Bay (*hexagon*), at the Falkland Islands. The 200-m isobath is represented by *dashed lines*

Birds were caught upon returning to the colony with a net attached to a 2-m pole (Otley et al. 2005; Masello et al. 2010). As gentoo penguins at Cow Bay and elsewhere are skittish around their nests (Reilly and Kerle 1981), this minimised disturbance in the colony. To ensure sampling of breeding individuals, only those birds with a vascularised brood patch were sampled (Volkman et al. 1980). Birds were suspended in a harness, and their mass recorded with a 10-kg Pesola spring balance, accurate to 100 g. Stomach lavage followed Wilson (1984) with modifications appropriate to the species. Specifically, two observers handled the bird with one gripping the feet while supporting the body on their legs, and the other holding the beak while massaging the neck. Stomach samples were drained of excess water over a 0.5-mm sieve, sealed in zip lock bags and frozen within 12 h (Putz et al. 2001).

Birds were marked with a green, temporary, waterproof wax marker (ROTO.STIK) on the breast feathers and then released in the direction of the colony. This mark lasts for approximately 10 days, minimising the chance of repeat sampling. It also allowed post-identification of sampled birds to facilitate detection of possible abnormal behaviour. There was a negligible chance of birds being repeatedly sampled between breeding periods or within years, owing to the size of the colony.

Stomach content analysis

Prior to sorting, samples were left to thaw overnight. Each sample was then placed in a 0.5-mm sieve allowing excess water to drain off. Total wet mass was recorded. Mass of stones, accounting for on average 1.6 % (range 0–13 %), was removed from the total wet mass and not included in the diet analysis (Clausen et al. 2005). When possible, the undigested part (e.g. whole squid, fish, and crustaceans) of the stomach content was separated from the digested part (Herling et al. 2005). These items were identified, weighed and measured accordingly: cephalopods, dorsal mantle length (DML); fish, total length (TL), measured to the fin tip (only rock cod fish *Patagonotothen* spp. were suitable owing to digestion extent); and crustaceans, total length (CTL), where CTL is the measure from the anterior edge of the eye to the distal end of the telson. From the remaining digested material, a 350-g subsample was used to inspect for saccular otoliths, cephalopod beaks, crustacean carapaces, or other hard part remains, as this is equivalent to roughly half the total wet mass (Polito et al. 2011). The remaining total composition of the sample was calculated from this proportion. Where others have used dark-bottomed pans (Miller et al. 2009; Polito et al. 2011), it was found that a large green container ($\approx$350 mm × 200 mm) allowed easy inspection for both white otoliths and darker cephalopod beaks simultaneously. A small amount of the digested material ($\approx$25 g) was placed into the container. Water was added to a depth of approximately 20 mm. The material was then lightly agitated apart with a fine spatula to search for hard part remains. These remains were identified to the lowest possible taxonomic level by comparing them with an extensive reference collection housed by the Falkland Islands Fisheries Department (FIFD) and published reference material (Clarke 1986; Xavier and Cherel 2009).

Length frequency and reconstituted mass

Intact lobster krill (*Munida* spp.) carapaces were measured using vernier callipers to the nearest 0.1 mm. Two species/morphs, *Munida gregaria* and *Munida subrugosa*, are commonly found within the continental shelf waters of South America and the Falklands (Matthews 1932; Tapella and Lovrich 2006). There are conflicting views on whether or not these are separate species (Tapella and Lovrich 2006), so reconstituted mass for *Munida* spp. was calculated only from regressions relating to *Munida gregaria* as this was the only identifiable morph during the study. Similarly, rock cod fish were largely digested and only occasionally were whole individuals identified as *Patagonotothen ramsayii* or *Patagonotothen tessellata.* These two species are most common in inshore waters of the Falklands, and distinguishing species by otoliths is only possible for those larger than observed in the study (otolith >7 mm, Paul Brickle pers. comm.; study: >7 mm, $n = 2$ of 1707). Therefore, average length and mass from the two species were used (Huin 2005).

Otolith length (OL) from fish, lower rostral length (LRL) of squid beaks, and lower hood length (LHL) of sepiolid squid and octopods were measured using an eye-piece graticule in a dissecting microscope, regularly recalibrated with a graticule scale. Both cephalopod beaks and otoliths undergo a significant ontogenetic morphological change (Smale et al. 1995). Otoliths of larval fish are virtually identical, and with increasing size, otoliths may be identified to a particular order, then family and ultimately a species (Gon and Heemstra 1990). Reconstituted mass and length were calculated from morphometric equations for each species following reference material or from regression equations developed during the study (Online Resource 1). When left and right otoliths were found from the same species and of similar size, the highest number of either side was used as a conservative estimate for total number of fish (Miller et al. 2009). Eroded fish otoliths and cephalopod beaks that were not attached to flesh were considered as accumulated items and not included in the final calculations of mass for each species (Van Heezik and Seddon 1989; Thompson 1994; Clausen et al. 2005). Accumulated squid beaks were, however, included when calculating species composition and size class distribution of the cephalopod portion of the diet (Thompson 1994). In cases where whole prey could be identified, but no reference equations existed or could be developed, the wet mass was used (Clausen and Putz 2003). Proportional size compared to a single, undigested, exemplar specimen was used in the case of the bobtail squid (*Semirossia patagonica*).

Composition of samples

Prey items were first described in terms of percentage number (%*N*), mass (%*M*), and frequency of occurrence (%FO) (Duffy and Jackson 1986), where:

> %*N* is the proportion of the total number of individuals of one prey item compared to the total number of individuals of all prey items per sample.
>
> %*M* is the proportion of the total mass of one prey item compared to the total mass of all prey items per sample.
>
> %FO is the proportion of stomachs containing the prey type compared to all stomachs examined.

