Prey-field use by a Southern Ocean top predator: enhanced understanding using integrated datasets

Merel Bedford[1,2,*], Jessica Melbourne-Thomas[2,3], Stuart Corney[2], Toby Jarvis[3,4], Natalie Kelly[3,5], Andrew Constable[2,3]

[1]Institute for Marine and Antarctic Studies, University of Tasmania, Private Bag 129, Hobart, Tasmania 7000, Australia

[2]Antarctic Climate and Ecosystems Cooperative Research Centre, University of Tasmania, Private Bag 80, Hobart, Tasmania 7000, Australia

[3]Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia

[4]Echoview Software Pty. Ltd., GPO Box 1327, Hobart, Tasmania 7001, Australia

[5]CSIRO Computational Informatics and Wealth from Oceans Flagship, GPO Box 1538, Hobart, Tasmania 7001, Australia

ABSTRACT: An important challenge for understanding and managing marine ecosystems is determining the relationship between the distributions of prey species and the foraging of top predators. We examined the diet and foraging dynamics of breeding macaroni penguins *Eudyptes chrysolophus* from sub-Antarctic Heard Island and related these to prey distributions derived from active-acoustics and net-derived data in the foraging zone of the penguins. Consistent with previous findings, we found that penguin diets changed between the guard and crèche stages of the breeding cycle and that this change in diet corresponded with a switch from short foraging trips in the guard stage to significantly longer, offshore foraging trips in the crèche stage. We related these differences in diet and foraging to characteristics of the prey field — specifically, a relatively uniform distribution of krill over the shelf and in deeper, offshore waters, compared with an increasing abundance of fish further from shore. We developed a simple dynamic energy budget for macaroni penguins to explore whether targeting fish during the crèche stage was an energetically favourable strategy. Finally, we extrapolated our energy budget to estimate prey consumption at the colony scale as previous work has suggested that depletion near breeding colonies could contribute to prey switching. We found that prey switching during the crèche stage was energetically favourable and was most likely related to a reduction in foraging constraints, rather than prey depletion. This study shows the value of integrating data sets to address questions surrounding variation in diet and the use of alternative prey by marine predators.

KEY WORDS: Prey-specific foraging · Prey switching · Prey-field characteristics · Prey depletion · Ecosystem function · Active-acoustics · Macaroni penguins

INTRODUCTION

Understanding and predicting the response of food webs to climate-driven habitat change requires knowledge of the linkages between the distribution and abundance of prey species and the foraging behaviour and diets of predator species. In the Southern Ocean, these dynamics are further complicated by the recovery of seal and whale populations from industrial harvesting in the 18th to 20th centuries. Technological advances — particularly in biologging, acoustics and molecular analyses of diets — have resulted in significant progress in understanding predator diets and habitat use as well as prey population dynamics. For example, advances in molecular techniques have provided a much clearer picture of

predator diets (e.g. Deagle et al. 2007, Hückstädt et al. 2012, Jarman et al. 2013) and helped resolve key foraging locations (Quillfeldt et al. 2005, Cherel et al. 2007). In addition, recent studies of a range of Southern Ocean predator species have provided insights into the associations that the foraging of these species have with physical habitat variables and features such as bathymetry, frontal zones, sea ice and mesoscale eddies (Field et al. 2001, Bailleul et al. 2007, 2010, Bost et al. 2009, Hindell et al. 2011). Data are now becoming available that can address questions of predator-prey overlap, including variability in this overlap, and how the success of predator foraging strategies may be determined by access to sufficient high-value prey at critical times.

Studies of foraging behaviour and diets of marine mammals and birds are well advanced around the world, showing variability between individuals, and populations, in space and time (e.g. Bradshaw et al. 2004, Green et al. 2005, Hindell et al. 2011). In terms of prey species, active-acoustic technology (Bertrand et al. 2004) now provides a cost-effective means to characterise the distribution and relative abundance of pelagic taxa at a variety of scales (Kloser et al. 2009, Godø et al. 2012), allowing the availability to predators to be determined. Acoustic sampling has particular advantages in regions such as the Southern Ocean because of the expense associated with direct sampling in isolated environments and the potential to deploy acoustic sensors on fishing vessels and other 'ships of opportunity'. Limitations of acoustic sampling, particularly regarding identifying taxa (Horne 2000), can be supplemented by direct sampling using nets (Kloser et al. 2009, Oozeki et al. 2012 and references therein). Importantly, biases in different methods are better addressed through a combination of techniques (Kloser et al. 2009).

Despite these advances in observing and understanding predator and prey species in the Southern Ocean, the connection between predator foraging and prey-field dynamics in this region is still poorly characterised (Barlow & Croxall 2002b, Trathan et al. 2006). Very few studies have estimated direct links between the foraging behaviour of marine predators and the spatial and temporal characteristics of their prey-fields (Zamon et al. 1996, Cresswell et al. 2012, Sigler et al. 2012, Benoit-Bird et al. 2013) or assessed how predator-prey overlap may impact on the performance of predators.

It remains unclear how top predators in the Southern Ocean exploit prey fields and — for central-place foragers that are constrained to colonies during breeding (e.g. penguins) — how their foraging behaviour is shaped by limitations imposed during the breeding season. Key questions include the following: How do the physical cues to which these animals seem to respond (e.g. different water masses; Field et al. 2001) relate to the distribution of target prey species? How does the target prey distribution change over the course of the breeding cycle? Are predator diets constrained by the availability of prey species in different habitats (that may differ in accessibility)? Alternatively, are prey potentially targeted depending on specific nutritional requirements? What are the consequences of competition for prey in cases in which multiple predator species may have overlapping foraging ranges, such as around sub-Antarctic islands? Several studies have suggested that prey fields may in fact become depleted during breeding seasons around sub-Antarctic islands (Moore et al. 1999, Barlow & Croxall 2002a, Hindell et al. 2011). Answers to these questions are important in informing responses of food webs to changes in habitats and in spatial and temporal patterns of productivity under climate change (Constable et al. 2014). They are also important in considering interactions between predators and fisheries that may target the same species. In this article, we address some of these questions using macaroni penguins *Eudyptes chrysolophus* at sub-Antarctic Heard Island as a case study based on data from an integrated ecosystem study, the 2003–2004 Heard Island Predator-Prey Investigation and Ecosystem Study (HIPPIES; Gales et al. 2006, Deagle et al. 2007, 2008, Frydman & Gales 2007, van Wijk et al. 2010). Heard Island rises from the Kerguelen Plateau, which forms the largest topographical barrier to the Antarctic Circumpolar Current. This is an area of high biological productivity (van Wijk et al. 2010) and provides breeding habitat for a number of land-based predator species, including 4 penguin and 2 seal species on Heard Island (Woehler 2006).

