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Diet variability and reproductive performance of macaroni penguins *Eudyptes chrysolophus* at Bird Island, South Georgia

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ABSTRACT: We analysed summer diet and fledging mass of macaroni penguins *Eudyptes chrysolophus* breeding at Bird Island, South Georgia, during the crèche period (January and February) between 1989 and 2010. Crustaceans were the main prey accounting, for over 90% of the diet by mass. Antarctic krill *Euphausia superba* was the main prey, in 17 out of 22 years. Amphipods *Themisto gaudichaudii* were the main prey in 1994 and 2009, fish in 2004, and the euphausiids *Thysanoessa* spp. and *Euphausia frigida* in 2000. There was no clearly dominant prey group in 1999. Prey diversity and the frequency occurrence of *T. gaudichaudii* both increased with a decreasing proportion of *E. superba* in the diet. There was strong evidence that macaroni penguins have a sigmoidal functional response, indicating that this kind of response should be accounted for when devising ecosystem-based management reference points for seabirds. The energy and mass of all euphausiids combined (rather than *E. superba* in particular) in the diet were the most reliable predictors of chick fledging mass; the correlation between model-predicted and observed values was 0.84. The gross energy content of individual meals was often above average in years when the diets contained fewer euphausiids, but fledging mass was always below average in these years. Although macaroni penguins are able to feed on a variety of prey types, chick growth was always severely impacted by a shortage of euphausiids due to higher energy or time costs associated with feeding on alternative prey types. Given their reliance on euphausiids, macaroni penguins would be particularly vulnerable to potential climate-driven declines in krill stocks.

KEY WORDS: Macaroni penguin · Krill · Ecosystem monitoring · Diet · Switching · Functional response · Concorde fallacy

INTRODUCTION

Marine ecosystems are difficult to sample, but an understanding of ecosystem structure and variability can be developed using data from long-term monitoring studies of selected land-based predators. By examining the diets of predators we can obtain information about their prey preferences, foraging behaviour and ecology. Diets might be expected to reflect the relative abundance or proportion of prey items in the ecosystem, so it is possible to consider predators as integrated indicators of ecosystem structure. Diet data, along with measures of reproductive output can be used to understand predator responses to prey availability (Boyd & Murray 2001, Reid & Croxall 2001, Reid et al. 2005a), and are essential for the development of plausible foodweb models (e.g. Murphy et al. 2007a, Hill et al. 2012).

Macaroni penguins *Eudyptes chrysolophus* have been described as the most important avian consumers in global marine ecosystems, with an estimated consumption of more than 8 million tonnes of

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prey per year (Boyd 2002, Brooke 2004). One of the largest populations of macaroni penguins breeds at South Georgia in the Scotia Sea (Croxall et al. 1984, Williams 1995). The main prey is Antarctic krill *Euphausia superba* (Barlow et al. 2002), but amphipods and fish can also make up a significant proportion of the diet, particularly in years in which *E. superba* is less readily available in the local environment (Croxall et al. 1999, Waluda et al. 2010).

At Bird Island (54° 00′ S, 38° 02′ W; Fig. 1), located off the north-western tip of South Georgia, the macaroni penguin population consists of around 46 500 breeding pairs inhabiting 3 rookery sites (Trathan et al. 2006, 2012). The demography and diet of this population has been regularly monitored since the 1970s. Initial diet samples obtained during the chick-rearing periods of 1977, 1980, 1985 and 1986 were dominated by *Euphausia superba* (between 94 and 98% by mass) in all years (Croxall & Prince 1980, Croxall et al. 1988b, 1997). Since 1989, diet data have been collected annually during the crèche period using standardised methods (CCAMLR 2004) as part of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Programme (CEMP) (Agnew 1997). The objective of CEMP is to detect changes in the Southern Ocean ecosystem and to distinguish the potential effects of commercial fishing from other drivers of change.

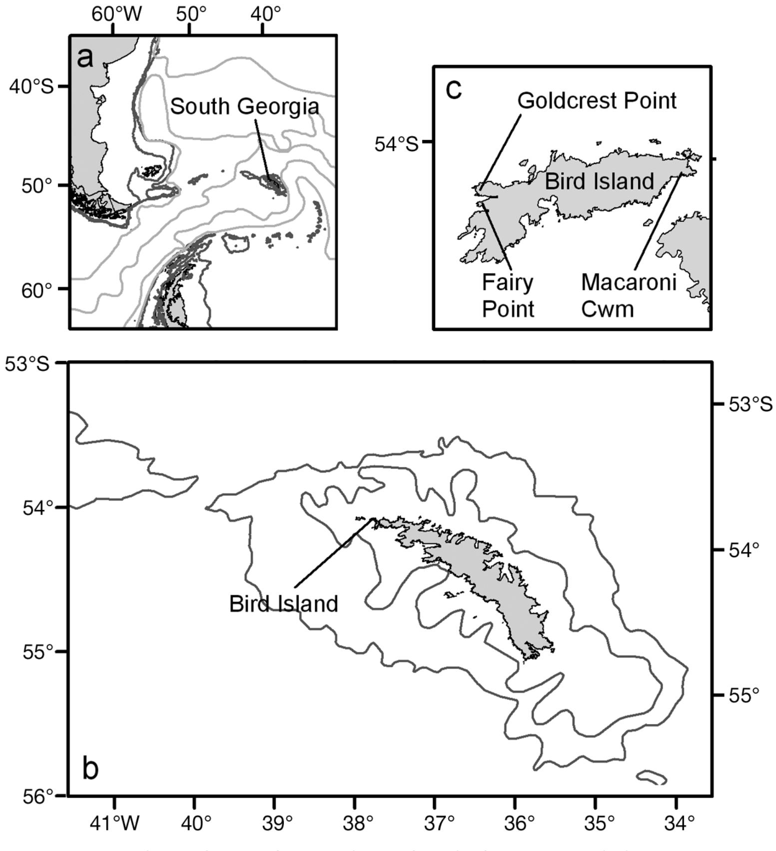

Fig. 1. Northern Scotia Sea with (a) South Georgia and the major fronts of the Antarctic Circumpolar Current (light grey), (b) Bird Island with location of 200 and 1000 m bathymetric contours shown in dark grey, and (c) Bird Island locations of macaroni penguin colonies at Goldcrest Point (~35 000 pairs), Fairy Point (~500 pairs) and Macaroni Cwm (~11 000 pairs)

Macaroni penguins are diving predators, making the majority of their dives during the day to median depths of between 10 and 60 m (Croxall et al. 1988a, 1993, Hart et al. 2010). The main feeding region for the population breeding at Bird Island is to the northwest of the island (Trathan et al. 2006, Waluda et al. 2010). Energy is delivered to the chick as regurgitated stomach contents, with both parents undertaking foraging trips while the chicks are at the crèche stage (Barlow & Croxall 2002).

