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Changes in diet and trophic position of a top predator 10 years after a mass mortality of a key prey

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After the disappearance of primary prey, seabirds exhibit gradually decreased breeding performance, and eventually the population size drops. Results are presented of an investigation into the diet of little penguins (*Eudyptula minor*) at Phillip Island, Australia, during a period when their key prey, pilchard (*Sardinops sagax*), declined dramatically. Data from stomach flushing (1982–2006) were used, supported by stable isotope (δ^{15}N, δ^{13}C) analyses of blood samples (2003, 2004, and 2006). The effect of the pilchard mortality on penguin diet was immediate, the birds shifting to a diet almost devoid of pilchard, and this was followed by 2 years of low breeding success, with considerably fewer penguins coming ashore. During periods when pilchard was not part of the diet, penguins consumed prey of a higher trophic level, e.g. higher values of δ^{15}N. Variability in penguin blood δ^{15}N coincided with years of low prey diversity. The disappearance of pilchard resulted in a decrease in prey diversity and led penguins to "fish up" the foodweb, possibly because of the simplified trophic structure. After 1998, however, breeding success re-attained average levels and the numbers of penguins coming ashore increased, probably because of increased abundance of prey other than pilchard after a 3-year period of food scarcity. Although little penguins apparently compensated over time, a less-flexible diet could make them ultimately vulnerable to further changes in their foodweb.

Keywords: diet changes, diet diversity, foodweb, pilchard mortality, seabird ecology, stable isotopes.

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Introduction

The natural or human-induced removal of key species in marine ecosystems has profound effects on foodwebs, leading to trophic cascades or ecological regime shifts (Österblom *et al.*, 2007; Baum and Worm, 2009). Seabird data have been used to detect such changes in marine ecosystems. Seabirds are highly sensitive to changes in food abundance and diversity, whether related to climate, exploitation, or both (Crawford and Dyer, 1995; Reid and Croxall, 2001; Crawford, 2007; Frederiksen *et al.*, 2007; Ainley and Blight, 2009). Several studies have shown that after the disappearance of a primary prey, whether through climate-related change or commercial fisheries, seabirds exhibit decreased breeding performance and eventually lower population size (Frank *et al.*, 2005; Myers *et al.*, 2007; Baum and Worm, 2009). However, resulting changes in seabird populations are often gradual, being detected over several years, and are often non-linear (Furness and Tasker, 2000; Montevecchi, 2007; Piatt *et al.*, 2007). Rarely have examples of carry-over effects of an acute alteration of the availability of a key prey of seabirds been documented (Österblom *et al.*, 2006, 2007; Crawford, 2007).

In 1995, there was a mass mortality of pilchard *Sardinops sagax* throughout southern Australia and New Zealand (Griffin *et al.*, 1997), the largest mortality of a single marine fish species ever recorded (Jones *et al.*, 1997; Whittington *et al.*, 1997). Deaths were reported over 5000 km along the southern Australian coast, which represents the total range of the species in Australia (Griffin *et al.*, 1997; Jones *et al.*, 1997). The mortality, apparently caused by a herpesvirus spreading at 30 km d^{-1}, decimated ~70% of the population, seriously depleting the southern Australian stocks of pilchard in a very short time (Jones *et al.*, 1997; Gaughan *et al.*, 2000; Gaughan, 2002; Murray and Gaughan, 2003). Further pilchard mortality was recorded in 1998, but on a much smaller scale (Gaughan *et al.*, 2000; Ward *et al.*, 2001b).

The pilchard was a key component of southern Australia's marine foodweb, present in the diet of several top predators (Kailola *et al.*, 1993), and one of the most abundant commercial species in southern Australia (Gaughan *et al.*, 2000; Ward *et al.*, 2001b). However, despite the potential impact on the ecosystem of the disappearance of pilchard from southern Australia, few studies monitored the ecological effects of the mortality in the marine system (Bernoth, 2007; Whittington *et al.*, 2008).

Little penguins *Eudyptula minor*, as top predators, may be good monitors of change in their marine system. They are central-place

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foragers with one of the smallest foraging ranges among seabirds (<20 km; Collins *et al.*, 1999; Hoskins *et al.*, 2008), and their breeding success is strongly related to food availability (Chiaradia and Nisbet, 2006). At Phillip Island, Victoria, Australia, during the 1980s, the pilchard was a key prey in the diet of little penguins (Montague and Cullen, 1988; Cullen *et al.*, 1992). The breeding onset of penguins seemed to be related to an increased presence of pilchard in their diet, and its absence delayed breeding onset and coincided with poor breeding success (Cullen *et al.*, 1992). Anchovy *Engraulis australis* were equally important in penguin diet (Cullen *et al.*, 1992) and their patterns of abundance in the area were similar to those of pilchard (Hobday, 1992); however, anchovy mortality was not recorded in 1995 (Jones *et al.*, 1997). Therefore, the pilchard mortality provided a natural experiment in which the trophic response of a top predator such as the little penguin to changes in its marine ecosystem could be examined.

