CSIRO PUBLISHING
www.publish.csiro.au/journals/emu *Emu*, 2009, **109**, 204–213

Diet composition, continuity in prey availability and marine habitat – keystones to population stability in the Snares Penguin (*Eudyptes robustus*)

Thomas Mattern[A,D], *David M. Houston*[B], *Chris Lalas*[C], *Alvin N. Setiawan*[A] *and Lloyd S. Davis*[A]

[A]Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand.
[B]Department of Conservation, Private Bag 68908, Newton, Auckland, New Zealand.
[C]PO Box 31, Portobello, Dunedin, New Zealand.
[D]Corresponding author. Email: t.mattern@eudyptes.net

Abstract. Worldwide, crested penguins (*Eudyptes* spp.) are in decline and it is suspected that reduced prey availability plays an important role. However, the population of Snares Penguins (*E. robustus*) does not follow this trend, with its population being stable if not slightly increasing. To assess whether the success of the Snares Penguins is a result of a rich and stable prey resource within the breeding range of the species, we examined the dietary composition of breeding Snares Penguins by analysis of stomach contents, and analysed ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes in feathers of living penguins and historical specimens. The food brought ashore by the Penguins was dominated by a single species of krill, *Nyctiphanes australis* (~60% of wet weight of the stomach samples); fish (~30%) and cephalopods (~10%) seemed to form only a minor portion. However, numbers of fish otoliths and cephalopod beaks in the samples suggest that these prey classes are more important food source for adult Penguins while at sea. Stable isotope ratios of Snares Penguin feathers collected between 1880 and 2004 revealed no temporal trend in either $\delta^{13}C$ or $\delta^{15}N$ indicating no significant changes in marine productivity or general composition of the diet of Snares Penguins in the past 120 years. We discuss our findings in the light of declining population trends and changing stable isotope ratios recently detected in Rockhopper Penguins (*E. chrysocome*), and conclude that the Snares Penguins benefit from stable prey availability as a function of the oceanographic setting of their breeding habitat.

Introduction

Seabird populations are often greatly affected by changes in the marine environment, especially if such changes alter the abundance or diversity of their prey (e.g. Becker and Beissinger 2006; Lee *et al*. 2007). Penguin populations are particularly influenced by environmental changes. Compared with flying seabirds, most species of penguin, when breeding, do not range far from their nesting sites owing to frequent chick-feeding and so depend on abundant food near their breeding colonies (Williams 1995). Such limited foraging ranges make them particularly vulnerable to environmental changes that affect the abundance of prey (Davis and Renner 2003). Population trends of crested penguins (*Eudyptes* spp.) worldwide seem to demonstrate this in a concerning way. Of the six species of crested penguin, all currently listed as globally threatened by the IUCN (IUCN 2009), four species have declined considerably through the 20th century, the main reasons suspected being reduced prey availability as a result of environmental changes (e.g. oceanic warming, Cunningham and Moors 1994), or competition with fisheries, or both (Ellis *et al*. 2007).

Populations of crested penguins breeding in New Zealand's subantarctic region (see Fig. 1) have declined significantly, as with worldwide trends. The Fiordland Penguin (*E. pachyrhynchus*), which breeds along the south-western coast of New Zealand's South Island is believed to have declined over the past 40 years, although the extent of the decline is not clear (Taylor 2000). On the subantarctic Antipodes Islands, the population of Erect-crested Penguins (*E. sclateri*) appears to have declined by 50% in the last 30 years (Taylor 2000) and on Campbell Island, numbers of Rockhopper Penguins (*E. chrysocome*) today are only one-tenth of what they were 50 years ago (Cunningham and Moors 1994). Recent studies suggest that these declines could be a result of decreasing oceanic productivity and accompanying fundamental changes in food webs (Hilton *et al*. 2006).

Interestingly, such a declining population trend is not evident in another New Zealand crested penguin – the Snares Penguin (*E. robustus*). The species is endemic to the Snares Islands, some 200 km south of New Zealand's South Island (Fig. 1). Its population is considered stable (Amey *et al*. 2001) and, in fact, numbers might even have increased slightly between the 1960s and the 1980s (Warham *et al*. 1986). If the population declines of other species of crested penguins were a result of changes in their oceanic habitat, it seems that the Snares Penguins were largely unaffected by such changes.

However, the interpretation of the Snares Penguin's apparent success is difficult. Although the general biology of the species

 10.1071/MU08001 0158-4197/09/030204

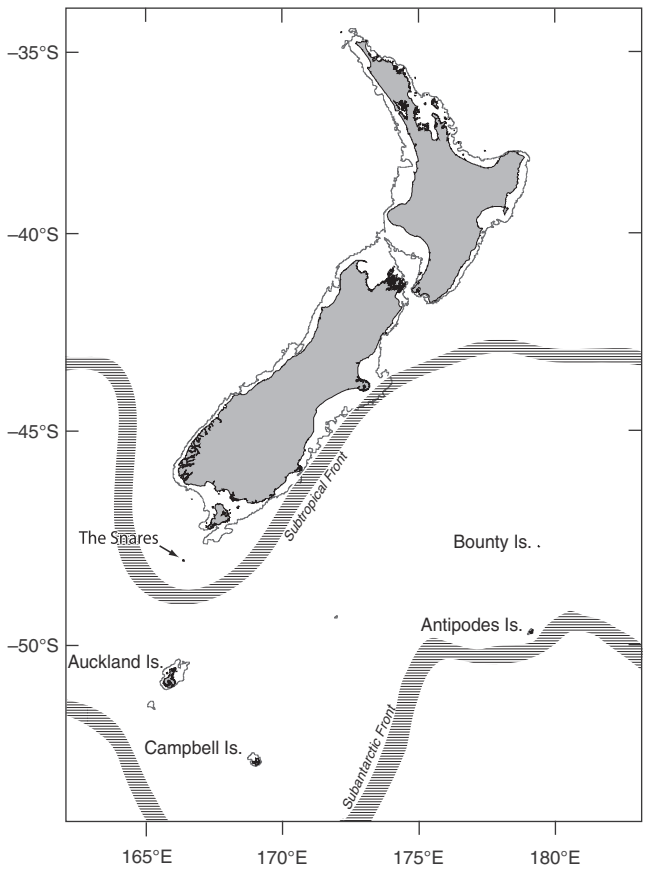

Fig. 1. New Zealand's subantarctic region and breeding locations of Snares Penguin and other crested penguins. Snares Penguins only breed on the Snares Islands. Fiordland Penguins inhabit the south-western coast of the South Island. Rockhopper Penguins breed on Campbell and Antipodes Islands, and Erect-crested Penguins breed on Antipodes and Bounty Islands. The approximate locations of the two main oceanic frontal systems are indicated (hatched). Warm, subtropical water (>12°C) dominates the regions north of the Subtropical Front (encompassing the Snares Islands and Fiordland), whereas cool (<12°C) subantarctic waters surround the remaining subantarctic Islands. A thin grey line indicates the 100-m depth contour.

has been described by Stonehouse (1971) and, in more detail, by Warham (1974), there is little information on its biology. In the face of prey-related population declines, information about the diet of Snares Penguins would be invaluable. However, the only published data on the diet of Snares Penguins are in Cooper *et al*. (1990) and Marchant and Higgins (1990), both of which merely list prey species without providing any detailed information about prey quantities or quality of data. Such lack of information makes it difficult to put present-day observations into a historical context and, as a result, interpretation of population trends often involves a considerable degree of speculation (e.g. Cunningham and Moors 1994; Guinard *et al*. 1998).