Here, we describe the diets of macaroni penguins during crèche for the 22 yr period from 1989 to 2010. While macaroni penguins breeding at Bird Island have been described as 'dependent predators' of *Euphausia superba* (Croxall & Prince 1987, Reid et al. 1999a), some studies have reported a decline in the relative proportion of *E. superba* in macaroni penguin diets since the late 1980s (Reid & Croxall 2001, Barlow et al. 2002). Both of these earlier analyses considered data from 1989 to 2000, and by doubling the length of the time series, we are able to better understand these observations in the context of long-term variability. We examine individual and inter-annual variability in diet composition and prey dominance and assess the influence of diet on fitness using the mass of chicks at fledging as an indicator of reproductive output.

MATERIALS AND METHODS

Diet sampling

Diet samples were obtained from macaroni penguins at the Goldcrest Point colony, Bird Island, South Georgia (Fig. 1). Samples were obtained during the crèche period (January and February) from 1989 to 2010, using the stomach lavage methods described in Wilson (1984) and Williams (1991). Samples were usually obtained over a 4 wk period with 10 birds sampled each week as they returned to the colony to feed their chicks (Table 1). All diet sampling procedures used were regulated by the British Antarctic Survey Ethical Review Committee in collaboration with Cambridge University and the UK Home Office.

Each diet sample was drained through 2 sieves (3.35 and 250 µm) and weighed to calculate wet meal mass per penguin. No samples were recorded as empty stomachs. Each sample was then sorted into the crustacean, fish and cephalopod components and the constituent parts weighed. Crustaceans were identified to species where possible. Fish otoliths were separated and counted from all diet samples, used to identify fish species and to calculate lengths using regression equations (Reid & Arnould 1996). Cephalopods were identified from beaks by comparison with a reference collection held at the British Antarctic Survey, with regression equations used to relate the lower rostral length to the original mantle length where possible (Clarke 1986, Rodhouse et al. 1990). The number of prey species observed in each year was recorded.

Mean mass at fledging

The mean mass of chicks at fledging in each year was used as a simple index of reproductive performance for the population of macaroni penguins breeding at Bird Island. Annual fledging mass was calculated as the mean mass of approximately 100 fledging birds sampled just prior to their departure from the colony (mid-February) each year. Fledging weights were obtained from the smaller macaroni penguin colony (approximately 500 pairs of breeding birds) at Fairy Point, adjacent to the Goldcrest Point colony (approximately 35 000 pairs) (Fig. 1). As part of the Bird Island long-term monitoring programme, macaroni penguin de-

Table 1. Summary of diet samples obtained from macaroni penguins at Bird Island 1989–2010 (n = 856). Data are by percentage mass and percentage frequency of occurrence of main taxa and by main crustacean prey. (–) not recorded. Data summarised by year, overall mean values (in bold) calculated for all individual samples

Year	No. of samples	No. of species	Meal mass (g)	Meal energy (kJ)	Crustaceans		Fish		Cephalopods		*E. superba*		Other euphausiids		*T. gaudichaudii*	
					% mass	% freq	% mass	% freq	% mass	% freq	% mass	% freq	% mass	% freq	% mass	% freq
1989	40	3	362	1727	98.2	100.0	1.8	40.0	<0.1	2.5	98.2	100.0	–	–	–	–
1990	40	3	318	1395	99.9	100.0	<0.1	35.0	0.1	2.5	99.9	100.0	–	–	–	–
1991	40	8	212	825	99.3	100.0	0.1	35.0	0.6	22.5	79.6	90.0	0.7	5.0	19.0	75.0
1992	40	3	464	1786	99.9	100.0	0.1	10.0	–	–	99.4	100.0	–	–	0.5	32.5
1993	40	4	370	1778	92.1	100.0	5.9	27.5	2.0	10.0	89.8	97.5	–	–	2.3	50.0
1994	40	16	276	1091	85.5	100.0	13.6	50.0	0.9	22.5	11.6	42.5	3.6	37.5	70.3	92.5
1995	40	4	212	1013	89.8	97.5	9.8	40.0	0.4	5.0	63.5	82.5	–	–	26.3	65.0
1996	17	3	210	866	99.9	100.0	0.1	5.9	–	–	99.9	100.0	–	–	<0.1	5.9
1997	39	7	524	2072	99.7	97.4	0.1	20.5	0.2	2.6	98.7	97.4	<0.1	2.6	1.0	15.4
1998	40	4	292	1197	93.5	100.0	6.5	40.0	<0.1	2.5	79.7	90.0	–	–	13.8	60.0
1999	40	8	191	956	79.0	100.0	21.0	57.5	<0.1	2.5	24.7	57.5	24.3	60.0	30.0	87.5
2000	40	7	391	1809	80.7	100.0	19.3	70.0	<0.1	5.0	19.5	52.5	43.3	90.0	17.8	70.0
2001	40	4	548	2120	100.0	100.0	<0.1	2.5	–	–	99.9	100.0	–	–	0.1	5.0
2002	40	10	425	2056	84.7	97.5	15.3	75.0	<0.1	15.0	73.4	82.5	0.6	10.0	10.8	57.5
2003	40	10	473	2090	92.1	100.0	7.9	85.0	<0.1	15.0	53.9	70.0	15.0	72.5	23.2	95.0
2004	40	10	397	2272	53.9	95.0	46.1	90.0	–	–	32.9	75.0	0.2	27.5	20.9	85.0
2005	40	6	396	1861	98.8	100.0	1.2	22.5	–	–	52.3	57.5	30.8	50.0	15.7	67.5
2006	40	3	254	1065	99.9	100.0	0.1	7.5	–	–	99.9	100.0	–	–	<0.1	7.5
2007	40	3	237	920	99.8	100.0	0.2	22.5	–	–	99.8	100.0	–	–	<0.1	32.5
2008	40	9	319	1397	83.1	100.0	16.9	82.5	–	–	52.5	80.0	12.4	47.5	18.2	82.5
2009	40	19	502	2138	78.5	100.0	21.4	97.5	0.1	27.5	8.9	57.5	10.2	82.5	59.1	97.5
2010	40	6	167	660	99.7	100.0	0.3	20.0	–	–	91.2	100.0	8.1	30.0	0.3	32.5
Mean		2.4	346	1612	90.7	99.6	9.1	43.6	0.2	6.3	64.4	82.8	6.8	29.0	19.6	52.0

mographic data are obtained from the Fairy Point colony, which is a satellite of the Goldcrest Point colony. Birds from both colonies use the same foraging areas and access the open ocean via the same inlet (Trathan et al. 2006).