Samples were then described by an integrative value, the index of relative importance (IRI) (Pinkas et al. 1971):

$$\mathrm{IRI} = \%\mathrm{FO} \times (\%N_{\mathrm{sum}} + \%M_{\mathrm{sum}})$$

This is a modification of the index where the original term of percentage by volume was replaced with %*M* (Koen Alonso et al. 1998). It incorporates from all samples, in a given sampling period, the summed value of %*N* and %*M*. Percentage FO has the advantage of being fast, with stomachs scored for the presence or absence data. It is, however, most appropriate when prey items are of similar size (Duffy and Jackson 1986). The IRI is most sensitive to %FO, which is a multiplicand, rather than %*M* and %*N* which are addends, but helps reduce the biases introduced by numerous small or a few very large items occurring in only one or a few stomachs (Duffy and Jackson 1986). It further reduces numerous tables making multiple comparisons which may lead to "data narcosis" (Duffy and Jackson 1986). As the index does not have a set scale, percentage index of relative importance was calculated (%IRI), where:

> %IRI is the proportion of each species IRI relative to the total sum of IRI for a given sampling period.

This allowed for easier interpretation of the IRI and for a standard measure to compare different sampling periods (Cortes 1997; Huin 2005). Analyses could then be conducted on those prey items that were represented by >2 %IRI (Koen Alonso et al. 2000). As the IRI relies on the summed information for each sampling period, there is no variation in the result. Therefore, percentage mass (%*M*) was chosen to compare prey items at the level of the sampling unit (each penguin), again as this favours samples with varying prey size (Duffy and Jackson 1986; Ratcliffe and Trathan 2011).

Data analysis

All data analyses were performed using R version 3.0.1 (R Core Team 2013). As historical data (2002/2003 and 2003/2004) were represented by relatively small sample sizes, extensive sampling during the chick guard period of 2011/2012 allowed us to determine whether these samples were sufficient to represent the major prey items for each period. Specifically, prey species accumulation curves were plotted for each sampling period (package: vegan; function: specaccum) and the Chao estimator (Chao 1987) determined (package: vegan; function: specpool). Comparisons were made for intra-annual variation between chick guard and crèche periods and long-term variation through analysis of all chick guard data. Univariate and multivariate normality was assessed with Shapiro–Wilks and multivariate Shapiro–Wilks tests (package: mvnormtest; function: m.shapirotest), respectively. Bartlett's test and multivariate Levene's test (package: vegan; function: betadisper) were used to assess for univariate and multivariate homogeneity of variance, respectively. Means with standard deviations are given, and significance was assumed at $p < 0.05$ unless otherwise stated.

Differences in species composition were first visually assessed with ordination via nonmetric multidimensional scaling (nMDS) (package: vegan; function: metaMDS with autotransform = "F"), using the arc-sin-transformed percentage by mass data. The function ordispider (package: vegan) was applied to the ordination which plots the centroid (weighted mean) for each treatment. Centroids further apart indicate greater dissimilarity. Statistical differences in species assemblages were assessed using an ADONIS test (package: vegan; function: adonis with distance = "bray"). This function partitions sums of squares for multivariate data and is analogous to nonparametric MANOVA (Anderson 2001; Birk et al. 2012). It is similar to ANOSIM but is believed to be statistically more robust (Peay et al. 2010; Oksanen et al. 2015). Significance was tested against 999 null permutations. Where appropriate, SIMPER tests (package: vegan; function: simper) were performed post-ADONIS to assess which species had the most influential cumulative contribution to sample similarity. These tests are limited as they only compare two groups of samples at a time (Clarke and Warwick 2001). Univariate tests among individual prey species percentage mass, and size, included Kruskal–Wallis tests, followed by post hoc Mann–Whitney *U* tests with Bonferroni correction.

Results

A total of 3314 prey items were identified from 69 gentoo penguin stomach contents examined over four seasons, comprising 2249 individual fish, 412 individual cephalopods, 648 individual crustaceans, and five other individual items, which included two gastropods, and a single mytilid, nacellid, and venerid. A total of 17 of the 31 prey items were identified to species level over the study period (Table 1).

Combined across each individual sampling period, a total of eight prey items contributed >2 %IRI. These included: fish, rock cod *Patagonotothen* spp., Falkland herring *Sprattus fugensis*, Bull blenny *Cottoperca gobio,* and juvenile fish too small for identification; cephalopods, Patagonian squid *Doryteuthis gahi*, *Gonatus antarcticus,* and juvenile cephalopods; and one crustacean, *Themisto gaudichaudii*. The three most important items for all sampling periods were rock cod, Patagonian squid, and then Falkland herring.

Reliability of sample size

From the samples collected, prey species accumulation curves (Fig. 2) indicated that sampling was extensive enough to represent the major prey items as indicated by all accumulation curves reaching a plateau. The highest number of expected major prey items (>2 % IRI) in the diet occurred during the 2011/2012 crèche period with the Chao estimator indicating six prey items. For all sampling