We can compensate for the dearth of historical diet data, to some extent, by the analysis of stable isotope ratios of carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) in historical samples. This approach hinges on changes in stable isotope ratios in response to variations in ecological processes over time. In aquatic ecosystems, for example, long-term decline of primary production may result in reduced growth rates of phytoplankton and decreasing carbon ratios (Laws *et al*. 1995). Hence, temporal variations in $\delta^{13}C$ can be used as an indicator for an ecosystem's carrying capacity (Schell 2000; O'Reilly *et al*. 2003). Within a marine ecosystem, $\delta^{15}N$ increases with the trophic level of a food web's component so that varying nitrogen ratios within historical samples reflect changes in dietary composition (Hilton *et al*. 2006). To investigate historical trends in diet, long-term series analysis of stable isotope ratios in feather samples were found to be a useful source of information (e.g. Thompson *et al*. 2005); feathers are metabolically inert after growth and as such provide an isotopic signature of diet shortly before or during feather growth (Hobson and Wassenaar 1997).

The aim of this study was to investigate if the population stability of the Snares Penguin is a function of composition and long-term stability of prey. First, since the population of Snares Penguins appears to be enduring we assumed that availability of prey was not a limiting factor. Owing to the pelagic setting of the Snares Islands, we expected to find primarily planktonic prey, reflecting the high oceanic primary production characteristic of the region (Murphy *et al*. 2001). To test this assumption, we studied the dietary composition of breeding Snares Penguins using analysis of stomach contents. Second, as historic and contemporary estimates of population give no indication for declines in Snares Penguins, we predicted that the current prey resource would be comparable to that of the past. This prediction was tested by performing stable isotope analysis in feathers from living Snares Penguins as well as dated museum specimens. We discuss our findings with regard to other, generally declining, crested penguin populations in the New Zealand region.

Methods

Study site and species

Fieldwork was conducted on North-east Island (48°09′S, 166°36′E), the main Island of the small Snares Archipelago. Snares Penguins lay at the end of September and beginning of October (Warham 1974). During incubation, Snares Penguins have stringent patterns of nest attendance, with both parents guarding and incubating the eggs for ~10 days, before all the breeding males synchronously leave the colonies around 14 October each year to forage for 2 weeks (Warham 1974; T. Mattern, pers. obs.). Upon return of the males, the females go to sea for about 1 week before returning to the nest to feed the newly hatched chicks. Hatching occurs in late October to early November. The male Penguins stay with the chicks for the entire guard phase until chicks start to form crèches in mid-November. Thus, it is solely the females' duty to provide food for the young chicks on a daily basis (Warham 1974).

Dietary sampling

In October and November 2002, that is the late incubation and early chick-rearing stages, we collected stomach samples from a total of 24 adult Snares Penguins returning from the sea at the main landing site in Station Cove, North-east Island. Samples were taken from birds that were presumed to be breeders since non-breeders were likely to return with empty stomachs as they

had no offspring to provision. Breeding status of arriving birds could not be assessed but Penguins that seemed to loiter onshore were assumed to be potential non-breeders. Therefore, only birds with short resting times after landing were chosen for sampling. Suitable individuals were selected from groups of Penguins heading towards the pathways into the forest and to the colonies.

After capture, bill-measurements were taken to determine sex (Warham 1974) and birds were then weighed in cloth bags to assess body condition. Males and females lighter than 3.1 and 2.4 kg, respectively (lower ranges of mean weights published in Warham 1974), were considered unfit for stomach sampling. The birds were relieved of their stomach contents by water offloading (Wilson 1984) and flushed until clear water indicated complete retrieval of stomach contents, which was usually the case after three flushes. The samples were processed immediately after flushing was completed.

Between 21 and 24 October we sampled nine male penguins (mean $\pm$ s.d., weight 3.9 ± 0.2 kg) returning from long-term foraging trips during the incubation stage. All of these birds had very few identifiable items in their stomachs so that further sampling of males was deemed unjustifiable. Between 2 and 8 November, after chicks had hatched in most nests, we sampled stomachs of 15 female Penguins (mean weight 2.7 ± 0.1 kg) that were assumed to return to feed chicks. The limited number of penguins used in this study was a result of permit constraints.

Stomach content analysis

Following Ridoux (1994), each sample was divided into the food load (fresh fraction, such as entire specimens, fleshy remains of fish and squid, digested matter) and accumulated material (hard-part remains, including cephalopod beaks and fish otoliths). The food load was sorted into different containers according to prey class: crustaceans, cephalopods and fish. After sorting, water was decanted before the material was transferred onto filter paper to extract further excess liquid. Filter paper was replaced if saturated until water ceased to permeate from the food material into the paper. The wet weight of each entire subsample was determined to the nearest 0.1 g using an electronic bench scale (Ohaus HH120, Ohaus Corporation, Pine Brook, NJ, USA), before the material was transferred into storage containers with 99% ethanol for further analysis. Subsamples of the food load were then sorted for identifiable taxa and components that were beyond identification. Prey taxa were identified using published keys (crustaceans, Kirkwood 1982; cephalopods, Roper *et al*. 1969 and Lu and Ickeringill 2002; fish, Paulin *et al*. 1989). Identified prey taxa were separated from the subsample and weighed after removal of excess liquid. Entire specimens of a given taxon were measured to determine standard body and individual wet weight.

Crustaceans (krill) represented a considerable portion of most samples collected from females. Generally the number of individual krill in a sample was large. As a consequence, a random crustacean subsample (~3–4 g, ~100–150 individuals) were scooped using a spatula from the drained material and identified in detail. Wet weight for individual crustaceans was <0.1 g and beyond the resolution of the bench scale.

Accumulated material provided additional information on cephalopod and fish species that were taken by the Penguins but not necessarily present or identifiable in the food load. Otoliths were identified using Hecht (1987) and Lalas (1983), differentiated for taxon and sorted into pairs to determine the number of individual prey items. Otolith lengths from two species (Redbait (*Emmelichthys nitidus*) and Red Cod (*Pseudophycis bacchus*)) were determined to the nearest 0.01 mm by analysing high resolution photos of sorted otolith collections in custom written digital-dimensioning software (L.-G. Ellenberg and T. Mattern, unpubl. data). Squid beaks were identified, using Roper *et al*. (1969) and Lu and Ickeringill (2002), sorted and measured under a microscope.

Standard length and weight of prey were either measured directly from entire specimens (following Ridoux 1994) or calculated from length of otoliths and dimensions of cephalopod beaks by applying published allometric equations: for the fish Redbait and Red Cod, from Gales and Pemberton (1994, and corrigendum); and for the cephalopods Arrow Squid (*Nototodarus sloani*) from Fraser and Lalas (2004), Warty Squid (*Morotheutis ingens*) from Bolstad (2006), and Violet Squid (*Histioteuthis atlantica*) from Hedd and Gales (2001).

To determine the relative importance of different prey, we calculated the proportional contribution of each prey class and each species to the individual food loads (percentage of the total wet weight of the food load, or 'proportional mass contribution') and to accumulated material (percentage of the total number of prey items, i.e. otoliths and squid beaks, or 'proportional prey item contribution'). We used these percentage values to calculate median values and ranges of the contribution of each prey class and species across all samples where the respective class or species occurred.

Feather samples and stable isotope analysis

After completion of breeding in mid-January, Snares Penguins forage for ~70 days to replenish body reserves in preparation for their annual moult which begins in late March (Warham 1974). As moulting penguins are restricted to land (i.e. there is no food intake during feather growth; Williams 1995), stable isotope signatures in penguin feathers reflect the penguins' diet during their pre-moult foraging period (Hilton *et al*. 2006).

Stable isotope analysis was performed on feather samples of 54 adult Snares Penguins. Half of the samples were contemporary samples that were collected from living individuals on the Snares Islands during field work of the breeding seasons 2003 (10 samples) and 2004 (17 samples). The remaining feather samples were obtained from museum skins with known collection dates, which ranged from 1888 to 2000 (Table 1); some of the collection locations of the early 20th century samples were either not known or seemed doubtful. From each individual, 3–5 feathers were either cut off at the base (of living individuals) or plucked (museum specimens) from the birds' lower backs and stored in zip-loc bags until further analysis.

Stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) were determined in all samples using continuous-flow isotope-ratio mass spectrometry (Thermo Finnigan MAT Delta^{Plus}, Thermo Finnigan MAT GmbH, Bremen, Germany). The analysis was conducted at the stable isotope laboratory of the National Institute for Water and Atmospheric Research (NIWA),

Table 1. Overview of historic feather samples obtained from museums for stable isotope analysis

Collection	Sampling year (sample size)
Museum of New Zealand, Te Papa Tongarewa, Wellington, NZ	1915 (4), 1972 (2), 1955 (1), 1972 (3), 1977 (2), 1987 (1), 2000 (3)
Canterbury Museum, Christchurch, NZ	1970 (1)
Natural History Museum, London, UK	1897 (2), 1998 (1), 1905 (1)
Natural History Museum, Vienna, Austria	1888 (2)
American Museum of Natural History, New York, USA	1895 (4), 1947 (1)

Wellington, New Zealand; for a detailed description of the analysis process see Hilton *et al*. (2006). Results are given in units of parts per thousand (‰) and indicate the relative deviation of the samples' isotope ratios from international standards – Pee Dee Belemnite (PDB) and atmospheric nitrogen for $\delta^{13}C$ and $\delta^{15}N$ respectively.

In the past two centuries, the amount of ^{13}C in the biosphere has been increasingly diluted by ^{12}C released by human burning of fossil fuels (Keeling 1979). This process, known as the 'Suess Effect', has resulted in an exponentially accelerating decrease in $\delta^{13}C$ signals in the world's oceans (Bacastow *et al*. 1996). This has also affected carbon isotope composition in penguin feathers so that systematically decreasing $\delta^{13}C$ ratios in historic samples occur independent of changes in oceanic productivity (Hilton *et al*. 2006). Following Hilton *et al*. (2006, Appendix A), we corrected our $\delta^{13}C$ data for the 'Suess Effect' using the $\delta^{13}C$ maximum annual rate of change of 0.0018‰ ('subtropical zone').

Sizes of historical samples varied but were small and not equally distributed over time (Table 1). Pooling samples according to certain time intervals did not enhance the analytical outcome. For basic comparison between years we calculated annual means of $\delta^{13}C$ or $\delta^{15}N$, and performed an analysis of variance (ANOVA) with Tukey's post-hoc test (Minitab 15, Minitab Inc., State College, PA, USA). Results are given as means ± s.d., unless otherwise indicated.

Results

For all samples ($n = 24$), a total of 24 different species from 23 families were identified (Table 2). Sample volumes and the volume of diagnosed prey remains differed considerably between males returning from foraging trips, which lasted up to 14 days, and trips by females provisioning chicks, which consisted of 1–3 days at sea.

Diet of males returning from long trips

Of nine males returning from long trips, one regurgitated only bile, and the other eight males had very little material, and that mainly digested, in their stomachs. The median food-load mass was 14.6 g (range 1.7–56.8 g, $n = 8$). With the exception of one bird that had 47 fresh, undigested Long-snouted Pipefish (*Leptonotus norae*) in its stomach, there was little identifiable material in the food loads (median weight of identifiable food 0.8 g, range 0.1–49.5 g, $n = 8$). Three samples contained the euphausid *Nyctiphanes australis* (henceforth called krill) in different states of digestion and which contributed between 0.1 g and 0.3 g (median 0.1 g) to the wet weight of the identifiable portion of the food load. Unidentifiable fish remains ($n = 5$ birds), Long-snouted Pipefish ($n = 5$) and Hector's Lanternfish (*Lampanyctodes hectoris*, $n = 1$) contributed between 0.1 g and 47.2 g (median 0.6 g) to the food load in seven birds. Six birds contained some fleshy remains of cephalopods (median weight 0.1 g, range 0.1–2.3 g); identifiable species were Arrow Squid ($n = 1$) and Pelagic Octopus (*Ocythoe tuberculata*, $n = 2$). All birds containing fleshy prey remains also had eroded otoliths or cephalapod beaks, or both, in their stomachs. Two additional samples contained only squid beaks among the digested material. Only one bird had otoliths that could be indentified, as Red Cod, Thornfish (*Bovichtus psychorolutes*), and Long-snouted Pipefish. Besides Arrow Squid ($n = 8$), only Warty Squid ($n = 2$) and Violet Squid ($n = 1$) could be identified from beaks. Owing to the meagre outcome of sample volume in male Penguins, we limited the quantitative and qualitative analysis of the diet composition to the samples obtained from females provisioning chicks.

Meal size and general prey composition of diet of female penguins

Wet weights of food loads in the 15 females returning from short trips during chick-guard phase ranged between 17.4 g and 162.6 g (median 74.1 g). Two of the females had only some digested material, cephalopod beaks (Warty Squid in one, unidentifiable beaks in both birds) and unidentifiable otoliths (one bird) in their stomachs and were thus excluded from the analysis of contribution of prey class and species to the food load. The samples obtained from the remaining 13 birds comprised 2.0 g to 112.7 g (median 30.3 g) of identifiable material. Krill was present in all 13 samples, and fleshy remains of fish and cephalopods in 11 and 10 samples respectively. One sample contained two small salps (*Salpidae*). Judging from the identifiable portions of the food brought ashore by the females, crustaceans were the most important prey class with a proportional mass contribution to the individual food loads that ranged around a median 64% (interquartile range (IQR) 22–88%), followed by fish (median 29%, IQR 17–41%) and cephalopods (median 10%, IQR 4–32%) (Fig. 2*a*).

Species composition in food loads of females

The stomach samples of females were dominated by krill, which contributed a median 61% (IQR 22–79%, $n = 13$; Fig. 2*b*) to the wet mass of the food load. Fresh fish remains consisted chiefly of Hector's Lanternfish (*Lampanyctodes hectoris*), which made up ~21% of the wet mass of the food load (IQR 4–42%). Specimens of Long-snouted Pipefish were present in five females; in four of these the mass contribution of this species ranged between 2 and 12% (median 4%) while in a fifth female, Pipefish constituted 26% of the wet weight of the food loads (Fig. 2*b*). Intact specimens of Redbait, Thornfish and Conger Eel (*Gnathophis habenatus*) were present in individual samples. While the latter species contributed little weight (3%) to the identifiable stomach

Table 2. Prey species taken by Snares Penguins ($n = 24$) during the early stages of the breeding season in October–November 2002

FOO, frequency of occurrence ($n = 24$ stomach samples); %W, percentage of pooled mass in food load; %N, numerical abundance (i.e. percentage of total number of beaks and otoliths in accumulated material). %W and %N were calculated from pooled samples (total food load mass 1402.6 g; total number of individual squid beaks and otoliths 1114). Mean size and mass of prey (±s.d.) were either derived from measurements of fresh specimen (superscript 'F') or else were calculated from allometric equations (see Methods for details). Values marked with superscript 's' were determined from random subsamples of pooled material. Only identifiable portions of food load (559.8 g, or 40% of total pooled mass) and accumulated materials ($n = 832$, or 74.6% of all items) were included in the analysis. Note that one Red Cod otolith pair was omitted from the sample as it was significantly larger (estimated size of fish 153 mm and mass 32.6 g) than the other Red Cod otoliths and would have unduly biased the estimation of mean size and mass