Energy content of meals

The energy content of each meal was calculated from the wet mass of each prey component and published data on energy content (kJ g^{-1}) of prey, assuming a constant mass–energy conversion for each prey type. Energy values from the same area and season (Scotia Sea during austral spring) were used whenever possible, but equivalent values from other areas and seasons were used as necessary. The energy content of *Euphausia superba* was calculated using a mean value for males and females (Clarke 1980). A single energy value was used for each of: euphausiids other than *E. superba*, based on *Thysanoessa macura* (Torres et al. 1994); amphipods, based on *Themisto gaudichaudii* (Ciancio et al. 2007); and cephalopods, based on a mean value for muscular squid (Clarke et al. 1985) (Table 2). The energy content of fish was calculated based on the species composition for each year, with energy values for key species given in Table 2. In years in which fish flesh was present but could not be identified to species level (i.e. years in which no otoliths were recovered) a mean value of 5.83 kJ g^{-1} (the mean of all fish species listed in Table 2) was used to calculate the energy content of fish.

Analyses

In this study we (1) describe the frequency of occurrence, meal mass, energy and diversity of prey in individual diets, (2) examine variability in diet composition and prey dominance within and between years, and (3) examine the relationship between diet and the mean mass of chicks at fledging. Non-linear least squares analyses were used to examine the relationship between meal composition and fledging weights. Analyses were done in the statistical package R (v2.13; R Development Core Team 2011). We used the corrected Akaike Information Criterion (AIC_c) and calculated the correlations between modelled and observed values to compare 24 models of the relationship between diet, indicated by various metrics, and fledging mass. The diet metrics included were the meal mass (wet mass in grams) or energy content (kJ) of each prey group and all groups combined, and the model forms included both 2- and 3-parameter asymptotic models.

RESULTS

Individual diet variability

In total, 856 diet samples were obtained from macaroni penguins between 1989 and 2010. Meals comprised crustaceans, fish and cephalopods, with crustaceans occurring in 853 diet samples (99.6%), and the remaining 3 samples containing only fish. The

Table 2. Energy content for key prey species of macaroni penguins

	Family	Species	Energy (kJ g^{-1})	Source
Cephalopods	[*See Table 3 for species names*]		4.27	Clarke et al. (1985)
Fish	Channichthyidae	*Champsocephalus gunnari*	5.4	Lea et al. (2002)
		Pseudochaenichthys georgianus	4.55	Vanella et al. (2005)
	Gempylidae	*Paradiplospinus gracilis*	4.6	Cherel & Ridoux (1992)
	Myctophidae	*Electrona antarctica*	7.93	Donnelly et al. (1990)
		Electrona carlsbergi	6.57	Clarke & Prince (1980)
		Krefftichthys anderssoni	8.23	Cherel & Ridoux 1992, Tierney et al. (2002) (mean value)
		Protomyctophum bolini	6.1	Data for *P. tenisoni* used; Lea et al. (2002)
		Protomyctophum choriodon	6.1	Data for *P. tenisoni* used; Lea et al. (2002)
	Nototheniidae	*Lepidonotothen larseni*	4.9	Staniland et al. (2007)
Crustaceans	Euphausiidae	*Euphausia superba*	4.645	Clarke (1980) (mean of male and female)
		Thysanoessa macura	5.038	Torres et al. (1994)
	Hyperiidae	*Themisto gaudichaudii*	3.1	Ciancio et al. (2007)

crustacean component was dominated by euphausiids, in particular *Euphausia superba*, which was present in 709 samples (83%). Other species of euphausiids (*E. frigida* and *Thysanoessa* spp.; not always identified to species level so included here as a single prey group) were present in 248 samples (29%), and the hyperiid amphipod *Themisto gaudichaudii* was present in 445 samples (52%).

Fish remains were present in 373 diet samples (44%). A total of 11 species of fish from 6 families were identified, with *Champsocephalus gunnari* and *Krefftichthys anderssoni* the most frequently recorded species (Table 3). Mean estimated standard lengths were between 26 mm (*Muraenolepis microps*) and 278 mm (*Paradiplospinus gracilis*) (Table 3).

Cephalopod remains were present in 54 diet samples (6%). A total of 7 cephalopod species from 5 families were identified, with *Kondakovia longimana* the most frequently recorded species (Table 3). Estimated mean mantle lengths were between 41 mm (*K. longimana*) and 200 mm (*Martialia hyadesi*) (Table 3).

The mean (±SD) mass of all 856 diet samples was 346 ± 214 g (Table 1, Fig. 2a). The diet was composed of crustaceans (314 ± 212 g), fish (32 ± 86 g) and cephalopods (0.6 ± 9 g). The most common crustacean prey were *Euphausia superba* (236 ± 231 g),

Table 3. Prey species recorded in the diet of macaroni penguins from 1989 to 2010. Mean length is given as standard length for fish and mantle length for cephalopods. (–) data not available

	Family	Species	No. of years	No. of samples	Frequency (%)	Mean length (mm)	Years present in diet
Cephalopods	Brachioteuthidae	*Brachioteuthis picta*	2	4	0.47	–	1991, 1994
	Cranchidae	*Galiteuthis glacialis*	1	1	0.12	–	2002
	Onychoteuthidae	*Kondakovia longimana*	3	33	3.86	41	1991, 1994, 2009
	Ommastrephidae	*Martialia hyadesi*	4	22	2.57	200	1991, 1994, 2002, 2003
	Onychoteuthidae	*Moroteuthis knipovitchi*	1	1	0.12	158	2009
	Psychroteuthidae	*Psychroteuthis glacialis*	1	2	0.23	–	2009
	Brachioteuthidae	*Slosarczykovia circumantarctica*	1	3	0.35	–	2009
Fish	Bathydraconidae	*Parachaenichthys georgianus*	1	1	0.12	238	2004
	Channichthyidae	*Champsocephalus gunnari*	13	87	10.16	132	1993–95, 1997, 1999, 2000, 2002–05, 2008–10
	Channichthyidae	*Pseudochaenichthys georgianus*	2	8	0.93	165	1994, 2003
	Gempylidae	*Paradiplospinus gracilis*	1	1	0.12	278	2009
	Muraenolepididae	*Muraenolepis microps*	2	18	2.10	26	2008, 2009
	Myctophidae	*Electrona antarctica*	8	50	5.84	45	1994, 2000–05, 2009
	Myctophidae	*Electrona carlsbergi*	4	8	0.93	69	2002–04, 2009
	Myctophidae	*Krefftichthys anderssoni*	8	80	9.35	59	1994, 1998, 1999, 2002, 2004, 2008–10
	Myctophidae	*Protomyctophum bolini*	1	1	0.12	63	2009
	Myctophidae	*Protomyctophum choriodon*	7	20	2.34	81	1994, 1997, 1999, 2003, 2004, 2008, 2009
	Nototheniidae	*Lepidonotothen larseni*	10	41	4.79	99	1994, 1997, 1999, 2001–05, 2007, 2009
Crustaceans	Euphausiidae	*Euphausia superba*	22	709	82.83	42	1989–2010
	Euphausiidae	*E. frigida/Thysanoessa* spp.	12	248	28.97	–	1991, 1994, 1997, 1999, 2000, 2002–05, 2008–10
	Hyperiidae	*Themisto gaudichaudii*	20	445	51.99	–	1991–2010
	Bougisidae	*Primno macropa*	1	2	0.23	–	2009
	Crangonidae	*Notocrangon* spp.	2	3	0.35	–	1997, 2009
	Calanoida	*Euchaeta antarctica*	2	2	0.23	–	2008, 2009
	Calanoida	*Rhincalanus gigas*	2	2	0.23	–	2008, 2009