Table 1 Prey species identified during the study

Sampling period		2002/2003 guard $n = 5$		2003/2004 guard $n = 5$		2011/2012 guard $n = 28$		2012/2013 guard $n = 10$	
Scientific name	Common name	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)
Crustaceans		1.5	(20)	1.6	(60)	12	(86.7)	12.4	(100)
Campylonotus vagans	Prawn	–	–	–	–	<0.1	(3)	<0.1	(10)
Euphausiid spp.	Krill	–	–	–	–	0.1	(20)	–	–
Munida gregaria	Lobster krill	1.6	(20)	0.1	(20)	–	–	0.4	(10)
Munida spp.	Lobster krill	<0.1	(20)	–	–	0.5	(10)	<0.1	(10)
Munida spp. (juvenile)	Juvenile lobster krill	–	–	–	–	0.5	(30)	<0.1	(10)
Paguridae	Hermit crab	–	–	–	–	0.3	(17)	0.1	(20)
Sphaeromatidae	Isopod	–	–	–	–	0.2	(30)	<0.1	(10)
Themisto gaudichaudii	NA	–	–	**5.6**	**(60)**	**5.9**	**(73)**	**4.9**	**(90)**
Cephalopod		26.7	(80)	2.5	(20)	14	(93.3)	17.9	(100)
Muusoctopus	Octopus	–	–	–	–	<0.1	(10)	<0.1	(10)
Cephalopoda (juvenile)	Juvenile squid	–	–	–	–	0.6	(30)	**6.1**	**(90)**
Gonatus antarcticus	NA	–	–	–	–	0.1	(20)	<0.1	(20)
Doryteuthis gahi	Patagonian squid	**8.4**	**(80)**	0.2	(20)	**9.2**	**(73)**	**6.5**	**(70)**
Moroteuthis ingens	Greater hooked squid	0.1	(20)	–	–	0.4	(10)	0.4	(20)
Semirossia patagonica	Mickey mouse/bobtail squid	–	–	–	–	0.1	(13)	<0.1	(10)

Sampling period		2011/2012 crèche $n = 10$		2012/2013 crèche $n = 11$		ALL $n = 69$	
Scientific name	Common name	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)
Crustaceans		9.3	(70)	(0.4)	(27.3)	7.2	(70.8)
Campylonotus vagans	Prawn	–	–	–	–	<0.1	(3)
Euphausiid spp.	Krill	–	–	–	–	<0.1	(8)
Munida gregaria	Lobster krill	–	–	–	–	0.1	(4)
Munida spp.	Lobster krill	–	–	<0.1	(9)	0.2	(8)
Munida spp. (juvenile)	Juvenile lobster krill	0.4	(30)	<0.1	(9)	<0.1	(20)
Paguridae	Hermit crab	<0.1	(10)	–	–	<0.1	(11)
Sphaeromatidae	Isopod	0.7	(20)	–	–	0.1	(17)
Themisto gaudichaudii	NA	**5.7**	**(40)**	<0.1	(18)	0.1	(56)
Cephalopod		17	(90)	5.1	(63.6)	12.6	(81.9)
Muusoctopus	Octopus	–	–	–	–	<0.1	(6)
Cephalopoda (juvenile)	Juvenile squid	<0.1	(10)	<0.1	(18)	<0.1	(30)
Gonatus antarcticus	NA	**6.5**	**(50)**	–	–	0.2	(18)
Doryteuthis gahi	Patagonian squid	**13.2**	**(50)**	**12.9**	**(64)**	**12.8**	**(65)**
Moroteuthis ingens	Greater hooked squid	–	–	<0.1	(9)	0.3	(10)
Semirossia patagonica	Mickey mouse/bobtail squid	0.7	(20)	<0.1	(9)	0.1	(11)

Sampling period		2002/2003 guard $n = 5$		2003/2004 guard $n = 5$		2011/2012 guard $n = 28$		2012/2013 guard $n = 10$	
Scientific name	Common name	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)
Fish		71.9	(100)	95.6	(100)	74	(93.3)	69.7	(100)
Fish (juvenile)	Juvenile fish	–	–	–	–	<0.1	(7)	**2.3**	**(60)**
Agonopsis chiloensis	Snail fish	–	–	–	–	0.1	(7)	0.1	(20)
Champsocephalus esox	Icefish	–	–	–	–	<0.1	(3)	<0.1	(10)
Cottoperca gobio	Bull blenny	0.6	(20)	**13.6**	**(40)**	0.1	(3)	1.1	(30)
Dissostichus eleginoides	Patagonian toothfish	–	–	–	–	0.1	(7)	–	–
Harpagifer bispinis	Magellanic spiny plunderfish	–	–	–	–	<0.1	(3)	–	–

Table 1 continued

Sampling period		2002/2003 guard $n = 5$		2003/2004 guard $n = 5$		2011/2012 guard $n = 28$		2012/2013 guard $n = 10$	
Scientific name	Common name	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)
Macruronus magellanicus	Patagonian grenadier	0.5	(40)	–	–	0.1	(3)	–	–
Micromesistius australis	Southern blue whiting	–	–	–	–	<0.1	(3)	<0.1	(10)
Patagonotothen spp.	Rock cod	**87.3**	(**100**)	**80.5**	(**80**)	**80.6**	(**93**)	**77.7**	(**100**)
Perciformes	NA	–	–	–	–	<0.1	(7)	–	–
Salilota australis	Red cod	1.4	(80)	–	–	0.4	(10)	0.2	(20)
Sprattus fugensis	Falkland herring	–	–	–	–	0.7	(20)	–	–
Thysanopsetta naresi	Small flounder	–	–	–	–	–	–	<0.1	(10)
Other		0	(0)	0	(0)	<0.1	(10)	0	0
Mytilid	Mussel	–	–	–	–	<0.1	(3)	–	–
Venerid	Clam	–	–	–	–	<0.1	(3)	–	–
Gastropod	Sea snail	–	–	–	–	–	–	–	–
Nacellid	Limpet	–	–	–	–	<0.1	(7)	–	–