Macaroni penguins are the most abundant penguin species breeding on Heard Island, with an estimated population of >1 million breeding pairs (Woehler & Green 1992, Woehler 2006). They have several breeding locations on the island, one of which is the colony on Capsize Beach (53.162° E, 73.642° S; Fig. 1). This colony consists of approximately 50 000 breeding pairs (Deagle et al. 2008), made up of a number of smaller sub-colonies (Trebilco 2004). Macaroni penguins have 2 distinct stages within their breeding cycle: the guard and the crèche stage. During the guard stage, male penguins stay ashore while female penguins feed, returning regularly to the colony to feed their chicks. During the crèche stage, both
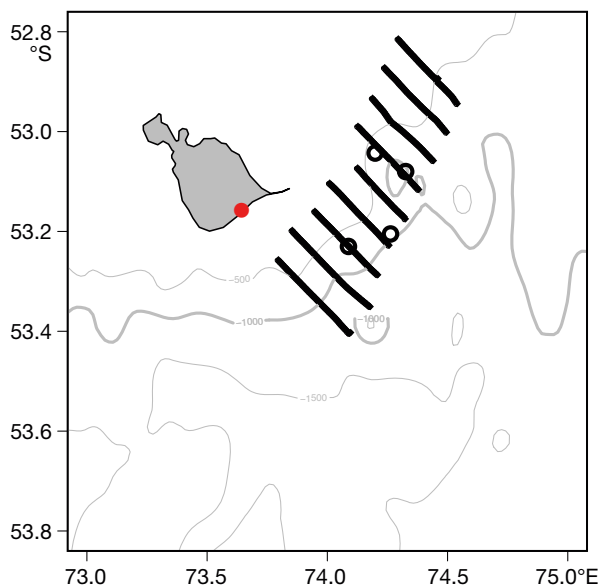
Fig. 1. Locations of the acoustic transects (thick black lines) and 4 net haul stations (circles) southeast of Heard Island. Grey isolines: bathymetry at 500 m intervals with the edge of the shelf at 1000 m depth indicated by the thicker line. Red dot: location of Capsize Beach

males and females forage as the chicks can be left alone for longer periods (Barlow & Croxall 2002b, Trathan et al. 2006).

Macaroni penguins are a useful test case for considering questions regarding prey-field use for several reasons: they are abundant and relatively easy to study; they travel relatively small distances on foraging trips (which constrains the required area for sampling the prey field); and studies of macaroni penguin foraging and energetics have been conducted in other regions of the Southern Ocean (e.g. Brown 1987, Barlow & Croxall 2002b, Green et al. 2002, 2003, Trathan et al. 2006), thus providing opportunities for regional comparisons.

Through this case study, we aim to:

(1) Determine the relationship between prey consumption (diet) in selected foraging areas of macaroni penguins and the availability of prey in these areas;

(2) Characterise spatial patterns in foraging trips of macaroni penguins during the guard and crèche stages of their breeding cycles;

(3) Evaluate whether differences in foraging strategies between guard and crèche stages meet with expectations from analyses of energetic requirements (including the potential of prey depletion) by developing energy budgets (Brown 1987, Kooijman 2012) for this colony.

METHODS

Diet and tracking data were obtained for macaroni penguins from a sub-colony on Capsize Beach at Heard Island (Fig. 1) to characterise foraging behaviour and diets during different stages of the breeding cycle. The foraging zone, which was located to the southeast of the island, was determined in near-real-time during the voyage from the tracking data, using HeardMap (Frydman & Gales 2007). The foraging zone comprised both shelf habitat (defined here as <1000 m depth, following Green et al. 1998) and deeper offshore areas further to the southeast. The prey field was assessed in the penguin foraging zone using active-acoustics (echosounder) and trawl nets (Fig. 1) as well as in the area to the northeast. The data were used to characterize and map zooplankton and pelagic fish distributions in key foraging areas around Heard Island.

Data used in this study were accessed via requests to the Australian Antarctic Data Centre (AADC; https://data.aad.gov.au/); raw data were collected at sea and on land during the HIPPIES cruise (RV 'Aurora Australis') in December 2003 to February 2004. Much of the initial processing of predator diet and foraging data was undertaken during the voyage and has been previously reported (e.g. Deagle et al. 2007, 2008, van Wijk et al. 2010). Relevant collection methods are summarised in Table 1. Here, we provide details on specific methods used, including detailed analyses of the active-acoustic data, and the development of simple energy budgets (Brown 1987, Kooijman 2012).

Diet

Diet data (biomass, g) were combined to form 4 groups: fish, krill, amphipods and squid. Percentages of each component were calculated for the overall diet for each of the guard and crèche stages. As per Deagle et al. (2007), unidentified materials were assumed to have the same proportional composition as the remaining sample. Similarities between samples from different breeding stages were visualised using non-metric multidimensional scaling (MDS) in PRIMER (Clarke & Gorley 2006).

Foraging

For the purpose of the HIPPIES project, only female birds were targeted for both the diet samples and

Table 1. Summary and references for data collection techniques applied during HIPPIES. For locations of prey-field data collection, refer to Fig. 1. –: unpublished data collected on the 2003–2004 HIPPIES cruise

Data type	Summary	Date of collection (dd/mm/yyyy)	Source
Predator diet	69 stomach samples collected (53 successful) using water-offloading technique	02/12/2003–03/02/2004	Deagle et al. (2007)
Predator foraging	106 birds tracked using Kiwisat Platform Terminal Transmitters	02/12/2003–03/02/2004	Trebilco (2004), Deagle et al. (2008)
Prey-field: acoustics	9 transects — 12, 38, 120 and 200 kHz — using a Simrad EK60 scientific echosounder system	31/12/2003–05/01/2004	–
Prey-field: nets	12 net hauls in each of 4 sampling stations using RMT-8 and IYGPT nets	31/12/2003–05/01/2004	–

tagging (Deagle et al. 2008), allowing for direct comparison between stages of the breeding cycle. We filtered the track data to remove noise from the tracks using the R (R Core Team 2014) package 'argosfilter' (Freitas 2012). We set the maximum speed at 15 km h^{-1}, following filtering methods of tracks by Frydman & Gales (2007) and Deagle et al. (2008). Individual track durations were determined by comparison of start and finishing times, and track distances were calculated with the R package 'trip' (Sumner 2012). In line with several previous studies (e.g. Barlow & Croxall 2002b, Trathan et al. 2006), tracks were removed if they represented cases where penguins (1) undertook abnormally long foraging trips (>5 d or >250 km in the guard stage; >16 d or >1300 km in the crèche stage), (2) travelled over land or returned to a different colony or (3) made very short foraging trips (<15 km), which would not add valuable information on pelagic habitat use.

We assume that this filtering process removed all non-breeders and birds that may have abandoned breeding. Based on descriptions of the tagging procedure and track analyses by Deagle et al. (2008), all tracks from the guard stage were identified as those from female penguins, and our filtering process removed any male tracks from the crèche stage. The remaining tracks were visualised using 2-dimensional kernel density plots generated with the 'smoothScatter' function from the R package 'lattice' (Sakar 2008), using the default values for the package. Areas for kernel densities were calculated using the R package 'raster' (Hijmans 2013).

Prey field

The prey field was sampled via acoustic transects and net hauls (Fig. 1) between 31 December 2003 and 5 January 2004. Active-acoustic data were collected at nominal frequencies of 12, 38, 120 and 200 kHz using a Simrad EK60 scientific echosounder system (Simrad 2001), calibrated in North West Bay, Tasmania, Australia (45.072° S, 147.309° E) in September 2003. Four transducers were mounted in sea chests in the forward part of the ship's hull and oriented to transmit pulses of sound (pings) vertically down into the water column. The 12 kHz data were used solely for seafloor detection and ranging, and the 38, 120 and 200 kHz data for describing and classifying the pelagic biota. For the 38, 120 and 200 kHz channels, samples of received echo power (P_r in dB re 1 W, indexed by date, time and geographic position) were logged every 3 to 8 m alongtrack and every 0.19 m from the face of each transducer to a range of 1000 m. The nominal vessel speed for data collection on each transect was 10 knots (19 km h^{-1}); in practice, samples were collected over a range of vessel speeds from ~6 to ~15 knots (11 to 28 km h^{-1}).