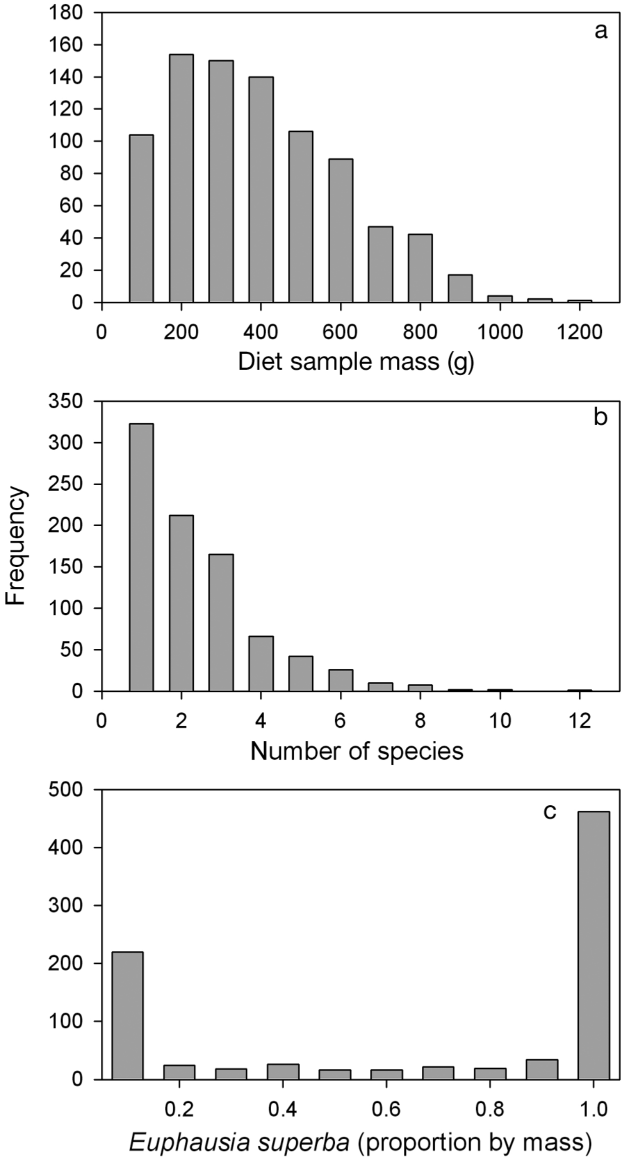

Fig. 2. Frequency occurrence of (a) diet sample mass, (b) number of species per sample and (c) proportion of *Euphausia superba* in diet samples

Themisto gaudichaudii (53 ± 116 g) and euphausiids other than *E. superba* (25 ± 85 g). The mean energy derived from meals was 1612 ± 1061 kJ (Table 1). The number of prey species recorded per sample was between 1 and 12 (mean ± SD: 2.4 ± 1.6) (Fig. 2b).

Euphausia superba was the main prey, but the proportion of this species in diets showed a distinct bimodal distribution, with 147 diet samples (17%) containing no *E. superba* and 277 (32%) containing only *E. superba* (Fig. 2c). To further examine prey dominance in diets we combined data into 3 main prey groups, these were 'euphausiids' (*E. superba*, *E. frigida*, *Thysanoessa* spp.), 'other crustaceans' (mostly amphipods; see Table 3) and 'fish'. In total, 357 of the 856 individual diet samples (42%) were composed entirely of a single prey type (317 were euphausiids, 37 other crustaceans, 3 fish). In 627 diet samples (73%), a single prey type represented >90% of diet mass (502 samples with euphausiids, 100 other crustaceans, 25 fish). We refer to this type of diet as 'dominated' by the majority prey type. Only 229 samples (27%) had no dominant prey type. We shall refer to this latter category as 'mixed' diets. All but 3 of these mixed diets included euphausiids.

Annual patterns of variability

Annual meal mass (mean ± SD) ranged between 167 ± 110 g (2010) and 548 ± 240 g (2001). Annual meal energy ranged between 660 ± 441 kJ (2010) and 2270 ± 1250 kJ (2004) (Fig. 3, Table 1). *Euphausia superba* was recorded in all 22 years, other species of euphausiids were present in 12 years and *Themisto gaudichaudii* was recorded in 20 years (Table 1). Fish were recorded in the diet in all 22 years, with otoliths recovered and species identified in 16 years (no species data were available for 1989 to 1992, 1996, 2006; see also Table 3). Cephalopods were present in 13 years (Table 1), with cephalopod beaks recovered in 5 years (1991, 1994, 2002, 2003, 2009; Table 3). *E. superba* was the main prey species (>50% of the annual total recorded diet mass) in 17 years, but contributed less than one third in 5 years (Fig. 4). There was no trend in the proportion of *E. superba* in the diet over the period of the study ($r = 0.03$. $p = 0.45$) and the 5 yr moving average indicates that this proportion has remained fairly constant at around 68% since the mid-1990s (Fig. 4). The proportion by mass of *E. superba* was negatively correlated with both the frequency of *T. gaudichaudii* (arcsine transformed data; $r = -0.88$, $p < 0.01$) and the number of species in the diet (*E. superba* data were arcsine transformed; $r = -0.81$, $p < 0.01$).