Sampling period		2011/2012 crèche $n = 10$		2012/2013 crèche $n = 11$		ALL $n = 69$	
Scientific name	Common name	%IRI	(%FO)	%IRI	(%FO)	%IRI	(%FO)
Fish		73.4	(100)	94.5	(100)	80.1	(95.8)
Fish (juvenile)	Juvenile fish	**3.1**	(**20**)	**3.4**	(**45**)	0.5	(21)
Agonopsis chiloensis	Snail fish	–	–	<0.1	(9)	<0.1	(7)
Champsocephalus esox	Icefish	0.8	(30)	0.1	(18)	0.1	(10)
Cottoperca gobio	Bull blenny	**3.3**	(**30**)	1.3	(9)	1.6	(15)
Dissostichus eleginoides	Patagonian toothfish	0.4	(10)	–	–	0.1	(4)
Harpagifer bispinis	Magellanic spiny plunderfish	–	–	–	–	<0.1	(1)
Macruronus magellanicus	Patagonian grenadier	–	–	–	–	0.1	(4)
Micromesistius australis	Southern blue whiting	0.1	(10)	0.1	(64)	<0.1	(14)
Patagonotothen spp.	Rock cod	**64.4**	(**90**)	**20.4**	(**64**)	**80.3**	(**89**)
Perciformes	NA	0.5	(40)	–	–	<0.1	(8)
Salilota australis	Red cod	–	–	–	–	<0.1	(13)
Sprattus fugensis	Falkland herring	–	–	**61.7**	(**73**)	**3.0**	(**20**)
Thysanopsetta naresi	Small flounder	–	–	–	–	<0.1	(1)
Other		0.3	(20)	0	(0)	0.1	(6.9)
Mytilid	Mussel	–	–	–	–	<0.1	(1)
Venerid	Clam	–	–	–	–	<0.1	(1)
Gastropod	Sea snail	0.2	(20)	–	–	<0.1	(3)
Nacellid	Limpet	–	–	–	–	<0.1	(3)

Prey species are categorised by major taxa and each sampling period. They are presented as percentage index of relative importance (%IRI) and frequency of occurrence (%FO). Bold represents those prey species, for a particular sampling period, which contributed >2 % IRI

Dashes indicate a prey species that was unobserved for a given sampling period

periods, there was zero deviation about the Chao estimator. As major prey items were found in at least two stomachs for each period, this was to be expected as once a species is found more than twice (doubletons), the estimator does not predict further increase in number of additional species.

General diet composition

The relative contributions of major prey taxa, by percentage mass, during all sampling occasions are shown in Fig. 3. The lowest contribution of fish (66 %) was seen during the 2011/2012 crèche period, compared to all other

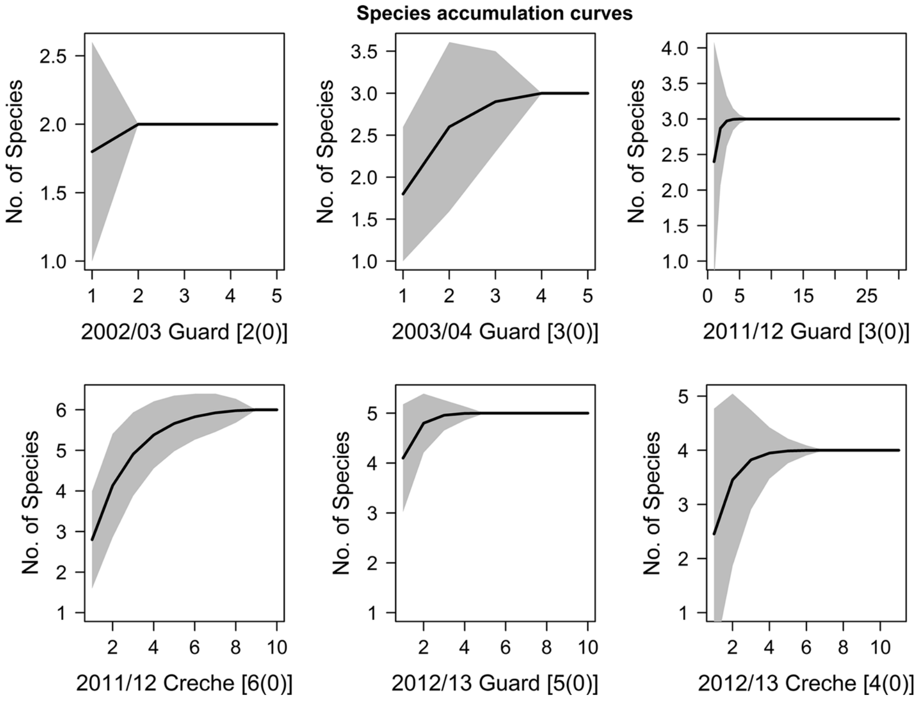

Fig. 2 Prey species accumulation curves for sampling periods. *Each plot* is labelled by the year and chick-rearing phase and includes the: [Chao estimator (Chao standard error)] (Chao 1987). *Bold line* represents the accumulation curve, with *grey shading* representing the 95 % confidence interval associated with the curve. Species used in *each plot* are those having >2 %IRI, for each sampling period

periods where fish contributed to 80 % of the diet. During the 2011/2012 crèche period, there was an increase in the contribution of squid to 32 %; otherwise, it accounted for a maximum of 14 %. Crustaceans did not appear in large quantities during any of the sampling periods (max. = 4 %). ADONIS indicated no significant differences between sampling occasions when comparing major prey taxa ($F_{5,63} = 1.94$, $R^2 = 0.13$, $p = 0.075$).

Temporal variation: breeding period

Variation in diet was evident both within and between the 2011/2012 and 2012/2013 breeding seasons. ADONIS indicated significant differences for the interaction of breeding season (inter-annual) and breeding period (intra-annual) ($F_{1,55} = 7.55$, $R^2 = 0.097$, $p = 0.002$), where breeding period contributed most significantly and explained 12 % of the variation ($F_{1,55} = 9.51$, $R^2 = 0.12$, $p = 0.001$) as opposed to breeding season which explained 7 % of the variation ($F_{1,55} = 6.07$, $R^2 = 0.07$, $p = 0.003$). Evidence of these results is reflected in the nMDS ordination (Fig. 4a), where the centroids of both crèche periods are separated from their respective guard periods and separated from each other, indicating an effect between breeding seasons for the crèche periods and within each breeding season. No seasonal effect was present between the guard periods.