The acoustic data was processed using Echoview v4. The raw P_r measurements were converted to (mean) volume scattering strength (S_v in dB re 1 m^2 m^{-3}, see MacLennan et al. 2002 and Table A1 of Jarvis et al. 2010 for further details) by accounting for transmission loss, the acoustic properties of the water column (which relate to temperature and salinity) and the properties of the echosounder system (determined from calibration experiments). Unwanted data were filtered out, including off-transect periods, near-surface noise (15 to 40 m depth, weather dependent), seafloor echoes, background and intermittent noise and samples beyond the nominal maximum range of the echosounder (1000, 250 and 100 m depth for the 38, 120 and 200 kHz data, respectively). For the acoustic transects, the 120 kHz frequency (with a wavelength of 12 mm and a nominal effective range of 250 m) was chosen as the best single fre-

quency for identifying acoustic signals from epipelagic biota.

The filtered S_v samples were resampled into discrete horizontal and vertical bins (mean S_v in 15-ping along-track by 2 m depth bins), and partitioned (classified) into biologically meaningful categories (hereafter 'acoustic taxa') based on their relative frequency response (Table 2, after Korneliussen & Ona 2003). Three acoustic taxa were identified — fish, small zooplankton (e.g. copepods) and large zooplankton (e.g. krill) — noting that there are no reliable frequency-difference models for these categories in the Heard Island area.

The backscatter values of the classified bins at 120 kHz were converted from S_v to nautical-area scattering coefficient (NASC or s_A in m^2 n mile^{-2}, see MacLennan et al. 2002). S_v is a volumetric acoustic density measurement that relates to individuals per cubic metre; NASC (hereafter 'acoustic biomass') is a real acoustic density measurement for a column of water of specified height that relates to individuals per square nautical mile. Note that the relationship between acoustic biomass and true biomass is not straightforward, and we have assumed that acoustic biomass reflects the general pattern of true biomass over space and time.

The acoustic biomass of each acoustic taxon was averaged over 500 m along-track intervals and summed over 0 to 100 m depth to provide measures of distribution and relative abundance for each prey group within the nominal diving range of macaroni penguins (<100 m; based on Green et al. 1998). Acoustic biomass values were log-normalised to account for some zero-inflation behaviour, and $\log(Y + 1)$ was applied for the zero values.

In each of the 4 sampling stations (Fig. 1), 12 net hauls were performed using RMT-8 (Rectangular Midwater Trawl) and IYGPT (International Young

Table 2. The multifrequency algorithms used to classify S_v bins into biologically meaningful categories (acoustic taxa), based on Korneliussen & Ona (2003)

Algorithm	Acoustic taxon
$S_{v, 120 - 38kHz} < 0$ dB	Fish
$S_{v, 120 - 38kHz} > 0$ dB	Zooplankton (e.g. copepods and krill)
$S_{v, 120 - 38kHz} > 0$ dB and $S_{v, 200 - 38kHz} > 0$ dB	Small zooplankton (e.g. copepods)
$S_{v, 120 - 38kHz} > 0$ dB and $S_{v, 200 - 38kHz} < 0$ dB	Large zooplankton (e.g. krill)

Gadoid Pelagic Trawl) nets for zooplankton and fish, respectively, at 0–100, 100–300 and 300–600 m depths. Two of the locations were over seafloor depths of 500 to 700 m; the other 2 were over seafloor depths of 900 to 1300 m. Data from the 0 to 100 m samples were used for the analyses of net-hauls, corresponding with data from the acoustics and published penguin diving depths. The data were combined to form 4 classes: zooplankton (predominantly krill and copepods), fish, jellyfish and squid. MDS and PERMANOVA (Anderson et al. 2008) were used to visualise and analyse differences between net hauls at different depths and locations.

Both day- and night-time acoustic transects and net hauls were performed during the HIPPIES cruise. Due to weather conditions, however, night-time samples were limited in number and clustered in space (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m526p169_supp.pdf). Samples were therefore not filtered by time of day to preserve a robust sample size. We have consequently not considered diurnal variability in prey availability and thus assumed that all sampled prey are available to the penguins. Bedford (2013) provides a more detailed treatment of diurnal patterns from acoustic transects. We note that the collection of active-acoustic and net-derived data during the HIPPIES cruise was undertaken over a short period (5 d) during the guard stage. Consequently, we have assumed that the acoustic biomass of biota in the sampling period is indicative of the availability of prey throughout the entire study period.

Energetics

To assess whether foraging strategies of macaroni penguins during different breeding stages were in accordance with expectations based on energetic requirements, we developed simple dynamic energy budgets (Brown 1987, Kooijman 2012), based on energy content of prey, energy requirements of chicks and energy expended by adults while foraging and at rest. We calculated energy budgets for male and female penguins, for a breeding pair (with a chick) and for the colony. We used results from the stomach samples in combination with published information to develop these models.

Energy densities (per g wet weight) of prey were determined from literature values, based on the species identified in stomach samples (Deagle et al. 2007) of the macaroni penguins. For krill, we used published energy densities for *Thysanoessa* spp.:

3.79 kJ g^{-1} (range: 2.30 to 5.04 kJ g^{-1}; Mårtensson et al. 1994, 1996, Torres et al. 1994). The energy density of amphipods (*Themisto* spp.) was estimated at 3.52 kJ g^{-1} (Whitman 2010) and that of squid at 3.64 kJ g^{-1} (Croxall & Prince 1982, van Pelt et al. 1997). Published energy densities for fish varied widely depending on species and locations (Clarke 1980, Clarke & Prince 1980, Lea et al. 2002, Tierney et al. 2002). We used energy densities for *Krefftichthys anderssoni* (97% of fish portion in diet samples) as published by Tierney et al. (2002) from sub-Antarctic Macquarie Island and those for *Electrona antarctica*, *E. carlsbergi*, *Gymnoscopelus nicholsi* and *G. fraseri* (combined 3% of fish portion in diet samples) as published by Lea et al. (2002), for a weighted average of 8.42 kJ g^{-1}. These values were used to calculate the average energy density of penguin diets for the guard and crèche stages, using the prey proportions from the diet samples.

The energy expenditure of macaroni penguin chicks was calculated based on an energy budget developed by Brown (1987). Differences between lengths of the breeding seasons at Marion Island (70 d) and Heard Island (60 d) required adjustment of the original budget. We assumed that the total energy expenditure of the chick was equal to that reported by Brown (1987). This budget covers all energy requirements including the demand on the parents for feeding the chicks (Green et al. 2007). No weighing of chicks was done during the 2003–2004 season; thus, the rate of growth for chicks was based on Brown (1987), with a mean weight at birth of 106 g and at fledging of 2.5 kg.

The energy expenditure of adult macaroni penguins was calculated using published average daily metabolic rates (ADMRs) for activities based on shore and at sea, during both the guard and crèche stages (Green et al. 2002). The daily metabolic rate (MR) of fasting males in the guard stage was based on data published by Davis et al. (1989). All values were converted from W kg^{-1} to kJ d^{-1}, assuming an average individual mass of 4.5 kg and 3.9 kg for male and female penguins, respectively (from Croxall et al. 1984, Davis et al. 1989, Green et al. 2002, 2007). These values were used to calculate energy requirements for foraging, resting on shore and fasting over selected time periods. The ratio of time spent at sea and on shore during guard and crèche stages was based on Barlow & Croxall (2002b) and lies within the ranges reported by Green et al. (2002, 2003). The total estimated energy expenditure of male macaroni penguins from the guard stage was added to expenditure during the crèche stage, on the assumption that lost bodyweight is regained by the completion of the breeding season, as per Green et al. (2007).