Inter-annual patterns in prey dominance are shown in Fig. 5. The most common situation was where more than 75% of diets were euphausiid-dominated (10 of 22 years). In 4 of these 10 years, 100% of diets were euphausiid-dominated. In 5 years, less than 25% of diets were euphausiid-dominated, and the remaining diets were either mixed (3 to 73% of diets) or dominated by other crustaceans (0 to 50%) or fish (0 to 23%). In 7 years,

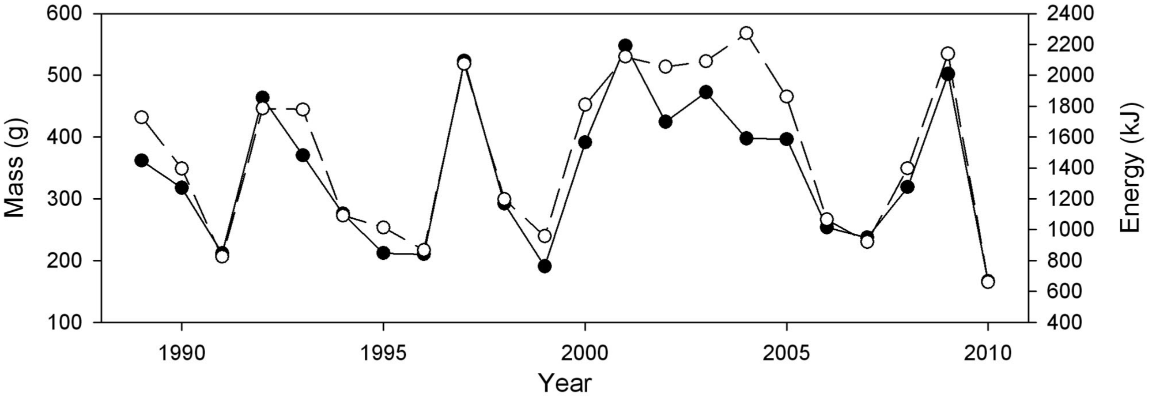

Fig. 3. Annual variability in meal mass (●) and energy derived from meals (○) of macaroni penguins 1989–2010

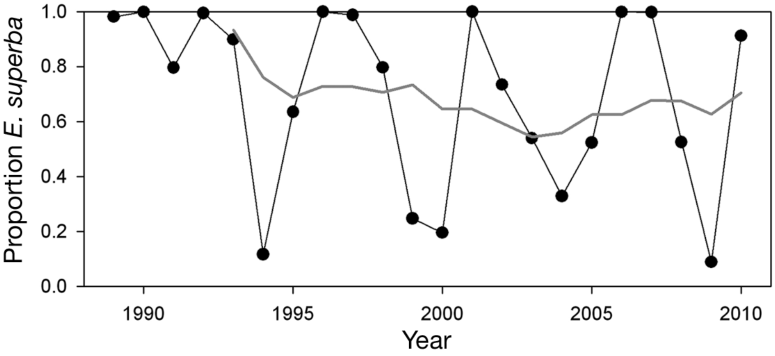

Fig. 4. Proportion of *Euphausia superba* (by mass) in the diet of macaroni penguins from 1989 to 2010. Grey line indicates 5 yr moving average (mean = 0.68)

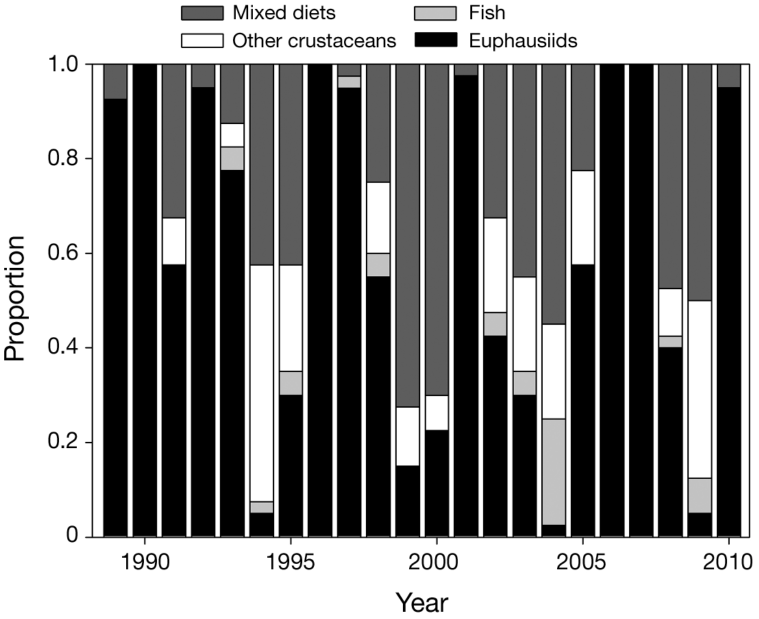

Fig. 5. Composition of macaroni penguin diets from 1989 to 2010. Diets are categorised as dominated (> 90% of a diet sample) by euphausiids, other crustaceans (mostly amphipods, *Themisto gaudichaudii*) or fish or as mixed diets where no individual prey group contributed > 90%

between 25 and 75% of diets were euphausiid-dominated, 23 to 55% were mixed, 8 to 50% were dominated by other crustaceans, and 0 to 5% were fish-dominated. Within years, the percentage of mixed diets varied between 0 (in 1990, 1996, 2006, 2007; Fig. 5) and 73% (1999). There were inevitable negative correlations between the proportion of euphausiid-dominated diets and the proportion of diets that were dominated by other crustaceans (arcsine transformed data; $r = -0.83$, $p < 0.01$) or fish (arcsine transformed data; $r = -0.55$, $p < 0.01$), or were mixed (arcsine transformed data; $r = -0.94$, $p < 0.01$).

Relationships between diet and fledging mass

The mean mass of chicks at fledging varied between 2.9 and 3.5 kg yr^{-1} (mean ± SD = 3.27 ± 0.18 kg; Fig. 6). Fledging mass was positively correlated with meal mass and energy, and with the crustacean, *Euphausia superba* and euphausiid components of the diet, but it was negatively correlated with the amphipod and fish components (Fig. 7). AIC_c provided most support for 3-parameter models with either mass or energy content of all euphausiids as the independent variable. The correlation between model-predicted and observed values for fledging weight was 0.84 for both of these models (Fig. 7, Table 4). AIC_c

provided a slightly lower level of support for 2-parameter models with the mass or energy of *E. superba* as the independent variable; the correlation between model-predicted and observed values was 0.68. The assumed relationship between mass and energy content was linear within each prey group, but varied across groups. Consequently, AIC_c did not distinguish between mass and energy models except when the independent variable included >1 prey group (i.e. all prey groups or all crustaceans). In these cases AIC_c supported the energy model more strongly than the mass model.