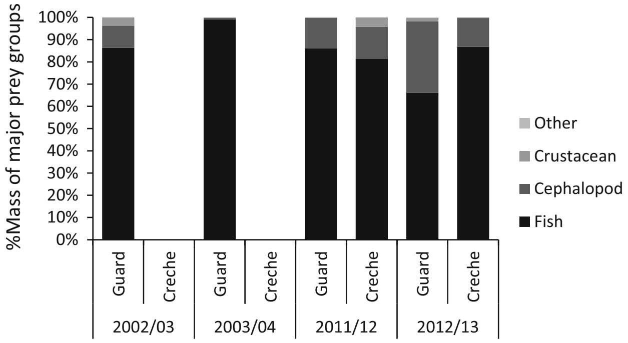

Fig. 3 Percentage mass contribution for major prey groups by sampling periods for gentoo penguins at Cow Bay over four seasons

This change in penguin diet within each breeding season was largely driven by the high proportion of Falkland herring, 53 %, in the 2012/2013 crèche period and the relatively low intake of rock cod in the 2011/2012 crèche period, 47 % (Fig. 5). As Falkland herring had zero contribution by %*M* during the 2011/2012 crèche and 2012/2013 guard period, comparisons were made only among rock cod and Patagonian squid for all four sampling occasions. Failing assumptions of normality, Kruskal–Wallis tests indicated significant differences for %*M* of consumed rock cod ($H_3 = 14.524$, $p = 0.002$). Post hoc testing indicated a significant difference for only the 2012/2013 crèche period where rock cod accounted for only 20 % of the diet compared to all other occasions where it accounted for on average 47–73 % ($p < 0.05$, all occasions). No difference by %*M* was observed for Patagonian squid ($H_3 = 1.313$, $p = 0.726$).

A significant difference in size of consumed rock cod ($H_3 = 124.130$, $p < 0.001$) and Patagonian squid

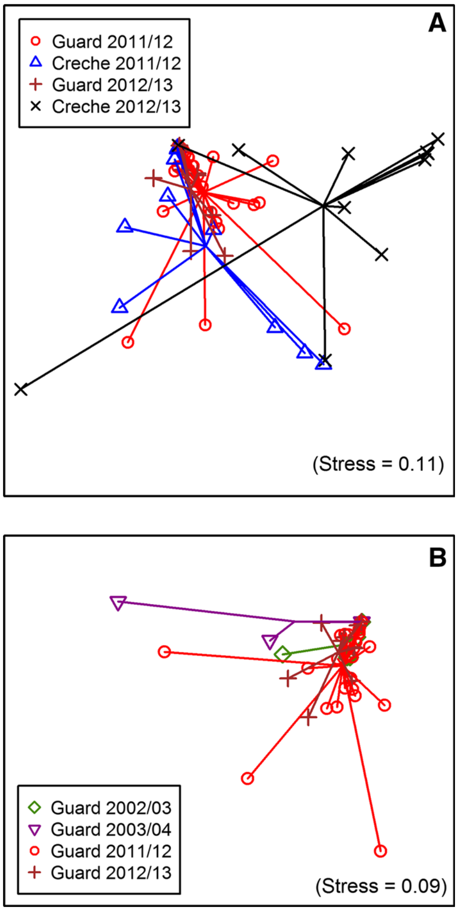

Fig. 4 Two-dimensional nMDS ordination, showing the grouping of diet samples for gentoo penguins at Cow Bay. **a** Breeding period comparison for guard and crèche periods of 2011/2012 and 2012/2013. **b** Inter-annual comparison for guard periods only. Prey items included are those that had >2 %IRI. Function ordispider: plots arms from samples which join at the centroid (weight mean) for each group of samples. *Centroids further apart* indicate greater dissimilarity

($H_3 = 14.936, p = 0.002$) was evident among the differing sampling occasions. For rock cod (Fig. 6a), gentoo penguins consumed larger fish during the 2011/2012 crèche period (median 101, range 62–173 mm) and post hoc testing indicated only this period to have significant differences from all others (2011/2012 guard, median 90, range 62–295 mm; 2012/2013 guard, median 87, range 51–206 mm; 2012/2013 crèche, median 87, range 72–119 mm). For Patagonian squid, post hoc tests indicated differences to lie between the periods of 2011/2012 (median 97, range 41–131 mm) and 2012/2013 (median 83, range 62–103 mm, $p < 0.001$) crèche periods, and the 2012/2013 guard (median 97, range 62–138 mm) and 2012/2013 crèche ($p = 0.011$) periods, although no observable pattern in size of Patagonian squid consumed was apparent (Fig. 6b).