	FOO (%)	%W	%N	Mean prey size ± s.d. (mm); (*n*)	Mean prey mass ± s.d. (g)
Crustaceans					
Krill (Euphausiacea : *Nyctiphanes australis*)	63	53.8	–	$12.9 \pm 2.6^{F,s}$ (250)	<0.1
Euphausiacea : *Euphausia lucens*	13	<0.1	0		
Unidentified Decapoda	8	<0.1	–		
Cephalopods					
Arrow Squid (Ommastrophidae : *Nototodarus sloani*)	75	1.7	35.2	90.0 ± 28.9 (293)	17.5 ± 14.3
Warty Squid (Onychoteithidae : *Morotheutis ingens*)	29	–	8.2	46.6 ± 17.4 (70)	8.1 ± 5.9
Violet Squid (Histioteuthidae : *Histioteuthis atlantica*)	21	–	6.4	41.9 ± 20.9 (54)	7.1 ± 5.2
Pelagic Octopus (Ocythoidae : *Ocythoe tuberculata*)	17	0.6	–	25.1 ± 12.2^{F} (12)	2.3 ± 1.2
Brachioteuthidae : ?*Brachioteuthis behni*	13	0.6	2.5		
Enoploteuthidae : ?*Enoploteuthis galaxias*	4	–	1.0		
Mastigoteuthidae : *Mastigoteuthis* spp.	4	–	0.6		
Cranchiidae : *Taonius* spp.	4	–	0.5		
Tunicates					
Unidentified Salpidae	4	<0.1	–		
Fish					
Long-snouted Pipefish (Syngnathidae : *Leptonotus norae*)	63	12.4	2.3	93.4 ± 21.9^{F} (68)	0.4 ± 0.1
Redbait (Emmelichthyidae : *Emmelichthys nitidus*)	33	6.9	7.9	120.2 ± 56.1 (66)	28.8 ± 12.2
Red Cod (Moridae : *Pseudophycis bacchus*)	29	–	27.4	32.4 ± 5.87 (227)	0.3 ± 0.2
Hector's Lanternfish (Myctophidae : *Lampanyctodes hectoris*)	25	2.3	–	52.6 ± 4.6^{F} (17)	0.3–0.2
Thornfish (Bovichthyidae : *Bovichtus psychorolutes*)	21	2.9	6.9	39.4 ± 21.9^{F} (16)	0.4 ± 0.2
Wharehou (Centrolophidae : *Sariolella brama*)	13	–	0.4		
Silverside (Argentinidae : *Argentina elongata*)	4	–	–		
Hoki (Merlucciidae : *Macruronus novaezelandiae*)	4	–	0.2		
Rockfish (Acanthoclinidae : *Acanthoclinus fuscus*)	4	0.2	–		
Silver Conger (Congridae : *Gnathophis habenatus*)	4	0.2	–		
Opalfish (Percophidae : *Hemerocoetes pauciradiatus*)	4	–	0.1		
Blue Moki (Latrididae : *Latridopsis ciliaris*)	4	–	0.5		

contents, Redbait (35%) and Thornfish (26%) added considerable portions to the food loads of the birds. In cephalopods, Pelagic Octopus occurred in four samples with a median proportional mass contribution to the food loads of 9% (IQR 2–35%). As fresh material, Arrow Squid (median mass contribution 7%, IQR 4–10%, $n = 4$) and *Brachioteuthis* sp. (4%, $n = 1$) formed only a minor portion. However, it could well be any of the cephalopod species found in the Penguins' diet might have been present as unidentifiable squid remains, which contributed ~10% (IQR 4–36%, $n = 10$) of wet mass to the food loads (Fig. 2*b*).

Species composition in accumulated material

Thirteen of the 15 females had otoliths in their stomachs. In five of these samples, otoliths were too degraded for identification. Where it occurred, Red Cod was the most numerous fish prey and made up ~47% (IQR 37–81%, $n = 6$) of all fish otoliths (Fig. 3*a*). Redbait otoliths were proportionally less numerous (median contribution 15%, IQR 7–22%, $n = 8$), as were Long-snouted Pipefish (*Stigmatopora macropterygia*) otoliths (median 4%, IQR 3–16%, $n = 6$). Contrasting with its occurrence as fresh material, Arrow Squid predominated the cephalopod beaks; it was found in 10 of the 13 samples and made up ~58% (IQR 36–71%) of prey items in the accumulated materials (Fig. 3*b*). Other important species that contributed considerably to the accumulated material in some samples were Warty Squid (median 41%, IQR 14–75%, $n = 4$), Violet Squid (median 36%, IQR 25–61%, $n = 4$) and *Brachitheutis* spp. (median 31%, IQR 5–62%, $n = 3$).

Size of prey species

Table 2 lists the measured or calculated mean size and mass of the most important prey species. There are some considerable differences in the sizes of fish prey taken by Snares Penguins. The allometric equations of Redbait otoliths show that this species is by far the largest (mean length 120.2 mm, $n = 66$, see Table 2) and heaviest (mean mass 28.8 g) type of prey in the diet. This is emphasised by one intact specimen weighing 38.9 g, and 145 mm long recovered from one female. Other fish species are considerably smaller, with mean lengths ranging from 30 mm to 93 mm and mean weights of 0.3–0.4 g. Similarly, Arrow Squid were the largest cephalopods (mean length 90.0 ± 28.9 mm, mean mass 17.5 ± 14.3 g); mean lengths of other cephalopod

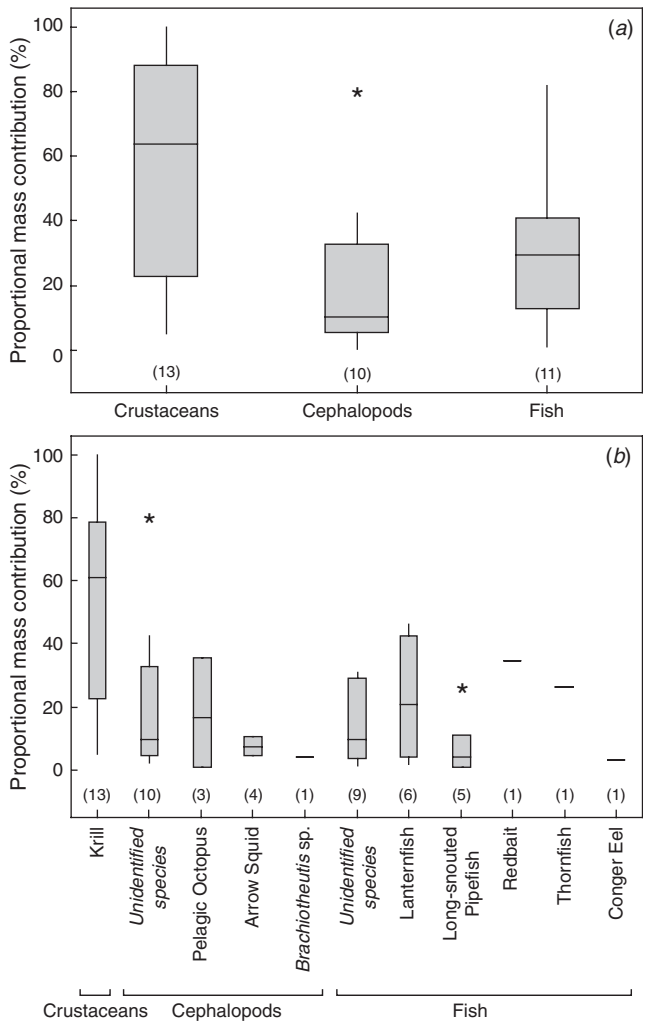

Fig. 2. Proportional mass contribution of (*a*) different prey classes and (*b*) prey species to the diagnostic remains of the food load of chick-provisioning female Snares Penguins. Only samples that contained identifiable diagnostic remains were included ($n = 13$ birds). Median mass of diagnostic remains in food loads (i.e. digested material not included) was 30.3 g (range 2.0–112.7 g); median food load mass was 82.0 g (range 25.0–163.0 g). Numbers in parentheses below each box indicate number of birds with the respective prey class or species in their stomachs. Asterisks denote outliers.