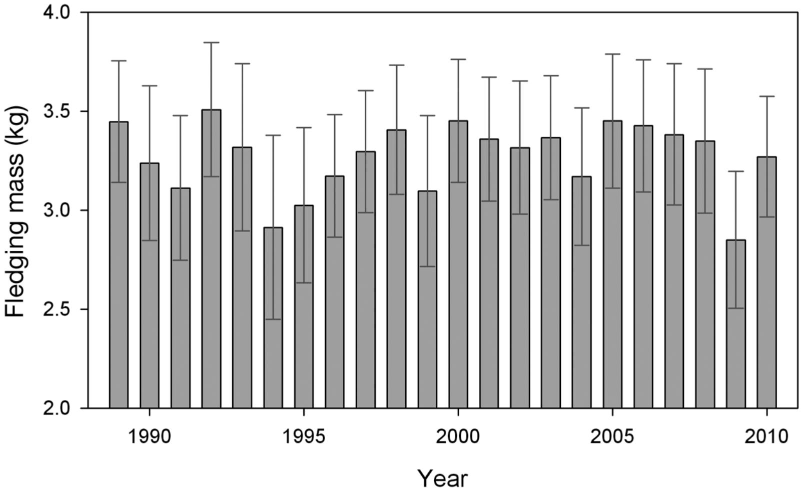

Fig. 6. Mean (±SD) annual fledging mass of macaroni penguins from 1989 to 2010. Overall mean = 3.27 kg

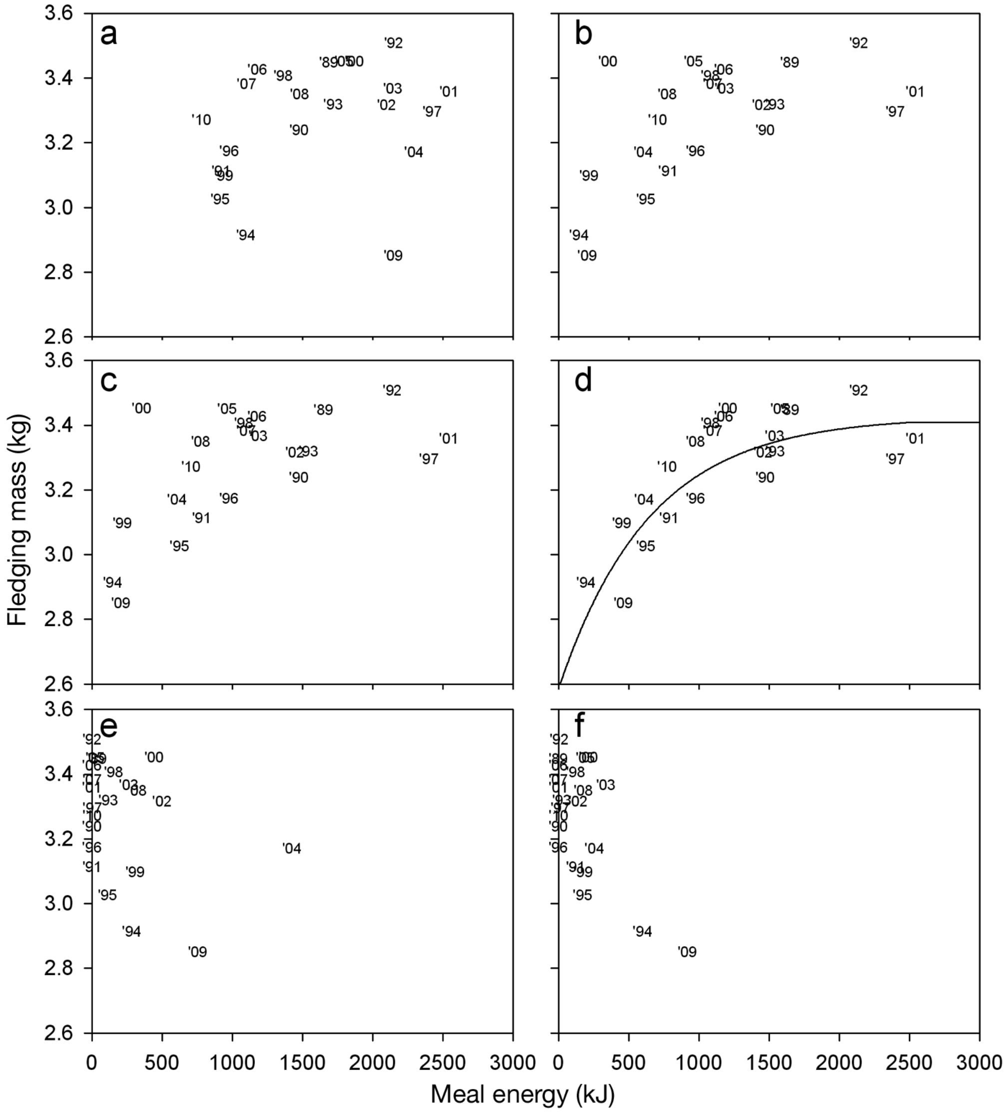

Fig. 7. Relationship between energy derived from diet (kJ) and fledging mass of macaroni penguins where meal energy is derived from (a) total diet, (b) all crustaceans, (c) *Euphausia superba* only, (d) all euphausiids (solid line shows fitted 3-parameter model, see Table 4), (e) fish only, or (f) *Themisto gaudichaudii* only

Table 4. Results of model fitting (diet versus fledging weight) using 2- and 3-parameter non-linear least squares analysis. x is calculated as either wet mass (g) or energy derived from prey (kJ) for each prey group and all diet components combined. **Bold**: best fit for each parameter (corrected Aikaike Information Criteria [AIC$_c$]). The correlation between model-predicted and observed values for fledging weight is also given for each model. Models — 3-parameter: $\text{fledging.wt} \approx a - b \cdot \exp(-c \cdot x)$; 2-parameter: $\text{fledging.wt} \approx a \cdot [1 - \exp(-c \cdot x)]$, where a, b and c are model parameters

	df	Meal mass (g)		Meal energy (kJ)	
		AIC$_c$	Correlation	AIC$_c$	Correlation
3 parameters					
All diet components	4	295.51	0.31	294.29	0.38
All crustaceans	4	293.27	0.43	288.44	0.59
E. superba	4	282.17	0.71	282.17	0.71
All euphausiids	4	271.01	0.84	**270.84**	**0.84**
Amphipods (*T. gaudichaudii*)	4	284.21	0.68	284.21	0.68
All fish	4	294.66	0.36	294.31	0.38
2 parameters					
All diet components	3	293.72	0.30	292.35	0.38
All crustaceans	3	291.69	0.41	287.18	0.57
E. superba	3	282.31	0.68	**282.31**	**0.68**
All euphausiids	3	288.98	0.51	289.17	0.51
Amphipods (*T. gaudichaudii*)	3	282.93	0.66	282.93	0.66
All fish	3	292.98	0.34	292.81	0.35

DISCUSSION

Crustacean dominance and variability in the contribution of *Euphausia superba*

This work presents data from 22 yr of diet sampling of macaroni penguins *Eudyptes chrysolophus* breeding at Bird Island, South Georgia. This is one of the longest and most comprehensive time series of penguin diet data available globally. Crustaceans dominated the diet, with Antarctic krill *Euphausia superba* the most commonly eaten prey species. The amount of *E. superba* in the diet was variable from year to year, providing over half of the diet by mass in 17 years of the study but less than one third in 5 years. Previous work has reported a decline in *E. superba* in macaroni penguin diets at Bird Island for the period between 1989 and 2000 (Reid & Croxall 2001, Barlow et al. 2002). Our Fig. 4 confirms low values (1999 and 2000) at the end of this period but, as with 1994 and 2009, these low values were followed by an immediate recovery.