To complete the energy budget for a breeding pair, energy requirements of both the parents and the chick were converted to food consumption requirements, using assimilation efficiencies of 73% for adults (Brown 1987) and 76% for chicks (Green et al. 1998). A final energy budget was created for food consumption by the 50 000 breeding pairs (Deagle et al. 2008) in the study colony, each consisting of a male, female and a chick. This value is necessarily an underestimate of the total requirements of the colony because it does not include non-breeding penguins (e.g. those who have not yet reached sexual maturity). The proportion of non-breeding macaroni penguins in the study colony may constitute a significant proportion. To the best of our knowledge, however, this is yet to be quantified (see also Trebilco 2004).

Impacts on prey

To gain a coarse understanding of the potential impact of foraging by macaroni penguins on prey biomasses within the penguins' prey field, we compared estimates of required food during the guard and crèche stages with available data on prey densities within the region. Acoustic data collected during the cruise were not sufficient to obtain a true estimate of biomass for the study area; hence, we used values published by Pruvost et al. (2005) for the Kerguelen Plateau region. Specifically, we calculated the area of the penguins' 'core' foraging area during each stage (the area in which the kernel density was >0.8; ~3000 km^2 and ~5300 km^2 in the guard and crèche stage, respectively) for calculations of prey biomasses from densities reported for zooplankton (krill and amphipods) and fish.

RESULTS

Diet

Stomach contents of the 53 penguins included in our analyses (Table 1) had a mean mass of 75 g (SD: ± 51.2 g), with a range of 12 to 216 g. There was no significant difference (p = 0.44) between the mass of the samples taken in the guard (n = 35) and crèche stage (n = 18). Overall, krill were the dominant prey species by mass (69%), and fish made up 22% of the samples, with the remainder being amphipods (8%) and squid (<1%). Specifics on the analyses of the
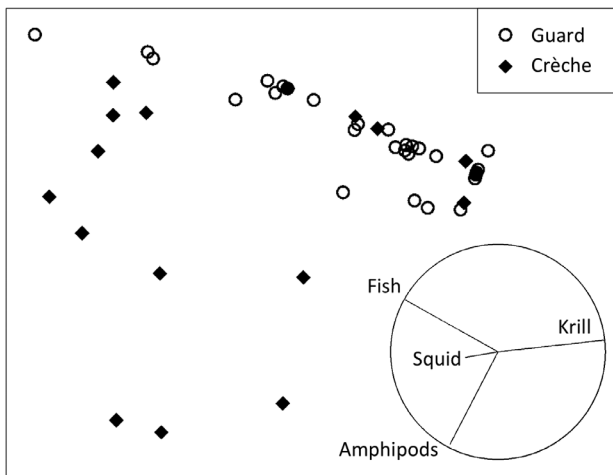
Fig. 2. Multidimensional scaling ordination (MDS) plot, with Bray Curtis similarities showing comparison of macaroni penguin diet composition (square root transformed) between the guard (O) and crèche (♦) stages. The vector overlay shows Pearson's correlations of response variables with the ordination axes. 2D stress = 0.03

stomach samples to species level can be found in Deagle et al. (2007).

PERMANOVA indicated a statistically significant difference in the composition and variability of the diet of macaroni penguins between the 2 stages (Pseudo-$F_{1,51}$ = 12.518, P(perm) < 0.002; PERMDISP $F_{1,51}$= 17.438, p < 0.002, Fig. 2). During the guard stage, krill made up the main component (83%) of the penguins' diet by mass, complemented by fish (16%). In the crèche stage, the diet was more varied: penguins continued to consume krill (43%), while fish provided a much larger proportion of the diet (33%), and amphipods increased from close to 0% to 23%. The percentage of squid in the diets of the macaroni penguins was minimal in both the guard and crèche stage (0.04 and 0.72%, respectively).

Foraging

After filtering, 51 tracks remained for the guard stage and 11 for the crèche stage. Based on analyses of foraging tracks, we defined the transition from

guard to crèche stage as occurring on 13 January. After filtering, the 2 longest tracks of the breeding season started on 13 and 15 January and were therefore classified as crèche stage tracks. This is consistent with previous studies, based on visual observations (Trebilco 2004, Deagle et al. 2008). Analyses of filtered tracks showed a significant difference in trip durations and the distances travelled by female macaroni penguins between the guard and crèche stages ($F_{50,10}$ = 0.012, p < 0.001; $F_{50,10}$ = 0.013, p < 0.001 respectively; Table 3, Fig. 3). Frequency of observations of macaroni penguins was higher on the shelf during the guard stage compared to the crèche stage (p < 0.005; 57.9 and 14.71%, respectively).

Prey field

Using data collected with the 120 kHz echosounder, and a frequency-difference algorithm using data from the 38, 120 and 200 kHz frequencies (Table 2), acoustic biomass (NASC) was estimated for fish, small zooplankton (e.g. copepods) and large zooplankton (e.g. krill) in the top 100 m of the water column over varying seafloor depths (Fig. 4A). Zooplankton were found everywhere at relatively low densities. Small zooplankton had greater acoustic biomass over the full range of seafloor depths (Fig. 4B) compared to large zooplankton (p < 0.001; Fig. 4C). Fish had lower mean acoustic biomass over shallower waters, but this increased over deeper seafloor depths (Fig. 4D). The patterns of acoustic biomass of zooplankton and fish were reasonably consistent across replicate transects.

Net hauls over deep waters revealed an abundance of both zooplankton and fish. On the shelf, zooplankton and squid were abundant, but fish were found in relatively small numbers. This is consistent with the results of the acoustic survey. In contrast, a PERMANOVA of the net hauls indicated no significant difference between the composition of catches at different locations (Pseudo-$F_{2,39}$ = 0.98, P(perm) = 0.45, Fig. 5). This result is related to the unbalanced design of the net haul sampling; however, the Pearson correlation overlay in Fig. 5 indicates that fish were more abundant in net

Table 3. Foraging dynamics of macaroni penguins during the breeding season (values adjusted to 3 significant figures)

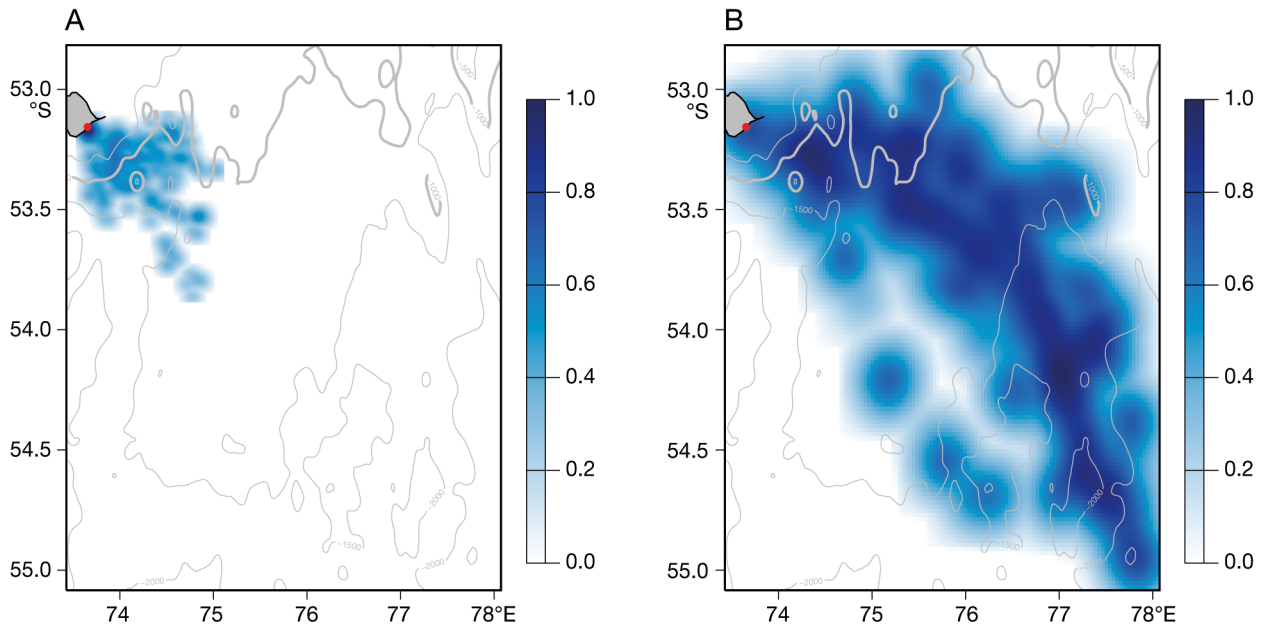| | Guard (n = 51) | | | Crèche (n = 11) | | | F | p |
	Mean ± SE	Min.	Max.	Mean ± SE	Min.	Max.		
Foraging duration (d)	1.51 ± 0.09	0.04	2.76	7.70 ± 1.75	1.17	15.4	0.01	< 0.001
Foraging distance (km)	109 ± 7.21	17.5	237	660 ± 140	81.6	1300	0.01	< 0.001