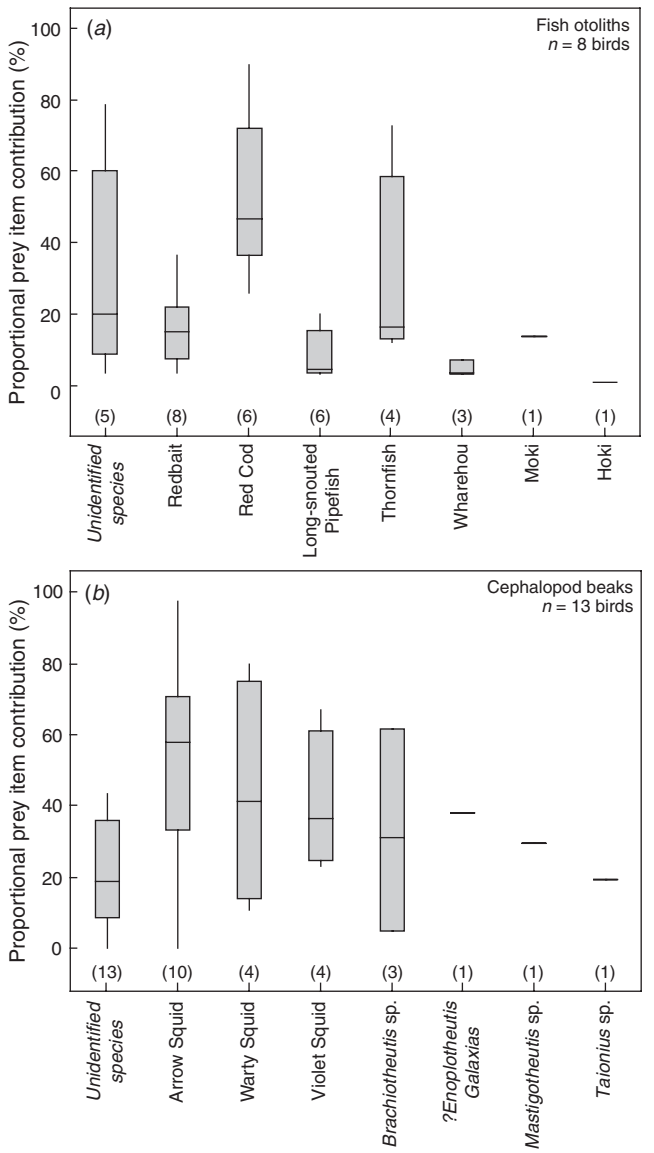

Fig. 3. Proportional contribution of different species of (*a*) fish and (*b*) cephalopods to the accumulated materials in stomach samples of chick-provisioning female Snares Penguins. Only samples that contained identifiable otoliths ($n = 8$ birds) and cephalopod beaks ($n = 13$ birds) where included in the analysis. Otoliths represented between 5 and 204 individual prey items (median 29 items); beaks derived from 5–52 individual cephalopods (median 30 items). Numbers in parentheses below each box indicate number of birds with the respective prey species in their stomachs.

species range from 25 mm to 47 mm, and mean weight from 2 g to 8 g. The sizes of all fish and cephalopod prey indicate that penguins primarily take larval and juvenile stages of the species.

Stable isotope ratios

The $\delta^{13}C$ or $\delta^{15}N$ values did not reveal clear trends in the diet of Snares Penguins over the past 120 years, although ratios seemed to be more varied in the first half of the 20th century (Fig. 4). The $\delta^{13}C$ values ranged between –15.15‰ and –18.51‰, and $\delta^{15}N$ ranged from 10.7‰ to 12.7‰. Stable isotope ratios in feathers sampled from living Snares Penguins were well within the range of ratios of historical samples. A comparison of pooled stable isotope ratios found no significant differences between years (ANOVA with Tukey's post-hoc: $\delta^{13}C$, $F_{14,53} = 1.05$, $P = 0.430$; $\delta^{15}N$, $F_{14,53} = 1.30$, $P = 0.254$).

Discussion

The importance of krill in the diet

The main component of food brought ashore by Snares Penguins was a single species of krill, *Nyctiphanes australis*; fish and cephalopods played only a secondary role (Fig. 1). This is

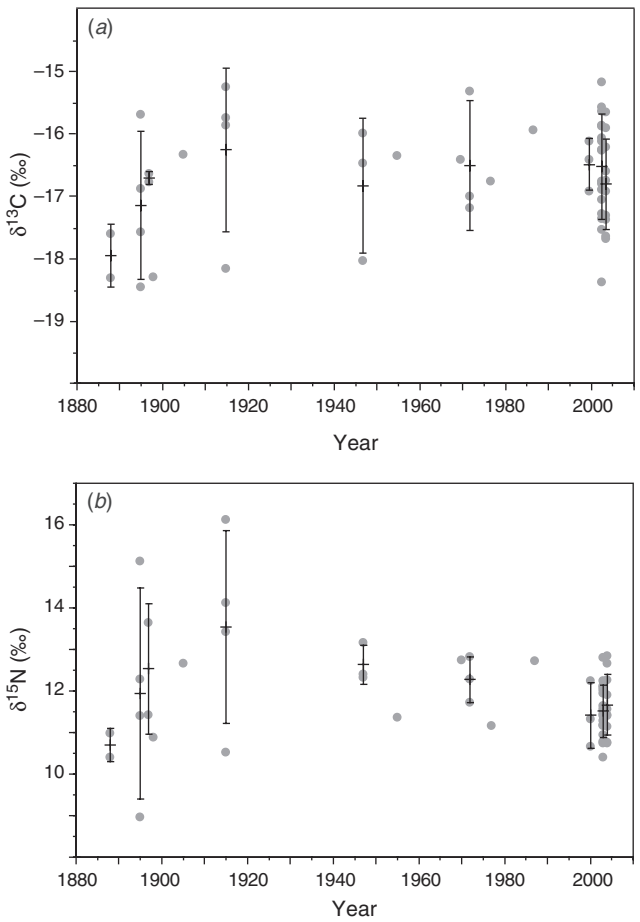

Fig. 4. Temporal trends in Snares Penguin feather stable isotope ratios. Grey markers represent individual values for ratios of (*a*) carbon ($\delta^{13}C$; corrected for Suess Effect, see Methods for details) and (*b*) nitrogen ($\delta^{15}N$). Annual means (–) and standard deviation (|) are provided for years for which more than one sample was available.

consistent with what had been suggested by Warham (1974) and the overview given in Cooper *et al*. (1990). Considering the dominance of krill in the diet of Snares Penguins, the biomass of *N. australis* in the waters around the Snares Island must be considerable. Dense swarms of this species are indeed a common occurrence even close inshore, and often close to the surface as a result of upwelling turbulences over submerged rocks and reefs (Fenwick 1978). The large amounts of undigested *N. australis* found in the food loads of Snares Penguins were most probably taken shortly before landing.

As such, krill represents a staple food for Snares Penguin chicks. Interestingly, it has been found that certain steroids from the cephalothorax region of euphausid krill act as a growth promoting factor in fish (Allahpichay and Shimizu 1985); this potentially renders it an excellent food source for growing penguin chicks too. Although fish and cephalopods contributed far less fresh material to the food loads it is nevertheless very likely that these prey are essential for the chicks as a balanced diet is imperative for the development (Romano *et al*. 2006). However, whether krill is an equally dominant food component in the diet of adult penguins is a different question. The presence of, at times, great numbers of fish otoliths and cephalopod beaks in the stomachs of Penguins indicates a higher intake of these prey than fresh remains delivered to the chicks would suggest.