The years in which *Euphausia superba* made up >99 % of the diet by mass occurred at approximately 5 yr intervals (1992, 1996, 2001, 2006, 2007). This is likely to be related to increased local abundance due to pulses of *E. superba* recruitment into the South Georgia ecosystem (Reid et al. 1999b, 2002, Murphy & Reid 2001, Murphy et al. 2007a,b). Similar patterns of *E. superba* recruitment have been reported in the diets of gentoo and chinstrap penguins breeding at Livingston Island in the South Shetland Islands (Miller & Trivelpiece 2007). The availability of *E. superba* was probably low in the South Georgia ecosystem in the 5 years when it made up less than one third of the diet of macaroni penguins (1994, 1999, 2000, 2004, 2009), with similarly low estimates of abundance in data from acoustic surveys and other predator diets (Croxall et al. 1999, Xavier et al. 2003, Waluda et al. 2010, S. Fielding pers. comm.).

Crustaceans other than *Euphausia superba* were the main prey in 3 years, with small euphausiids (*E. frigida*, *Thysanoessa* spp.) the most common prey group in 2000 and the hyperiid amphipod *Themisto gaudichaudii* dominant in 1994 and 2009. The results of our study are consistent with diet studies of macaroni penguins and the closely related royal penguins *Eudyptes schlegeli* elsewhere in the Southern Ocean where crustaceans (particularly euphausiids) are frequently recorded as the main prey (Table 5).

Fish and cephalopods in the diet

The majority of fish species recorded in diet samples occupy a pelagic or bentho-pelagic habitat, with the most commonly recorded species including the myctophid *Krefftichthys anderssoni*, the channichthid *Champsocephalus gunnari* and the notothenid *Lepidonotothen larseni.* Similar species fish have been reported in varying proportions in the diets of Antarctic fur seals (Reid & Arnould 1996, Reid et al. 2006), gentoo penguins (Hill et al. 2005, Reid et al. 2005b), and black-browed and grey-headed albatrosses (Reid et al. 1996, Xavier et al. 2003), which also breed at Bird Island. Fish can provide a significant proportion of the diet of macaroni and royal penguins breeding at other locations (Table 5). Myctophids, particularly *K. anderssoni, Protomyctophum tenisoni, P. normani* and *Electrona carlsbergi* (Brown & Klages 1987, Hindell 1988, Ridoux 1994, Green et al. 1998, Pichegru et al. 2011) are the most commonly observed fish in the diets of macaroni penguins throughout the

Southern Ocean, and *C. gunnari* is also important at Heard Island in certain years (Klages et al. 1989).

Cephalopods were rare in diet samples, and only 2 species (*Martialia hyadesi* and *Kondakovia longimana*) were present in 3 or more years of the study. Cephalopods were more common in years during which *Euphausia superba* was not a dominant prey group, particularly 2009, when the lowest amount of *E. superba* and the highest diversity of species were recorded. A number of cephalopod (and other) species not seen in other years were recorded in 2009 (Table 3). While cephalopods can make up a reasonable proportion of the diet of some species, e.g. king penguins *Aptenodytes patagonicus*, emperor penguins *A. forsteri* and little penguins *Eudyptula minor* (Croxall & Prince 1996), they probably occur in waters beyond the diving depth and range of breeding macaroni penguins except during unusual years. Cephalopods are similarly rare in the diets of macaroni penguins breeding at other locations in the South Atlantic, but can contribute a significant proportion of the diet at colonies in the Southern Indian Ocean (Table 5), with *K. longimana* the most commonly observed species at Crozet Island and Marion Island (Adams & Brown 1989, Ridoux 1994), and *Moroteuthis* spp. the most common cephalopod in the diets of royal penguins breeding at Macquarie Island (Hindell 1988).

Table 5. Summary of diet studies on macaroni penguins *Eudyptes chrysolophus* and royal penguins *E. schlegeli*. Data are the percentage of diet by mass (given as an approximate mean value if the original study examined data over multiple years). (–) item not recorded

Location	Species	Years	Crustaceans (%)	Fish (%)	Cephalopods (%)	Source
South Georgia (Bird Island)	Macaroni	1977, 80, 85, 86	97	3	–	Croxall et al. (1988b)
South Georgia (Goldcrest Point, Bird Island)	Macaroni	1989–2010	90.7	9.1	0.2	Present study
South Shetlands (Clarence Island)	Macaroni	1977	100	–	–	Croxall & Furse (1980)
South Shetlands (Gibbs Island)	Macaroni	1977	37	63	–	Croxall & Furse (1980)
South Shetlands (King George Island)	Macaroni	1978–79 to 80–81	96	4	<1	Jablonski (1985)
Heard Island (Red Island, Rogers Head, West Bay)	Macaroni	1986–87	76.7	23.2	0.1	Klages et al. (1989)
Heard Island (Rogers Head, Icicle Gully)	Macaroni	1992	58.6	41.4	–	Green et al. (1998)
Heard Island (Capsize Beach)	Macaroni	2003–04	77	22	<1	Deagle et al. (2007)
Crozet (Possession Island)	Macaroni	1980–81	60.9	28.7	9.8	Ridoux (1994)
Marion Island (Macaroni Bay)	Macaroni	1983–84, 84–85, 87–88	90	9	2	Brown et al. (1990)
Marion Island (Bullard Beach)	Macaroni	1994–95 to 2001–02	79	18	3	Crawford et al. (2003)
Marion Island	Macaroni	2008–09	86	12.1	1.9	Pichegru et al. (2011)
Macquarie Island (Bauer Bay)	Royal	1981–82	11	54	35	Horne (1985)
Macquarie Island (Sandy Bay)	Royal	1981–82	26.5	62	11.5	Horne (1985)
Macquarie Island (The Nuggets)	Royal	1984–85 and 85–86	51.4	45.7	2.9	Hindell (1988)
Macquarie Island (Sandy Bay)	Royal	1993–94 to 95–96	44.9	51.7	3.4	Hull (1999)