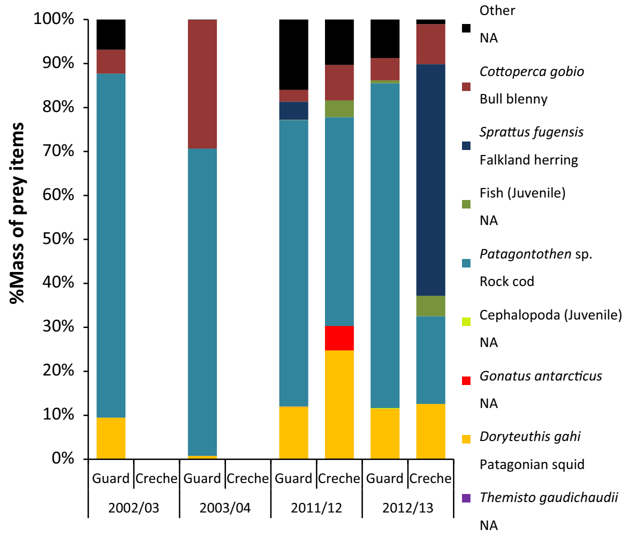

Fig. 5 Contribution of main prey items by percentage mass to the diet of gentoo penguins at Cow Bay during the different sampling occasions. Main prey items are those that had >2 %IRI

These results indicate a clear difference in diet over recently investigated seasons, where larger rock cod were taken during the crèche period of the 2011/2012 season and species composition changed between the chick guard and crèche periods in the 2012/2013 season and also between years for crèche periods. Inter-annual variation in diet during the guard phase was not evident.

Temporal variation: inter-annual

Only data from the chick guard period were used for the extended inter-annual comparison (due to above-mentioned differences between breeding periods and only guard data being available for the earlier period). The ADONIS test indicated no significant differences between chick guard periods for all years ($F_{3,44} = 1.39$, $R^2 = 0.086$, $p = 0.177$), with this result being reflected in the nMDS ordination where centroids overlap or are situated in close proximity to each other (Fig. 4b).

SIMPER analysis identified rock cod and Patagonian squid as the most influential prey items by mass for all pairwise comparisons, except those involving the 2003/2004 season where rock cod and bull blenny were most influential. This is reflected in the species contribution by $\%M$ for each sampling occasion (Fig. 5), and no difference being found for $\%M$ of consumed rock cod over all periods ($H_3 = 0.969$, $p = 0.808$). However, when comparing the size of rock cod consumed, there were significant differences between seasons ($H_3 = 108.963$, $p < 0.001$). Similar size items were taken in the recent years (2011/2012 and 2012/2013, see above; $p = 0.400$), whereas prey items were smaller in 2011/2012 as

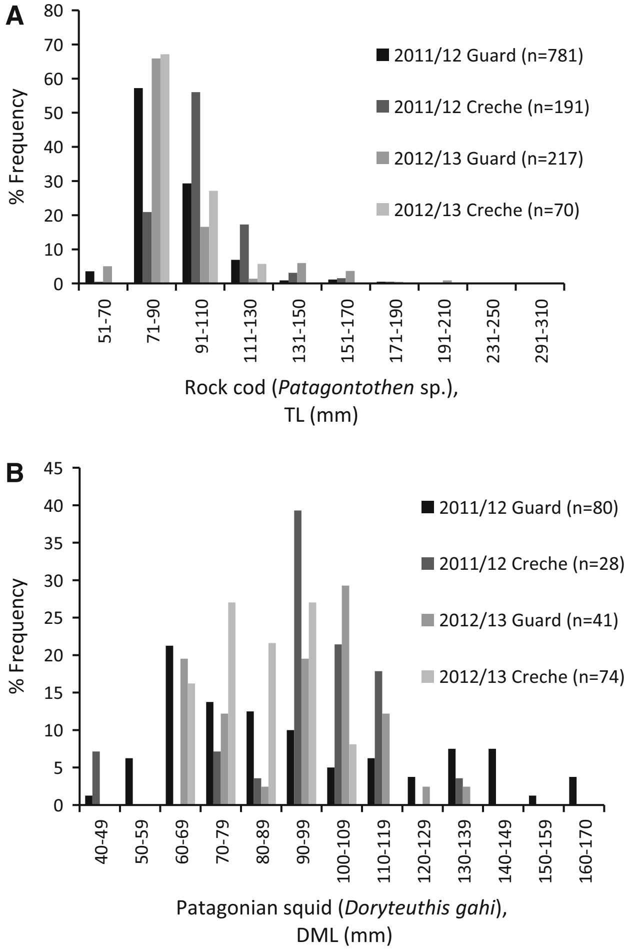

Fig. 6 Size-frequency histogram for **a** rock cod *Patagonotothen* sp. and **b** Patagonian squid *D. gahi* found in the diet of gentoo penguins at Cow Bay during the guard and crèche periods of 2011/2012 and 2012/2013. *n* = number of measurable prey items for each sampling period

compared to the 2002/2003 (median 83, range 19–292 mm, $p = 0.007$) season and in all cases smaller than those taken during the 2003/2004 season (median 116, range 44–177 mm, $p < 0.001$).

Discussion

General diet composition

This study provides the first detailed investigation of species consumed by gentoo penguins at Cow Bay, Falkland Islands. For the broad diet classification, fish were the main taxonomic group consumed by gentoo penguins, accounting for over 80 % of the diet by mass. This finding is consistent with a previous study at Cow Bay during the 1998/1999 guard period, where fish accounted for 98.6 % (Putz et al. 2001). Furthermore, our findings are consistent with a dietary trend across the Falklands, with fish dominant in gentoo penguin diet at breeding colonies in the north, while crustaceans are dominant at western and southern breeding colonies (Putz et al. 2001). At finer detail, the major prey items in this study were notothenioid fish rock cod, the Clupeidae, Falkland herring, and the loliginid squid Patagonian squid. All three of these items have been reported previously in the diet of gentoo penguins at the Falklands (Putz et al. 2001; Clausen and Putz 2002, 2003; Clausen et al. 2005), and other dietary studies over broad spatial ranges also report demersal fish, including notothenioids (Croxall et al. 1988; Bost et al. 1994; Coria et al. 2000).