Importance of fish and cephalopods

Fleshy fish remains brought ashore consisted chiefly of demersal species, such as Long-snouted Pipefish, Thornfish, and even Rockfish (*Acanthoclinus fuscus*), with the latter probably taken from one of the rock pools in Station Cove, where the penguins bathe. As these species were also found as entire specimens in the food loads it is clear that the Penguins prey on demersal species that live along the rocky shores and reefs of the Snares Islands (Paulin *et al*. 1989). This furthermore suggests considerable portions of the food of the Snares Penguin chicks is sourced from the immediate surroundings of the Island. Whether this pattern of prey provisioning persists throughout the breeding season is a different question as, in the face of large numbers of penguins and other seabirds on the Snares Islands, a prey-depletion halo effect occurring around the Island seems inevitable (Birt *et al*. 1987).

Judging from otoliths the most important fish species in the diet of Snares Penguins was Redbait. Although the numerical abundance of Redbait otoliths was low when compared, for example, to Red Cod otoliths (Fig. 3*a*), the specimens taken by the Penguins were much larger in length and mass, and thus more energetically valuable (Forero *et al*. 2002), than all other species (Table 2). Unlike Redbait, which is a planktivorous mid-water species, commonly found in New Zealand waters (Paulin *et al*. 1989), Red Cod is primarily a bottom dwelling species; but its larval and juvenile stages are pelagic and form part of the macro-zooplankton communities over the continental shelf that occur in association with patches of primary production (Habib 1973).

Squid beak frequencies show that Arrow Squid constitutes the bulk of the cephalopod prey of Snares Penguins (Table 2), although only small portions of this species were present in food loads (see Fig. 2*b*). This cephalopod is particularly abundant in the warmer (>12°C) waters west of the Subtropical Front (Smith *et al*. 1987; Jackson *et al*. 2000), which arches at a distance of some 200 km around the South and the East of the Snares Archipelago (Fig. 1). Arrow Squid is an important component in the diet of a wide range of pelagic vertebrates living and breeding in the area (e.g. penguins, van Heezik 1990; shearwaters, Cruz *et al*. 2001; albatross, James and Stahl 2000; fur seals, Harcourt *et al*. 2002) and is also an important species for commercial fisheries (Smith *et al*. 1987).

Interestingly, juvenile Warty Squid were the second most numerous cephalopod prey, though recorded considerably less frequently in the samples when compared with Arrow Squid (Table 2). Warty Squid is a typical deep-water species that prefers cool waters of <12°C (Jackson *et al*. 2000) and it seems unlikely that the Penguins encountered this type of prey in waters immediately surrounding the Snares Islands. Squid beaks may remain intact in seabird stomachs for up to 50 days, (Furness *et al*. 1984; Jackson and Ryan 1986) so that it is more likely that the Penguins caught Warty Squid in cooler waters beyond the Subtropical Front (Fig. 1), on long foraging trips before chicks hatched.

Comparison with other crested penguins in New Zealand

Like the Rockhopper and Erect-crested Penguins, Snares Penguins forage in a pelagic environment (Davis and Renner 2003). However, the former two species breed in cool subantarctic waters, which are characterised by reduced primary production presumably as result of iron deficiency (Boyd *et al*. 1999). The Snares Islands on the other hand are located in warm subtropical waters with higher primary production fuelled by nutrient introduction from the Tasman Sea (Murphy *et al*. 2001) (Fig. 1). The Fiordland Penguin breeds along the south-western coast of the South Island and utilises a marine habitat with oceanographic properties similar to the Snares region. Comprehensive reports on the dietary composition are only available for Fiordland Penguins (van Heezik 1989, 1990). There is no information about the feeding ecology of Erect-crested penguins other than that this species feeds on crustaceans and cephalopods (Marchant and Higgins 1990).

The main prey species reported for Fiordland Penguins are similar to those found in this study, although the importance of prey classes seems to differ (van Heezik 1989). Cephalopods (mainly Arrow Squid) made up most of the diet of Fiordland Penguins (85% of the reconstituted food mass), followed by crustaceans (13%, primarily krill *N. australis*) and fish (2%). However, it should be noted that the proportions of the prey classes were derived primarily from size estimations using allometric equations, so that the importance of cephalopods might be exaggerated (van Heezik 1989). Thus, it is imaginable that krill and fish might be more important food components of Fiordland Penguins. Overall, the comparability of the prey composition of Snares and Fiordland Penguins most likely reflects oceanographic similarity and relative proximity of their marine habitats. In this light, it seems unlikely that the Fiordland Penguin's decline is a result of substantial changes in the marine environment as such changes most likely would have had an effect on the Snares Penguin population too.

Rockhopper Penguins breeding on New Zealand's Campbell Island seem to have a considerably different diet compared with that of Snares Penguins, and also compared with principally krill-feeding Rockhopper Penguins elsewhere (see Cooper *et al*. 1990). According to rudimentary information published in Marchant and Higgins (1990), they predominantly forage for fish (91% of all prey items), apparently primarily demersal species, whereas crustaceans (~8%) and cephalopods (~2%) are of little relevance. Demersal fish species generally have a lower energetic value than pelagic fish (Vlieg 1982, 1984), so that it would appear that the pelagic species taken by Snares Penguins were better quality prey. Furthermore, if Rockhopper Penguins have to rely on demersal species as staple food, the foraging activities of the species are likely to be limited to narrow continental shelf areas around their breeding locations (see Fig. 1), whereas the foraging strategy of Snares Penguin, focusing on pelagic prey, has no such limitations.

Temporal trends in stable isotope ratios

Stable isotope ratios in feathers reflect the dietary preference of the Penguins during the foraging period before moulting (Hobson and Clark 1992; Bearhop *et al*. 2002). Before the moult, crested penguins generally stay at sea for several weeks, allowing them to forage further away from their nesting sites than during the breeding period (Davis and Renner 2003). As such it can be difficult to integrate the results of feather isotope ratios with observations of dietary composition made during the early chick-rearing phase. However, given that most adult Penguins return to their nesting sites to moult, it seems unlikely that the birds venture thousands of kilometres away from their breeding sites and probably stay within the same water masses in which they foraged throughout the breeding season. As such, temporal trends in feather isotopes can indeed provide information about the state of the marine habitat utilised during the breeding period.

Considering the graphical representation (Fig. 4*a*, *b*), stable isotope ratios in Snares Penguin feathers varied between 1880 and 1920. However, it is questionable whether this variation is an indicator for different feeding situations around the Snares Islands in the past. First, the age and breeding status of the historic samples could not be ascertained, that is the collected specimen might have been an adolescent bird or a non-breeder. Such birds are not tied to the Snares Islands until the end of the breeding season (Warham 1974) and therefore might have ventured further away during their pre-moult trips and fed in different regions than the breeding population (represented by contemporary feather samples). Second, some of the historic samples, including samples from 1897 and 1915 that account for most of the variation in isotope ratios, were not labelled properly so that the sampling location is either not known or in doubt. Whereas most of the breeding population of Snares Penguins returns to the Island to moult (Warham 1974), stragglers are regularly reported on the New Zealand mainland or even the Chatham Islands (Miskelly and Bell 2004). Therefore, some of the 'extreme' isotope values in historic feathers might be artefacts of the sampling location.

Stable isotope ratios in Snares Penguin feathers do not indicate obvious trends in either $\delta^{15}N$ or $\delta^{13}C$ over the past 120 years. The sample size of historic feathers was fairly small, which might have hindered the detection of finer temporal trends. However, on a broader scale our data do not suggest that Snares Penguins experienced any drastic changes in their prey composition. Carbon isotope ratios give no evidence for gross disparities in the marine productivity in the foraging areas of the Penguins in the course of the last century. Accordingly, nitrogen isotope ratios in all samples showed that the Penguins foraged on comparable trophic levels (Fig. 4*b*).