Fig. 3. Two-dimensional kernel density plots of Argos foraging tracks from macaroni penguins originating from Capsize Beach (red dot) in the (A) guard and (B) crèche stages. Grey isolines: bathymetry at 500 m intervals with the edge of the shelf at 1000 m depth indicated by the thicker line
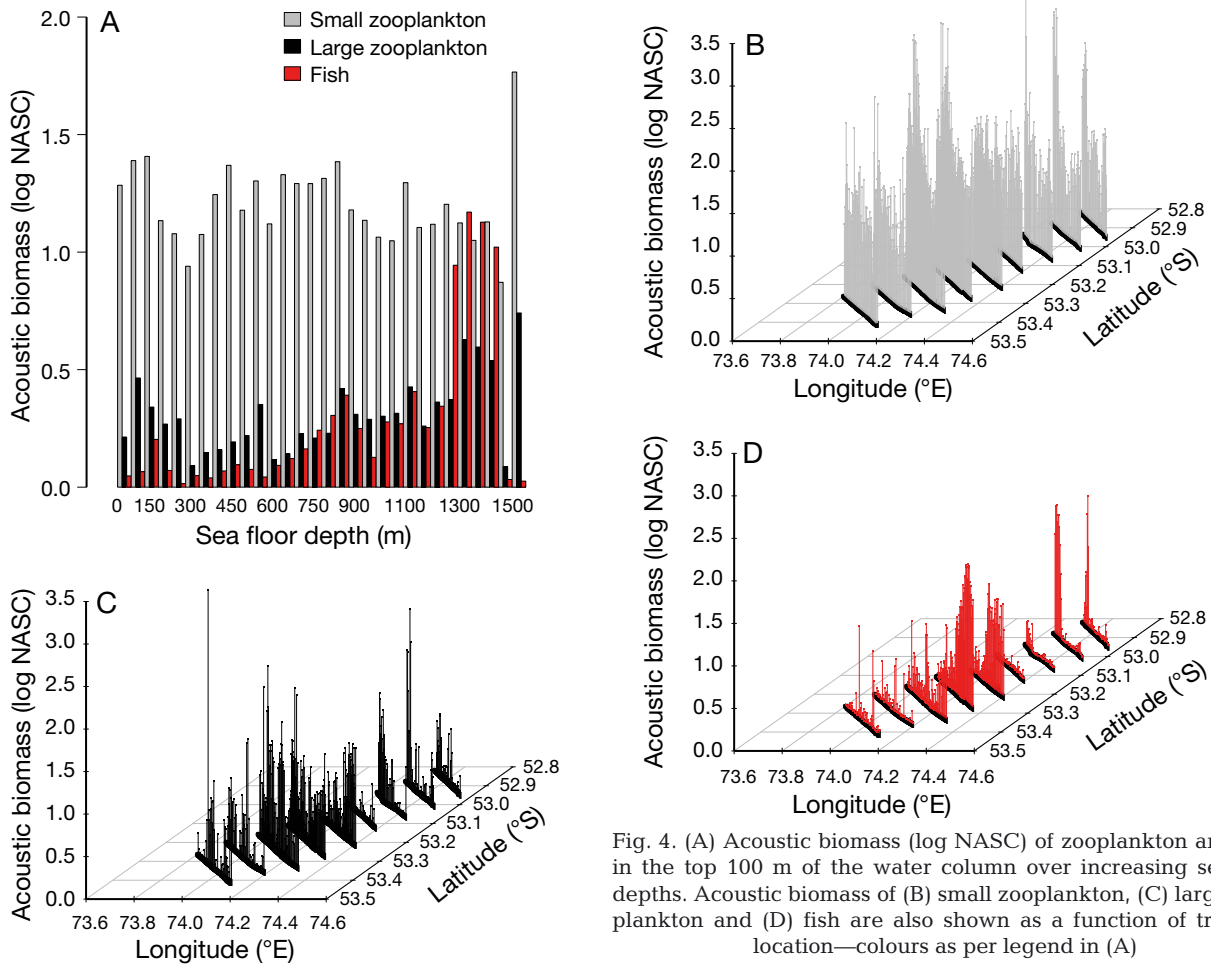

Fig. 4. (A) Acoustic biomass (log NASC) of zooplankton and fish in the top 100 m of the water column over increasing seafloor depths. Acoustic biomass of (B) small zooplankton, (C) large zooplankton and (D) fish are also shown as a function of transect location—colours as per legend in (A)
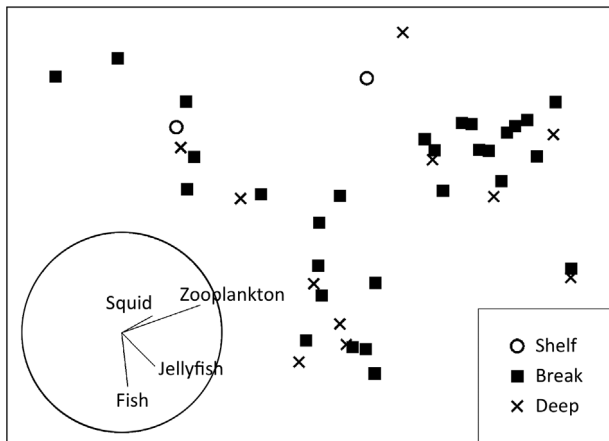
Fig. 5. Multidimensional scaling ordination of Bray Curtis similarities between net hauls (square root transformed) over the shelf, shelf-break and deep waters. The vector overlay shows Pearson's correlations of response variables with the ordination axes. 2D stress = 0.08

hauls conducted over the shelf break and in deeper waters than in the hauls conducted over the shelf.

Because of the southwest to northeast axis of the sampling design, the south-eastern portion of the core foraging area was not sampled. We assumed that the pattern of higher fish abundances in deeper waters extended to the southeast in the area not sampled. Higher abundances of fish in deeper waters have been reported around nearby Marion Island (Perissinotto & McQuaid 1992), supporting our assumption.