The fact that rock cod was the most dominant prey item in the study can be attributed to its high relative abundance which does not vary much throughout a year (Arkhipkin et al. 2001; Laptikhovsky et al. 2013). It spawns on the shelf break during the austral winter (Arkhipkin et al. 2013a) and then during the spring, juvenile, resting, and maturing adults move onto the shelf (Brickle et al. 2006), with a majority found towards the highest abundance of macrozooplankton in the north of the Falklands (Agnew 2002). The size of rock cod consumed in this study indicates a benthic feeding behaviour for gentoo penguins as the juvenile stage of rock cod is characterised by individuals <150 mm which are primarily benthic themselves (Laptikhovsky and Arkhipkin 2003).

Similarly, Patagonian squid that spawn in the autumn cohort take advantage of this summer macrozooplankton bloom (Arkhipkin et al. 2013b). Spawning occurs in shallow waters <50 m (Arkhipkin et al. 2013b), and the highest densities of squid eggs have been found on the north-east coast (Arkhipkin et al. 2000). At the Falklands, adults are typically found in the south, south-east, and north-east waters (Arkhipkin et al. 2013b). Due to ontogenetic migration, maturing adults move beyond the shelf and a bimodal size distribution in water <150 m deep is typically observed (Arkhipkin et al. 2013b). During the daytime, when gentoo penguins most often feed, Patagonian squid concentrate near the bottom. These concentrations include squid with DML of <80 mm in waters of <100 m depth and larger squid, DML 90–100 mm, being found in deeper water of 100–200 m depth (Arkhipkin et al. 2013b). This size range of squid fits well with the size consumed by gentoo penguins at Cow Bay and again points towards gentoo penguins being demersal foragers.

The third major prey item, Falkland herring, indicates gentoo penguins at Cow Bay can successfully utilise a pelagic foraging technique as these fish are associated with coastal, pelagic waters, typically schooling in the bottom layers of the water column around the Falklands (Laptikhovsky et al. 2001) in waters of 0–70 m depth (Whitehead et al. 1985). Around the Falklands, these fish spawn in

September and October with adults then moving inshore to feed after spawning (Agnew 2002). Large shoals of adults have even been reported to strand in coves around the Falklands (Agnew 2002). At-sea surveys indicate the largest populations are towards the north-west of the Falklands (Laptikhovsky et al. 2001; Agnew 2002; Baylis et al. 2013b). These fish were also observed as the highest component in the diet of the South American Fur Seal *Arctocephalus australis*, via faecal samples collected in October in this region (Baylis et al. 2013b). However, as it coincided with spawning, the authors suggest that the diet may reflect opportunistic foraging on a seasonally abundant prey item. Similar conclusions were drawn when investigating the diet of dogfish *Squalus acanthias* and catsharks *Schroederichtys bivius* (Laptikhovsky et al. 2001) and Patagonian toothfish *Dissostichus eleginoides* (Arkhipkin et al. 2003) whose diet had the highest proportion of Falkland herring during September–November and November–January, respectively, around the Falklands.

For the majority, these data all imply that gentoo penguins typically utilise a demersal feeding technique within the confines of the continental shelf, on readily available prey, as reported at other breeding locations (Trivelpiece et al. 1986, 1987; Wilson et al. 1998; Miller et al. 2009). We expect the location of Cow Bay would further promote a demersal feeding technique because the shelf slope, defined by the 200-m isobath, which is a depth towards the maximal ability of gentoo penguins, is approximately 100 km away. This is well beyond the 30-km average foraging range of gentoo penguins (Trivelpiece et al. 1987; Wilson et al. 1998; Miller et al. 2009). This argument is supported in the fact that demersal prey was also observed in the west of the islands at breeding colonies with similar bathymetry where there was a gently sloping seabed (Clausen et al. 2005).

In terms of pelagic feeding, this has been observed when gentoo penguins target krill (Bost et al. 1994; Hinke et al. 2007; Kokubun et al. 2010). The technique is more typical when the birds are foraging in deeper near-shore waters, as seen in Antarctica where gentoo penguins at Cape Sherriff had significantly more fish in their diet compared to those at Admiralty Bay, where the continental shelf edge (and hence, deep water) is closer to shore (Miller et al. 2010). Therefore, while pelagic appears more atypical than demersal foraging, clearly gentoo penguins at Cow Bay can apparently utilise both demersal and pelagic foraging techniques during the chick guard and crèche period. The preferred method is most likely influenced by variations in abundance and migration of major prey species in and out of feeding areas. Ultimately, a demersal foraging technique may be more beneficial as prey distribution is limited by the sea floor which increases spatial predictability of prey items (Kokubun et al. 2010).

Temporal variation: breeding period

This is the first study to explore differences in gentoo penguin diet between the guard and crèche periods at the Falklands. We revealed a shift in the primary prey species between the guard and crèche periods of the 2012/2013 chick-rearing season. Also notable was the significant difference in the size of rock cod consumed between the guard and crèche periods of the 2011/2012 season. Predictions based on optimal foraging theory may help to explain the dietary differences we observed between guard and crèche periods.

Optimal foraging theory predicts that animals should forage in a manner that maximises energy gain therefore promoting fitness (Emlen 1966; Macarthur and Pianka 1966). The theory may also be applied to the selection of different food items (Stephens and Krebs 1986), in particular larger items or those with higher energy content which would favour a reduced foraging duration. This might additionally be influenced by the breeding stage of an individual that has different energy requirements (Williams and Rothery 1990). As the capture of larger prey items is facilitated by larger body size (Williams 1991), one might expect gentoo penguins at the Falklands to consume the largest prey items at this location. However, those breeding at South Georgia had a diet consisting of 48 % fish, which were much larger (130–180 mm) (Reid et al. 2005), on average, than those consumed in this study (83–116 mm), despite these penguins exhibiting a smaller body size (see Lynch 2012).