In contrast to our findings, stable isotope ratios in feathers of Rockhopper Penguins from Antipodes Island revealed a decreasing trend in $\delta^{13}C$ since the late 19th century (Hilton *et al*. 2006). This indicates a potential relationship between population decline and reduced oceanic productivity. However, the same publication also found that no such trend in $\delta^{13}C$ was evident in feathers from the same species breeding on Campbell Island where the population also had experienced dramatic declines. Cunningham and Moors (1994) suggested that this decline could have resulted from a dietary shift from crustacean to fish prey in the face of rising sea surface temperatures; yet the lack of a clear temporal trend in $\delta^{15}N$ invalidates this hypothesis (Hilton *et al*. 2006). However, whether a shift from pelagic to demersal fish species could be revealed by $\delta^{15}N$ is another question.

Overall the dietary differences between Snares and Rockhopper Penguins reflect the disparity of the marine environments in which the two species forage. The generally low primary production of the cool subantarctic oceanic waters surrounding the breeding locations of Rockhopper Penguins limits the biomass of species at higher trophic levels (Bradford-Grieve *et al*. 2003). This probably makes the species more susceptible to small changes in the marine ecosystem. In contrast, Snares Penguins seem to benefit from increased productivity of warm subtropical waters around the Snares Islands (Heath 1985; Murphy *et al*. 2001). The high abundance of crustacean swarms and associated fish and squid even within close range of the Snares Islands underlines this fact (Fenwick 1978). Therefore, the secret to the success of the Snares Penguins might be rooted in the location of their breeding habitat.

Acknowledgements

We are especially grateful for the help we received from the many museums we contacted while searching for historic penguin skins. We thank in particular Gillian Stone (Te Papa Tongarewa, Museum of New Zealand, Wellington, NZ), Ernst Bauernfeind and Anita Gamauf (Naturhistorisches Museum, Wien, Austria), Robert Prys-Jones, Joanne Cooper and Mark Adams (Natural History Museum, London, England), Paul Scofield (Canterbury Museum, Christchurch, NZ), and Paul Sweet (American Museum of Natural History, New York, USA). We furthermore extend our gratitude to David Thompson and Sara Bury (NIWA, Wellington, NZ) for facilitating and conducting the stable isotope analysis, and to Uwe Piatkowski (IFM-GEOMAR, University of Kiel, Germany) for his enthusiastic help with cephalopod identification. Very special thanks to Ursula Ellenberg and Katrin Ludynia for help and support in the field, and to Lars-Gunnar Ellenberg for programming the otolith measuring software. We thank the Department of Conservation, Southland Conservancy, for issuing research permits and logistical support. This study was approved by the Department of Conservation and the Animal Ethics Committee of the University of Otago and complies with current laws of New Zealand.

References

Allahpichay, I., and Shimizu, C. (1985). Separation of growth promoting factors from non-muscle krill meal of *Euphausia superba. Bulletin of the Japanese Society of Scientific Fisheries* **51**, 945–951.

Amey, J. M., McAllister, A. K., Houston, D. M., and Tennyson, A. J. D. (2001). Census of the Snares crested penguin breeding population. *New Zealand Journal of Zoology* **28**(4), 432–433.

Bacastow, R. B., Keeling, C. D., Lueker, T. J., Wahlen, M., and Mook, W. G. (1996). The ^{13}C Suess effect in the world surface oceans and its implications for oceanic uptake of CO_2: analysis of observations at Bermuda. *Global Biogeochemical Cycles* **10**(2), 335–346. doi: 10.1029/96GB00192

Bearhop, S., Waldron, S., Votier, S. C., and Furness, R. W. (2002). Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiological and Biochemical Zoology* **75**, 451–458. doi: 10.1086/342800

Becker, B. H., and Beissinger, S. R. (2006). Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology* **20**(2), 470–479. doi: 10.1111/j.1523-1739.2006.00379.x

Birt, V. L., Birt, P., Goulet, D., Cairns, D. K., and Montevecchi, W. A. (1987). Ashmole's halo: direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series* **40**, 205–208. doi: 10.3354/meps040205

Bolstad, K. S. (2006). Sexual dimorphism in the beaks of *Moroteuthis ingens* Smith, 1881 (Cephalopoda : Oegopsida : Onychoteuthidae). *New Zealand Journal of Zoology* **33**, 317–327.

Boyd, P., LaRoche, J., Gall, M., Frew, R., and McKay, R. M. L. (1999). Role of iron, light, and silicate in controlling algal biomass in subantarctic waters SE of New Zealand. *Journal of Geophysical Research* **104**(C6), 13 395–13 408. doi: 10.1029/1999JC900009

Bradford-Grieve, J. M., Probert, P. K., Nodder, S. D., Thompson, D., Hall, J., Hanchet, S., Boyd, P., and Zeldis, J., *et al*. (2003). Pilot trophic model for subantarctic water over the Southern Plateau, New Zealand: a low biomass, high transfer efficiency system. *Journal of Experimental Marine Biology and Ecology* **289**, 223–262. doi: 10.1016/S0022-0981(03)00045-5

Cooper, J., Brown, C. R., Gales, R. P., Hindell, M. A., Klages, N. T. W., Moors, P. J., and van Heezik, Y. (1990). Diets and dietary segregation of crested penguins (*Eudyptes*). In 'Penguin Biology'. (Eds L. S. Davis and J. T. Darby.) pp. 131–156. (Academic Press: San Diego.)

Cruz, J. B., Lalas, C., Jillett, J. B., Kitson, J. C., Lyver, P. O. B., Newman, J. E., and Moller, H. (2001). Prey spectrum of breeding Sooty Shearwaters (*Puffinus griseus*) in New Zealand. *New Zealand Journal of Marine and Freshwater Research* **35**, 817–829.

Cunningham, D. M., and Moors, P. J. (1994). The decline of Rockhopper Penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* **94**, 27–36.

Davis, L. S., and Renner, M. (2003). 'Penguins.' (T. & A. D. Poyser: London.)

Ellis, S., Woehler, E. J., Skewgar, E., and Boersma, P. D. (2007). Penguin conservation assessment: summary document. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Fenwick, G. D. (1978). Plankton swarms and their predators at the Snares Islands. *New Zealand Journal of Marine and Freshwater Research* **12**(2), 223–224.

Forero, M. G., Hobson, K. A., Bortollotti, G. R., Donázar, J. A., Bertellotti, M., and Blanco, G. (2002). Food resource utilisation by the Magellanic penguin evaluated through stable-isotope analysis: segregation by sex and age and influence on offspring quality. *Marine Ecology Progress Series* **234**, 289–299. doi: 10.3354/meps234289

Fraser, M. M., and Lalas, C. (2004). Seasonal variation in the diet of blue penguins (*Eudyptula minor*) at Oamaru, New Zealand. *Notornis* **51**, 7–15.

Furness, B. L., Laugksch, R. C., and Duffy, D. C. (1984). Cephalopod beaks and studies of seabird diets. *Auk* **101**, 619–620.

Gales, R., and Pemberton, D. (1994). Diet of the Australian Fur Seal in Tasmania. *Marine and Freshwater Research* **45**, 653–664.

Guinard, E., Weimerskirch, H., and Jouventin, P. (1998). Population changes and demography of the Northern Rockhopper Penguin on Amsterdam and Saint Paul Islands. *Colonial Waterbirds* **21**(2), 222–228. doi: 10.2307/1521909

Habib, G. (1973). Aspects of the biology of the red cod (*Pseudophycis bachus*). Ph.D. Thesis, University of Canterbury, Christchurch.