Prey preferences

A greater variety of species was observed in the diet as the proportion of *Euphausia superba* declined. In years of very low *E. superba* (e.g. 1994, 2009) diet diversity was very high (Table 1). Macaroni penguins have previously been described as 'prey switchers' based on observations that they mainly feed on euphausiids but can feed on other prey when euphausiids are scarce (Croxall et al. 1999). Technically, the term 'prey switching' describes a tendency for predators to preferentially consume common prey types disproportionately more than less common prey types (Murdoch 1969). The term is usually applied to individual predators and is associated with a sigmoidal (type III) functional response, in which the predator's intake of a single prey type is disproportionately low at low densities, but increases rapidly to saturation as density increases (Holling 1959). Our analysis shows that the majority of individual diets were dominated by euphausiids, and there were 4 years in which every observed diet was euphausiid-dominated. This suggests that all individual macaroni penguins at Bird Island were euphausiid specialists under favourable conditions. When conditions were less favourable, mixed diets were most common, but diets dominated by non-euphausiid prey (fish or amphipods) still accounted for 15% of all observations. Macaroni penguins are capable of feeding on a variety of prey types during a foraging trip. Nonetheless, they generally forage in areas where aggregations of euphausiids occur predictably (Trathan et al. 2006, Waluda et al. 2010), and their non-euphausiid prey also tend to form aggregations. This tendency to feed on aggregated prey could, in itself, explain the high frequency of single-prey-type-dominated diets. We were unable to formally test the hypothesis that macaroni penguins are prey switchers by the above definition, but it is clear that they generally specialise on a single prey type during a trip. This provides some evidence for a sigmoidal functional response and a clear indication that their diets are not linear reflections of the relative density of different prey types in their foraging habitat. Cury et al. (2011) did not include this type of functional response in the analysis leading to their proposed ecosystem-based management reference point to account for the feeding requirements of seabirds. We suggest that sigmoidal functional responses should be included in such analyses.

Inter-annual variability in diets

In years in which there was a lower proportion of *Euphausia superba* in the diet, a corresponding increase in the frequency of *Themisto gaudichaudii* was observed. It is not clear whether this reflects the relative abundance of the 2 species in the local ecosystem or is an artefact of the population variability in *E. superba* described above. It is possible that this apparent switch could be related to the influx of different prey types caused by oceanographic variability, with *T. gaudichaudii* replacing *E. superba* in the environment close to South Georgia. This is linked to the location of the Southern Antarctic Circumpolar Front (SACCF) with warm (*T. gaudichaudii, Krefftichthys anderssoni*) and cold water (*E. superba, Electrona carlsbergi*) assemblages occurring to the north and south respectively of the SACCF between the South Orkneys and South Georgia (Ward et al. 2012). There is evidence of co-occurrence of these 'warm' and 'cold' water species in the diet of penguins. A total of 80 diet samples contained *K. anderssoni* of which 64 (80%) also contained *T. gaudichaudii*, and all 8 diet samples containing *E. carlsbergi* also contained *E. superba*. Oceanographic variability has been linked with prey diversity in the diets of *Eudyptes* spp. penguins at Marion Island (Brown et al. 1990), and have been suggested as a driver of prey variability in seabird diets in a variety of ecosystems elsewhere (Frederiksen et al. 2007, Montevecchi 2007, Springer et al. 2007, Thayer & Sydeman 2007).

Dietary influences on fledging mass

We used fledging mass as an indicator of the net benefits of foraging. Our results show that these net benefits are more strongly related to the energy content of euphausiids in the diet than to *Euphausia superba* in particular or the total energy content of all prey in general. The latter is a description of the gross benefits of foraging, but our results suggest that the costs per unit energy vary between prey types. One of the major costs is the time taken to locate prey. Macaroni penguin foraging trip duration (mean ± SD) can vary between 5 ± 4 and 24 ± 16 h during the crèche period, with penguins making longer trips or travelling a greater maximum distance from the colony during years of reduced *E. superba* availability (Trathan et al. 2006). There is an energy cost associated with pursuing and subduing prey, which tends to increase with prey size and mobility. There are also costs associated with digestion. Indeed, not all of the energy content of prey is available to the predator as some of it is associated with indigestible structures such as chitin. Fig. 7 shows that net benefits were lowest in 1994 and 2009 even though the gross energy content was above average in 2009. The majority of the gross energy came from amphipods in these years. 2004 was also characterised by above-average gross energy, in this case derived mainly from fish, and below average net benefits. It appears that the costs to a macaroni penguin of a unit of energy are generally higher for amphipods and fish than they are for euphausiids. Despite the lack of available information on costs, the high correlation between the modelled and observed values for fledging weights indicates the strong dependence of macaroni penguin reproductive output on the availability of euphausiids.

CONCLUSIONS

This study confirms that at South Georgia, crustaceans, particularly *Euphausia superba*, are the most important component of the diet of macaroni penguins, although the amount of *E. superba* can be very variable from year to year. The entire suite of land-based predator species monitored at Bird Island (macaroni and gentoo penguins, black-browed albatrosses and Antarctic fur seals) as part of CEMP are often described as 'krill-dependent predators' (Croxall & Prince 1987, Veit et al. 1993, Reid et al. 1999a). None of the Bird Island species is an obligate euphausiid feeder (Reid & Arnould 1996, Croxall et al. 1997, 1999). While euphausiids make up a greater proportion of the macaroni penguin diet than that of other species at Bird Island (Croxall et al. 1997, 1999), they are unimportant in the diets of some macaroni penguin populations elsewhere (Croxall & Furse 1980, Green et al. 1998) and in the closely related royal penguins at Macquarie Island (Horne 1985, Hindell 1988, Hull 1999). At Bird Island, however, our results support the characterisation of the macaroni penguin population as 'krill dependent'. Fledging mass is strongly dependent on the euphausiid component of the diet; this dependence appears to relate to the availability of euphausiids in general rather than *E. superba* in particular. Although macaroni penguins were capable of feeding on alternative prey, fledging weight was below average in all 4 years in which euphausiids composed less than half of the diet. We do not have any data on post-fledging mortality, but it is likely that the fitness of a fledgling is positively related to its weight (Van Heezik & Davis 1990, Olsson 1997, Moreno et al. 1999, McClung et al. 2004). This raises the possibility that macaroni penguins might commit the Concorde fallacy (Dawkins & Carlisle 1976) when *E. superba* is scarce: that is, foraging to feed an underweight offspring might reduce the parent's fitness compared to foraging to feed itself. The dependence of individual fitness on the availability of euphausiids also supports the hypothesis that localised specialisation on euphausiids has enabled macaroni penguins to become the most numerous avian predator on Bird Island (Barlow et al. 2002, Trathan et al. 2012), and consequently euphausiid availability is the main factor limiting population size. There is substantial uncertainty about the future availability of *E. superba* with some studies suggesting that climate change could cause a catastrophic decline (e.g. Murphy et al. 2007b). Our results, and those of Hill et al. (2012), suggest that macaroni penguins at South Georgia would be particularly vulnerable to such a decline.

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