The hypothesis with respect to capture of higher energy prey items is compelling, because it could help to explain the shift in prey items between the 2012/2013 guard and crèche periods. Of all three major prey items in the study, Falkland herring has the greatest energy density (7148 j g^{-1}) compared to rock cod (*P. tesellata* = 4034 j g^{-1}, *P. ramasayi* = 4798 j g^{-1}) and Patagonian squid (4952 j g^{-1}) (Ciancio et al. 2007). For the yellow-eyed penguin in New Zealand, European sprat *Sprattus sprattus* in the diet was associated with higher fledgling mass and greater reproductive success (van Heezik 1990), and the importance of this prey item as a higher energy target species was also recognised by Browne et al. (2011). Furthermore, in feeding trials on black-legged kittiwakes *Rissa tridactyla* and tufted puffins *Fratercula cirrhata,* those chicks that were fed higher energy density forage fish had higher growth increments (Romano et al. 2006). Therefore, in gentoo penguins at the Falklands, when higher energy prey items are available, these may be preferentially captured so as to provide even greater support for growing chicks compared to a diet of rock cod.

Temporal variation: inter-annual

The key difference in diet composition between years was in the size of rock cod consumed over the guard periods. Our findings are in contrast to Putz et al. (2001), who found marked differences in prey composition between years for gentoo penguins breeding at the Falklands. However, they investigated changes only between broad taxonomic divisions (fish, squid, crustacean) at the Falklands and in some years included different breeding colonies, which may bias results as diet is seen to vary greatly even at the scale of the archipelago (Lescroël et al. 2004; Clausen et al. 2005; Miller et al. 2010). There was, however, annual variation in the diet between the two crèche periods of the recent investigation.

This inter-annual difference in diet has been observed elsewhere for gentoo penguins in both size of fish and krill consumed and prey composition (Croxall et al. 1999; Coria et al. 2000; Bevan et al. 2002; Libertelli et al. 2004; Hinke et al. 2007). For example, Bost et al. (1994) found differences in the contribution of either *Euphausiids* or *Themisto gaudichaudii* over two seasons. Also, in a multispecies study conducted at South Georgia, changes in both predator diets and prey biomass estimated through acoustic surveys occurred on an annual basis. However, when assessing intra-annual variation, this same study found no marked differences present for either gentoo penguins or Antarctic fur seals *Arctocephalus gazella* (Croxall et al. 1999). This again points to temporal changes in species composition of gentoo penguin diet, in this study and others, being attributed largely to changes in prey availability within their foraging range (Volkman et al. 1980; Adams and Klages 1989; Coria et al. 2000; Libertelli et al. 2004). This argument is further supported by comparative studies at the Falklands (Clausen et al. 2005) and Kerguelen archipelago (Lescroël et al. 2004). These studies both found differences in diet during concurrent investigations at different colonies, which were reflective of known prey availability.

Ecological implications

Monitoring predator diet and prey abundance in the environment is fundamental in understanding predator–prey interactions (Reid et al. 2005). The fact that rock cod is the primary prey item for gentoo penguins at Cow Bay during the breeding period, could indicate a possible interaction with fisheries. Prior to 2006, rock cod was viewed as a bycatch species but has since been commercialised and catch per unit effort (kg h^{-1}) has increased 30-fold between 2002–2004 and 2009–2011. The ability for increased CPUE is thought to be possible because of increased rock cod population growth due to overfishing of southern blue whiting in the region which has reduced exploitative competition between these planktivorous fish (Laptikhovsky et al. 2013). Stocks of southern blue whiting declined from the 1990s, and in 2011–2012 total catches in Falklands and Argentinian waters were, conservatively, 25-fold less than they were between 1989 and 1995 (Laptikhovsky et al. 2013). For hake *Merluccius hubbsi*, *M. australis,* and kingklip *Genypterus blacodes*, whose diet also consisted of over 50 % rock cod, mean daily catches over the same period have increased five- and two fold, respectively, and are thought to be a consequence of increased rock cod abundance (Laptikhovsky et al. 2013). For gentoo penguins, breeding pair numbers have also increased from approximately 570 pairs in 2003/2004 (Huin 2005) to 1821 breeding pairs in 2012/2013 (Baylis et al. 2013a).

Population changes through shift in ecosystem structure, particularly change in prey availability, have been recognised elsewhere in seabirds. Furness and Barrett (1985) noted how the removal of some top predators and increased abundance in a forage fish, capelin *Mallotus villosus*, supported an increasing seabird population in Norway. Along with potential impacts of climate change, Lescroël and Bost (2006) suggest that reduced numbers in the gentoo penguin population at the Kerguelen archipelago may be related to depletion of fish stocks, in particular reduction in the mackerel icefish *Champsocephalus gunnari* which accounted for 40 % of the diet during the winter of 1987 (Lescroël et al. 2004), but now is no longer a viable commercial species in the region. Prey availability also played a role in population numbers of magellanic penguins *Spheniscus magellanicus* breeding along the Argentinian coastline in Patagonia. Those breeding colonies that were closest to required prey resources had the largest populations probably due to enhanced provisioning and associated increase in lifetime reproductive success (Wilson et al. 2005).

Conclusion

Gentoo penguins at Cow Bay, Falkland Islands, foraged primarily for demersal prey during the breeding period, which look to be readily available during this time. This was reflected in their two main prey items being rock cod and Patagonian squid, which, at the size consumed in this study, are found at or near the seabed. It would be valuable for future studies to assess how representative our findings are for other gentoo penguin breeding colonies at the Falkland Islands. In addition, given rock cod are one of the primary commercial resources at the Falkland Islands and the Falkland Islands holds the largest proportion of the global gentoo penguin population, it would be valuable for future research to investigate to what extent gentoo penguins and commercial fisheries interact in order to support the conservation and management of gentoo penguins.

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