Energetics

Calculated energy densities, based on the average proportions of different prey types in stomach sam-

ples collected during the guard and crèche stages, were 4.54 kJ g^{-1} and 5.27 kJ g^{-1} in the guard and crèche stage respectively (Table 4). During the guard stage, the largest mean contribution to energy density of the diet came from krill (70%), whereas during the crèche stage, this was replaced by fish (53%; Table 4).

The energy requirements of chicks change throughout the breeding period (Fig. 6; see also Brown 1987). For the first 18 d (at Heard Island), there is a rapid increase in energy required. This plateaus during the crèche stage to a peak in energy requirement at 42 d, before decreasing in preparation for fledging.

The converted ADMRs for adult penguins indicated that during the guard stage, the fasting MR of males was 1480 kJ d^{-1}, while the females had an ADMR of 2070 kJ d^{-1} on shore and 3010 kJ d^{-1} at sea. During the crèche stage, males had an ADMR of 2480 kJ d^{-1} on shore and 3530 kJ d^{-1} at sea, while the females had an ADMR of 2150 kJ d^{-1} on shore and 3060 kJ d^{-1} at sea. Throughout the duration of the guard and crèche stages, female macaroni penguins require approximately 2680 kJ d^{-1} and 2560 kJ d^{-1} respectively, and males require 3970 kJ d^{-1} in the crèche stage only (see Table S1 in the Supplement). The difference in energy requirements between male and female penguins during the crèche stage was predominantly due to the need by males to regain body mass lost while fasting in the guard stage.

The calculated energy budget (Table 5), using energy densities per meal, indicates that to sustain themselves and their chicks in the guard stage, females need to consume an average of 960 g of prey per day, of which approximately 150 g is provided to the chick. In the crèche stage, the females and males

Table 4. Energy density for a typical macaroni penguin diet during the guard and crèche stages of the breeding season, based on the proportions of diet components determined from stomach samples. See 'Methods: Energetics' for sources of data on individual energy values

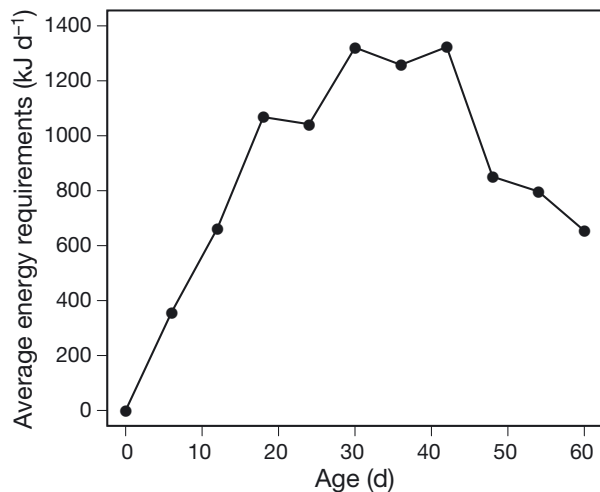| Prey	Energy value (kJ g^{-1})	Mean proportion of prey in samples (%)	Mean contribution to energy density of diet (kJ g^{-1})	Mean contribution to energy density of diet (%)	Total energy density of diet (kJ g^{-1})
Guard stage					
Krill	3.79	83.4	3.16	70	4.54
Fish	8.42	16.3	1.37	30	
Amphipods	3.52	0.26	0.01	0	
Squid	3.64	0.04	0.00	0	
Crèche stage					
Krill	3.79	42.8	1.62	31	5.27
Fish	8.42	33.3	2.80	53	
Amphipods	3.52	23.2	0.82	16	
Squid	3.64	0.70	0.03	0	

Fig. 6. Energy requirements of growing macaroni penguin chicks over the 60 d breeding period (adjusted from Brown 1987), based on a weight at birth of 106 g and weight at fledging of 2.5 kg

need to consume 850 g and 1150 g d^{-1}, respectively, including a combined total of approximately 300 g for the chick.

Impacts on prey

Assuming 50 000 breeding pairs (Deagle et al. 2008), a colony-wide energy budget indicates that during the guard stage, an estimated 1150 t of food was consumed by breeding female macaroni penguins from Capsize Beach. During the crèche stage, a combined estimate of 3700 t of food was consumed by female and male penguins. The estimate of total prey biomass consumed during the breeding period is close to 5000 t over approximately 60 d, from mid-December to mid-February. Using these minimum required levels of consumption and our coarse estimates of available fish and zooplankton biomass in the penguins' core foraging area, we estimate that the breeding population of penguins from Capsize Beach would have consumed <2% of available zooplankton prey and <1.5% of available fish prey during the guard stage. This population could have consumed approximately 2.5% of the remaining available zooplankton prey and approximately 5% of available fish prey during the crèche stage (see Table S2 in the Supplement).

DISCUSSION

Through our analyses of penguin diet and foraging behaviour, we found that prey switching by macaroni penguins in the crèche stage is evident; the guard stage diet was dominated by krill, whereas the crèche stage diet was more varied (Table 4). The observed prey switching was likely due to the release of foraging constraints in the crèche stage when female penguins are no longer required to feed the chicks on a daily basis and can thus make longer foraging trips. Our results did not provide evidence for prey depletion near breeding colonies (as postulated by authors such as Moore et al. 1999, Barlow & Croxall 2002b, Hindell et al. 2011), at least by the breeding population of macaroni penguins.

Implementation of a simple energy budget indicated that prey switching in the crèche stage was

Table 5. Energy budget for a macaroni penguin breeding pair (male, female and chick). Values (adjusted to 3 significant figures) are based on total energy requirements for adults from Table S1 in the Supplement at www.int-res.com/articles/suppl/m526p169_supp.pdf, energy requirements for chicks adjusted from Brown (1987; our Fig. 6) and energy density for diet from Table 4. AE: assimilation efficiency

	Energy (kJ d^{-1})	Energy density meal (kJ)	Prey required (g d^{-1}) at 73% adult AE and 76% chick AE	Proportion provided to chick[a]	Required prey consumption (g d^{-1})
Guard stage					
Female	2680	4.54	810	1.00	960
Male	–	4.54	–	–	–
Chick	520	4.54	150	–	–
Crèche stage					
Female	2560	5.27	670	0.60	850
Male	3970	5.27	1030	0.40	1150
Chick	1180	5.27	300	–	–

[a]Unequal division of parental responsibilities, calculated from Barlow & Croxall (2002b) and Trathan et al. (2006)

energetically more favourable for the penguins. The energy budget considered the added energy costs of extended foraging times and distances as well as the higher energy content of fish, which were the offshore prey targets. Our analyses of the acoustics and net-haul data back up our conclusions of prey switching in the later breeding stage. Fish were more abundant further from the island, over deeper waters, consistent with other findings (Perissinotto & McQuaid 1992, Pruvost et al. 2005). Zooplankton (krill), the main food source in the guard stage, were found consistently throughout the prey field.

Our results for macaroni penguin diets are consistent with previous studies on Heard Island (Klages et al. 1989, Green et al. 1998, Deagle et al. 2007, 2008), and show that krill are an important component of the diet, particularly during the guard stage (83% of biomass). There is little evidence of prey switching by macaroni penguins during the breeding season in other regions of the Southern Ocean. Penguins at South Georgia, however, are reported to target amphipods in years when the availability of Antarctic krill is low (Croxall et al. 1999). In contrast to other published results, our study shows that, although krill still comprise a substantial proportion of the diet in the crèche stage (43% of biomass; Table 4), prey switching is evident, with a significant increase in fish and amphipod consumption.