Harcourt, R., Bradshaw, C., Dickson, K., and Davis, L. (2002). Foraging ecology of a generalist predator, the female New Zealand fur seal. *Marine Ecology Progress Series* **227**, 11–24. doi: 10.3354/meps227011

Heath, R. A. (1985). A review of the physical oceanography of the seas around New Zealand – 1982. *New Zealand Journal of Marine and Freshwater Research* **19**, 79–124.

Hecht, T. (1987). A guide to the otoliths of Southern Ocean fishes. *South African Journal of Antarctic Research* **17**, 1–87.

Hedd, A., and Gales, R. (2001). The diet of shy albatrosses (*Thalassarche cauta*) at Albatross Island, Tasmania. *Journal of Zoology* **253**, 69–90. doi: 10.1017/S0952836901000073

Hilton, G. M., Thompson, D. R., Sagar, P. M., Cuthbert, R. J., Cherel, Y., and Bury, S. J. (2006). A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome. Global Change Biology* **12**, 611–625. doi: 10.1111/j.1365-2486.2006.01130.x

Hobson, K. A., and Clark, R. G. (1992). Assessing avian diets using stable isotopes. I: Turnover of ^{13}C in tissues. *Condor* **94**(1), 181–188. doi: 10.2307/1368807

Hobson, K. A., and Wassenaar, L. I. (1997). Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* **109**, 142–148. doi: 10.1007/s004420050068

IUCN (2009). The IUCN Red List of Threatened Species. Version 2009.1. (International Union for Conservation of Nature and Natural Resources.) Available at www.iucnredlist.org [Verified 22 July 2009].

Jackson, S., and Ryan, P. G. (1986). Differential digestion rates of prey by White-chinned Petrels (*Procellaria aequinoctialis*). *Auk* **103**, 617–619.

Jackson, G. D., Shaw, A. G. P., and Lalas, C. (2000). Distribution and biomass of two squid species off southern New Zealand: *Nototodarus sloanii* and *Moroteuthis ingens*. *Polar Biology* **23**, 699–705. doi: 10.1007/s003000000141

James, G. D., and Stahl, J.-C. (2000). Diet of southern Buller's albatross (*Diomedea bulleri bulleri*) and the importance of fishery discards during chick rearing. *New Zealand Journal of Marine and Freshwater Research* **34**, 435–454.

Keeling, C. D. (1979). The Suess effect: ^{13}Carbon-^{14}Carbon interrelations. *Environment International* **2**, 229–300. doi: 10.1016/0160-4120(79)90005-9

Kirkwood, J. M. (1982). A guide to the Euphausiacea of the Southern Ocean. *Australian National Antarctic Research Expeditions Research Notes* **1**, 1–45.

Lalas, C. (1983). Comparative feeding ecology of New Zealand marine shags (Phalacrocoracidae). Ph.D. Thesis, University of Otago, Dunedin.

Laws, E. A., Popp, B. N., Bidigare, R. R., Kennicutt, M. C., and Macko, S. A. (1995). Dependence of phytoplankton carbon isotopic composition on growth rate and $[CO_2]_{aq}$: theoretical considerations and experimental results. *Geochimica et Cosmochimica Acta* **59**(6), 1131–1138. doi: 10.1016/0016-7037(95)00030-4

Lee, D. E., Nur, N., and Sydeman, W. J. (2007). Climate and demography of the planktivorous Cassin's auklet *Ptychoramphus aleuticus* off northern California: implications for population change. *Journal of Animal Ecology* **76**, 337–347. doi: 10.1111/j.1365-2656.2007.01198.x

Lu, C. C., and Ickeringill, R. (2002). Cephalopod beak identification and biomass estimation techniques: tools for dietary studies of southern Australian finfishes. Science Report No. 6, Museum Victoria, Melbourne.

Marchant, S., and Higgins, P. J. (Eds) (1990). 'Handbook of Australian, New Zealand and Antarctic Birds. Vol. 1: Ratites to Ducks.' (Oxford University Press: Melbourne.)

Miskelly, C. M., and Bell, M. (2004). An unusual influx of Snares crested penguins (*Eudyptes robustus*) on the Chatham Islands, with a review of other crested penguin records from the Island. *Notornis* **51**, 235–237.

Murphy, R. J., Pinkerton, M. H., Richardson, K. M., Bradford-Grieve, J. M., and Boyd, P. W. (2001). Phytoplankton distributions around New Zealand derived from SeaWiFS remotely-sensed ocean colour data. *New Zealand Journal of Marine and Freshwater Research* **35**, 343–362.

O'Reilly, C. M., Alin, S. R., Plisnier, P.-D., Cohen, A. S., and MCKee, B. A. (2003). Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature* **424**, 766–768. doi: 10.1038/nature01833

Paulin, C., Stewart, A., Roberts, C., and McMillan, P. (1989). 'New Zealand Fish – A Complete Guide.' (Te Papa Press: Wellington.)

Ridoux, V. (1994). The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. *Marine Ornithology* **22**(1), 1–192.

Romano, M. D., Piatt, J. F., and Roby, D. D. (2006). Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. *Waterbirds* **29**(4), 407–414. doi: 10.1675/1524-4695(2006)29[407:TTJHOM]2.0.CO;2

Roper, C. F. E., Young, R. E., and Voss, G. L. (1969). 'An Illustrated Key to the Families of the Order Teuthoidea (Cephalopoda).' (Smithsonian Institution Press: Washington, DC.)

Schell, D. M. (2000). Declining carrying capacity in the Bering Sea: isotopic evidence from whale baleen. *Limnology and Oceanography* **45**, 459–462.

Smith, P. J., Mattlin, R. H., Roeleveld, M. A., and Okutani, T. (1987). Arrow squids of the genus *Nototodarus* in New Zealand waters: systematics, biology, and fisheries. *New Zealand Journal of Marine and Freshwater Research* **21**, 315–326.

Stonehouse, B. (1971). The Snares Crested Penguin. *Ibis* **113**, 1–7. doi: 10.1111/j.1474-919X.1971.tb05118.x

Taylor, G. A. (2000). Action plan for seabird conservation in New Zealand. Part A: threatened seabirds. Threatened Species Occasional Publication No. 16, Department of Conservation, New Zealand, Wellington.

Thompson, D. R., Bury, S. J., Hobson, K. A., Wassenaar, L. I., and Shannon, J. P. (2005). Stable isotopes in ecological studies. *Oecologia* **144**, 517–519. doi: 10.1007/s00442-005-0171-8

van Heezik, Y. (1989). Diet of the Fiordland Crested Penguin during the post-guard phase of chick growth. *Notornis* **36**, 151–156.

van Heezik, Y. (1990). Diets of yellow-eyed, Fiordland crested, and little blue penguins breeding sympatrically on Codfish Island, New Zealand. *New Zealand Journal of Zoology* **17**, 543–548.

Vlieg, P. (1982). Proximate and fatty acid composition of the flesh of New Zealand red cod, hoki and jack mackerel. *New Zealand Journal of Science* **25**, 155–158.

Vlieg, P. (1984). Proximate analysis of 10 commercial New Zealand fish species. *New Zealand Journal of Science* **21**, 99–104.

Warham, J. (1974). The breeding biology and behaviour of the Snares crested penguin. *Journal of the Royal Society of New Zealand* **4**(1), 63–108.

Warham, J., Spurr, E. B., and Clark, W. C. (1986). Research on penguins in New Zealand. WLRG Research Review, Wildlife Research Liaison Group, Wellington.

Williams, T. D. (1995). 'The Penguins.' (Oxford University Press: Oxford, MA, USA.)

Wilson, R. P. (1984). An improved stomach pump for penguins and other seabirds. *Journal of Field Ornithology* **55**, 109–111.

Manuscript received 8 January 2008, accepted 22 May 2009