Localised prey-field depletion has been suggested as a potential driver of foraging behaviour for central-place foragers during the breeding season (e.g. Moore et al. 1999, Barlow & Croxall 2002b, Hindell et al. 2011). Our coarse estimates for consumption of prey by the breeding macaroni penguin colony at Capsize Beach suggest that only approximately 1.5% of available zooplankton and fish prey would be consumed during the guard stage. This is necessarily an underestimate due to conservative estimates of the time spent at sea (we assumed an average of 45 to 65% of time spent at sea, but other estimates are as high as 68 to 75%; Green et al. 2002) and the exclusion of non-breeders. However, Trebilco (2004) found that non-breeding macaroni penguins had very different foraging behaviours than breeding penguins, particularly concerning the distances foraged.

Inclusion of foraging by the full estimated population of 1 million breeding macaroni penguins on Heard Island to the energy budget takes total prey consumption to approximately 30% of the available prey (see Table S2 in the Supplement). Inclusion of prey consumption by other land-based predator species (seals, penguins and flying birds) that use the same high-productivity area for foraging at a similar time of year (Green et al. 1998, Moore et al. 1999, van Wijk et al. 2010, Hindell et al. 2011) would further increase the total volume of prey taken during the breeding season. Nonetheless, there was no strong evidence that prey depletion around the island was responsible for the observed prey switching by macaroni penguins in the crèche stage in our study. Our results are more consistent with prey switching due to the energy densities per weight for fish and reduced foraging constraints in the crèche stage leading to greater access to fish in offshore areas.

Based on modelling results for Adélie penguins, *Pygoscelis adeliae*, Cresswell et al. (2012) found that quality rather than quantity of the prey field was important in predicting foraging behaviour of penguins. In our case, the observed change in diet and prey-field use for macaroni penguins is primarily determined by the change in constraints on foraging trip duration between guard and crèche stages. The shift in behaviour appears likely to be due to the lack of available fish in the near-shore environment, reinforcing the conclusion of Cresswell et al. (2012).

Due to the logistical difficulty of concurrently sampling predators and prey fields, the integrated approach of combing prey-field dynamics, energy budgets and information on predator foraging behaviour has not been broadly applied in trophic studies for Southern Ocean ecosystems. As such, the HIPPIES data provide a rare opportunity to evaluate how Southern Ocean predators use and respond to the distribution of their prey. Our results provide insights into constraints on foraging strategies between 2 stages of the breeding cycle of macaroni penguins at Heard Island. Furthermore, the development of simple energy budgets is an important step in the development of fully dynamic models for top predators that can inform fisheries and conservation management about responses of predators and food webs to changes in habitats under climate change.

Insights from this kind of integrated study can be used to inform predictions of the responses of predators to climate-driven changes in prey availability as well as potential impacts from fishing activities. Key directions for future work include more targeted evaluation of spatial gradients in prey fields and how predators might use these selectively; development of algorithms to better delineate dominant taxa using acoustic data and of more specific target-strength models so that true biomass can be estimated; targeted sampling of prey fields in non-foraging areas; studies of prey-field use outside of the breeding season; and studies that evaluate and integrate prey-field use by multiple predator species.

LITERATURE CITED

Anderson M, Gorley R, Clarke K (2008) PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E, Plymouth

Bailleul F, Charrassin JB, Ezraty R, Girard-Ardhuin F, McMahon CR, Field IC, Guinet C (2007) Southern elephant seals from Kerguelen Islands confronted by Antarctic Sea ice. Changes in movements and in diving behaviour. Deep-Sea Res II 54:343–355

Bailleul F, Cotté C, Guinet C (2010) Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. Mar Ecol Prog Ser 408:251–264

Barlow KE, Croxall JP (2002a) Provisioning behavior of macaroni penguins *Eudyptes chrysolophus.* Ibis 144:248–258

Barlow KE, Croxall JP (2002b) Seasonal and interannual variation in foraging range and habitat of macaroni penguins *Eudyptes chrysolophus* at South Georgia. Mar Ecol Prog Ser 232:291–304

Bedford M (2013) Prey-field use by top predators of the Southern Ocean: understanding foraging dynamics of macaroni penguin *Eudyptes chrysolophus* near Heard Island. BMarSc (Hons) thesis, University of Tasmania, Hobart, available from http://eprints.utas.edu.au/22465/

Benoit-Bird KJ, Battaile BC, Heppell SA, Hoover B and others (2013) Prey patch patterns predict habitat use by top marine predators with diverse foraging strategies. PLoS ONE 8:e53348

Bertrand A, Segura M, Gutiérrez M, Vásquez L (2004) From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. Fish Fish 5:296–316

Bost CA, Cotté C, Bailleul F, Cherel Y and others (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. J Mar Syst 78:363–376

Bradshaw CJA, Hindell MA, Sumner MD, Michael KJ (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. Anim Behav 68:1349–1360

Brown CR (1987) Energy requirements for growth and maintenance in macaroni and rockhopper penguins. Polar Biol 8:95–102

Cherel Y, Hobson KA, Guinet C, Vanpe C (2007) Stable isotopes document seasonal changes in trophic niches and winter foraging individual specialization in diving predators from the Southern Ocean. J Anim Ecol 76:826–836

Clarke A (1980) The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia. J Exp Mar Biol Ecol 43:221–236

Clarke K, Gorley R (2006) PRIMER v6: user manual/tutorial. PRIMER-E, Plymouth

Clarke A, Prince PA (1980) Chemical composition and calorific value of food fed to mollymauk chicks *Diomedea melanophris* and *D. chrysostoma* at Bird Island, South Georgia. Ibis 122:488–494

Constable A, Melbourne-Thomas J, Corney S, Arrigo K and others (2014) Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. Global Change Biol 20:3004–3025

Cresswell KA, Wiedenmann JR, Mangel M (2012) A model of parental conflict: predicting provisioning behavior of penguin partners in response to local changes in krill. Ecol Modell 246:68–78

Croxall J, Prince P (1982) Calorific content of squid (Mollusca: Cephalopoda). Br Antarct Surv Bull 55:27–31

Croxall JP, Ricketts C, Prince PA (1984) Impact of seabirds on marine resources, especially krill, of South Georgia waters. In: Whittow GC, Rahn H (eds) Seabird energetics. Plenum Press, New York, NY, p 285–317

Croxall J, Reid K, Prince P (1999) Diet, provisioning and productivity responses of marine predators to differences in availability of Antarctic krill. Mar Ecol Prog Ser 177: 115–131

Davis R, Croxall J, O'Connell M (1989) The reproductive energetics of gentoo *Pygoscelis papua* and macaroni *Eudyptes chrysolophus* penguins at South Georgia. J Anim Ecol 58:59–74

Deagle BE, Gales NJ, Evans K, Jarman SN, Robinson S, Trebilco R, Hindell MA (2007) Studying seabird diet through genetic analysis of faeces: a case study on macaroni penguins *Eudyptes chrysolophus.* PLoS ONE 2:e831

Deagle BE, Gales NJ, Hindell MA (2008) Variability in foraging behaviour of chick-rearing macaroni penguins *Eudyptes chrysolophus* and its relation to diet. Mar Ecol Prog Ser 359:295–309

Field I, Hindell M, Slip D, Michael K (2001) Foraging strategies of southern elephant seals *Mirounga leonina* in relation to frontal zones and water masses. Antarct Sci 13: 371–379

Freitas C (2012) argosfilter: Argos locations filter. R package version 063. R Foundation for Statistical Computing, Vienna. Available at http://CRAN.R-project.org/package =argosfilter

Frydman S, Gales N (2007) HeardMap: tracking marine vertebrate populations in near real time. Deep-Sea Res II 54: 384–391

Gales N, Constable A, Williams R (2006) A new era in conservation science: ecosystem scale experiments at Heard Island. In: Green K, Woehler E (eds) Heard Island: Southern Ocean sentinel. Surrey Beatty & Sons, Chipping Norton

Godø OR, Samuelsen A, Macaulay GJ, Patel R and others (2012) Mesoscale eddies are oases for higher trophic marine life. PLoS ONE 7:e30161

Green K, Williams R, Green M (1998) Foraging ecology and diving behaviour of macaroni penguins *Eudyptes chrysolophus* at Heard Island. Mar Ornithol 26:27–34

Green JA, Butler PJ, Woakes AJ, Boyd I (2002) Energy requirements of female macaroni penguins breeding at South Georgia. Funct Ecol 16:671–681

Green JA, Butler P, Woakes A, Boyd I (2003) Energetics of diving in macaroni penguins. J Exp Biol 206:43–57

Green JA, Boyd IL, Woakes AJ, Warren NL, Butler PJ (2005) Behavioural flexibility during year-round foraging in macaroni penguins. Mar Ecol Prog Ser 296:183–196

Green JA, Boyd IL, Woakes AJ, Green CJ, Butler PJ (2007) Feeding, fasting and foraging success during chick rearing in macaroni penguins. Mar Ecol Prog Ser 346: 299–312

Hijmans RJ (2013) raster: geographic data analysis and modeling. R package version 2.1-49. R Foundation for Statistical Computing, Vienna

Hindell MA, Lea MA, Bost CA, Charrassin JB and others (2011) Foraging habitats of top predators, and Areas of Ecological Significance, on the Kerguelen Plateau. In: Duhamel G, Welsford D (eds) The Kerguelen Plateau: marine ecosystem and fisheries. Société Française d'lchtyologie, Abbeville, p 203−215

Horne JK (2000) Acoustic approaches to remote species identification: a review. Fish Oceanogr 9:356−371

Hückstädt L, Burns J, Koch P, McDonald B, Crocker D, Costa D (2012) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287−301

Jarman SN, McInnes JC, Faux C, Polanowski AM and others (2013) Adélie penguin population diet monitoring by analysis of food DNA in scats. PLoS ONE 8:e82227

Jarvis T, Kelly N, Kawaguchi S, van Wijk E, Nicol S (2010) Acoustic characterisation of the broad-scale distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (30-80° E) in January-March 2006. Deep-Sea Res II 57:916−933

Klages N, Gales R, Pemberton D (1989) Dietary segregation of macaroni and rockhopper penguins at Heard Island. Wildl Res 16:599−604

Kloser RJ, Ryan TE, Young JW, Lewis ME (2009) Acoustic observations of micronekton fish on the scale of an ocean basin: potential and challenges. ICES J Mar Sci 66: 998−1006

Kooijman SALM (2012) Energy budgets. In: Hastings A, Gross LJ (eds) Encyclopedia of theoretical ecology. University of California Press, Berkeley, CA, p 249−258

Korneliussen RJ, Ona E (2003) Synthetic echograms generated from the relative frequency response. ICES J Mar Sci 60:636−640

Lea MA, Nichols PD, Wilson G (2002) Fatty acid composition of lipid-rich myctophids and mackerel icefish *Champsocephalus gunnari*—Southern Ocean food-web implications. Polar Biol 25:843−854

MacLennan DN, Fernandes PG, Dalen J (2002) A consistent approach to definitions and symbols in fisheries acoustics. ICES J Mar Sci 59:365−369

Mårtensson PE, Nordøy E, Blix A (1994) Digestibility of crustaceans and capelin in harp seals (*Phoca groenlandica*). Mar Mamm Sci 10:325−331

Mårtensson PE, Gotaas A, Norddy E, Blix A (1996) Seasonal changes in energy density of prey of northeast Atlantic seals and whales. Mar Mamm Sci 12:635−640

Moore GJ, Wienecke B, Robertson G (1999) Seasonal change in foraging areas and dive depths of breeding king penguins at Heard Island. Polar Biol 21:376−384

Oozeki Y, Hu F, Tomatsu C, Kubota H (2012) Development of a new multiple sampling trawl with autonomous opening/closing net control system for sampling juvenile pelagic fish. Deep-Sea Res I 61:100−108

Perissinotto R, McQuaid CD (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. Mar Ecol Prog Ser 80:15−27

Pruvost P, Duhamel G, Palomares M (2005) An ecosystem model of the Kerguelen Islands' EEZ. In: Palomares M, Pruvost P, Pitcher T, Pauly D (eds) Modeling Antarctic marine ecosystems. Fisheries Centre Research Reports 13(7). Fisheries Centre, University of British Columbia, Vancouver, p 40−64

Quillfeldt P, McGill RAR, Furness RW (2005) Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. Mar Ecol Prog Ser 295:295−304

R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, www.R-project.org

Sakar D (2008) Lattice: multivariate data visualization with R. Springer, New York, NY

Sigler MF, Kuletz KJ, Ressler PH, Friday NA, Wilson CD, Zerbini AN (2012) Marine predators and persistent prey in the southeast Bering Sea. Deep-Sea Res II 65−70:292−303

Simrad (2001) Simrad EK60 scientific echo sounder: instruction manual, rev.c (857-164204/C). Simrad AS, Horten

Sumner MD (2012) trip: spatial analysis of animal track data. R package version 11-12. R Foundation for Statistical Computing, Vienna. http://CRAN.R-project.org/package= trip

Tierney M, Hindell MA, Goldsworthy SD (2002) Energy content of mesopelagic fish from Macquarie Island. Antarct Sci 14:225−230

Torres JJ, Donnelly J, Hopkins TL, Lancraft TM, Aarset AV, Ainley DG (1994) Proximate composition and overwintering strategies of Antarctic micronektonic Crustacea. Mar Ecol Prog Ser 113:221−232

Trathan PN, Green C, Tanton J, Peat H, Poncet J, Morton A (2006) Foraging dynamics of macaroni penguins *Eudyptes chrysolophus* at South Georgia during brood-guard. Mar Ecol Prog Ser 323:239−251

Trebilco R (2004) Macaroni penguin *Eudyptes chrysolophus* foraging ecology at Heard Island: behaviour and environmental influences. BSc (Hons) thesis, University of Tasmania, Hobart

van Pelt TI, Piatt JF, Lance BK, Roby DD (1997) Proximate composition and energy density of some North Pacific forage fishes. Comp Biochem Physiol A 118:1393−1398

van Wijk EM, Rintoul SR, Ronai BM, Williams GD (2010) Regional circulation around Heard and McDonald Islands and through the Fawn Trough, central Kerguelen Plateau. Deep-Sea Res I 57:653−669

Whitman LD (2010) Variation in the energy density of forage fishes and invertebrates from the Southeastern Bering Sea. MS thesis, Oregon State University, Corvallis, OR

Woehler E (2006) Status and conservation of the seabirds of Heard Island and the McDonald Islands. In: Green K, Woehler EJ (eds) Heard Island, Southern Ocean sentinel. Surrey Beatty & Sons, Chipping Norton

Woehler E, Green K (1992) Consumption of marine resources by seabirds and seals at Heard Island and the McDonald Islands. Polar Biol 12:659−665

Zamon JE, Greene CH, Meir E, Demer DA, Hewitt RP, Sexton S (1996) Acoustic characterization of the three-dimensional prey field of foraging chinstrap penguins. Mar Ecol Prog Ser 131:1−10