Previous studies of the diet of little penguins used flushed-stomach analyses, which yield prey-species composition, but such data can be complemented with stable isotope analyses to inform on trophic interactions between predator and prey (Barrett *et al.*, 2007; Inger and Bearhop, 2008). Measurements of the stable isotope ratios of carbon (δ^{13}C) and nitrogen (δ^{15}N) can provide trophic-level and space-use information of consumers in marine foodwebs (Hobson and Welch, 1992; Forero *et al.*, 2002; Hobson *et al.*, 2002). The use of δ^{13}C analyses can additionally provide information on feeding on inshore or benthically linked prey vs. offshore or pelagic prey (Hobson and Welch, 1992; France, 1995). In contrast to conventional dietary approaches, the stable-isotope method can trace assimilated food and integrate dietary information in the blood over longer periods (about a month for seabirds of medium size; Hobson and Wassenaar, 2008) than stomach analyses (often less than a day), which represent a single or at most few feeding events.

Predicting the diet changes of a predator in response to major reductions in its primary prey is difficult because it will depend on the relative abundance of alternative prey and the foraging limitations of the predator, in little penguin a range of 20 km (Collins *et al.*, 1999). However, penguins could have shifted to a more diverse diet, as removal of the then highly abundant pilchard facilitated the expansion of other less abundant species in other areas (Ward *et al.* 2001a). Within that context, we examined not only shifts in diet, but also possible changes in the foodweb of little penguins, when the availability of a key prey varied dramatically.

Here, long-term data from flushed stomachs (1982–2006), supported by δ^{13}C and δ^{15}N analyses (2003, 2004, 2006) of penguin blood and of their prey, were used to investigate possible changes in diet and trophic position in little penguins at Phillip Island, Australia, following the mortality of pilchard in 1995.

Methods

First, we examined whether the initial change in penguin diet after the pilchard mortality in 1995 (Chiaradia *et al.*, 2003) had persisted 10 years after the event, which we then related to changes in breeding success and population parameters. Second, the trophic positions of penguins and their prey were determined over 3 years of below- and above-average breeding success, a parameter considered a proxy for food availability (Chiaradia and Nisbet, 2006). Third, the isotopic foodweb of penguins was constructed before and after the pilchard mortality, using prey isotope values and prey proportion from the long-term conventional stomach-flushed dataset to determine whether penguins moved up or down in trophic position. Finally, penguin diet diversity was investigated, because shifting the balance between a predator and its main prey can increase or decrease the diversity of the predator's diet (Croxall *et al.*, 1999).

Two sites at Summerland Peninsula, Phillip Island, Victoria, Australia (38°15′S 145°30′E) were used in this study—Parade and Radio-Tracking Bay, which are about 1 km apart. Both sites have about 100 nests marked individually, with an annual nest occupancy of ~60%. All birds were weighed and sexed, then injected with transponders (Trovan and Allflex, Australia) for individual identification. Bill depth was used to determine the sex of adults (Gales, 1988; Arnould *et al.*, 2004) and DNA analysis to sex chicks in 2003 and 2004, using polymerase chain reaction amplification of the *CHD* gene (Fridolfsson and Ellegren, 1999). This technique for determining the sex of little penguins has been validated (Overeem *et al.*, 2006). A custom-made hand-held transponder reader recorded the presence of birds with transponders in the colony (Chiaradia and Kerry, 1999). Parental status, such as pre-laying, incubation, chick guard, and chick post-guard, was determined during regular visits to both colonies (details on the breeding stages are provided by Chiaradia and Kerry, 1999). The Parade site was visited three times per week (Chiaradia and Nisbet, 2006) and the Radio-Tracking Bay every 2 weeks (Chiaradia *et al.*, 2003).

Breeding success was determined as the number of chicks fledged per pair (cpp). Data were standardized as relative values in relation to the long-term mean. For the years when diet data were available, years were grouped in below-average (≤0.7 cpp, years 1985, 1987, 1995, and 2004) and above-average (>0.7 cpp, 1986, 1996, 1998, 2000, 2001, 2002, 2003, 2005, and 2006) breeding success, for a comparison with diet diversity.

Daily beach counts of penguins were used as a proxy for population change. Little penguins always return to shore after sunset, most crossing the beach during the first 2 h after sunset (Stahel and Gales, 1987; Daniel *et al.*, 2007), providing a good indication of daily attendance. Birds were counted at the Parade colony every day for 50 min after the first group of penguins crossed the beach. Data were standardized as relative mean values in relation to the long-term mean.

Stomach-flush samples were collected from 1982 to 2006 at Phillip Island. Data for 1982 and 1983 were from Montague and Cullen (1988, their Table 5). Although shown in Figure 1, they were not used in statistical analyses, because information on individual samples was not available. Data collected between 1985 and 1987 are from Cullen *et al.* (1992) and represent the period before the pilchard mortality. Although those samples were collected during the breeding period, the breeding status of individual birds was unknown. Therefore, all analyses performed with these data were grouped per year and not examined at the level of breeding stage. No data were available by stage between 1988 and 1994. Data from 1995 to 2006 (but no samples in 1997 and 1999) were collected at pre-laying, incubation, guard, and post-guard stages. Adults were trapped as soon as they arrived on the beach and food samples collected from marked birds with known recent breeding histories. Stomach samples were collected by stomach-flushing, according to the method of Gales (1987), later modified by Chiaradia *et al.* (2003). Samples were frozen at −20°C for later analysis (see details in Chiaradia *et al.*, 2003).

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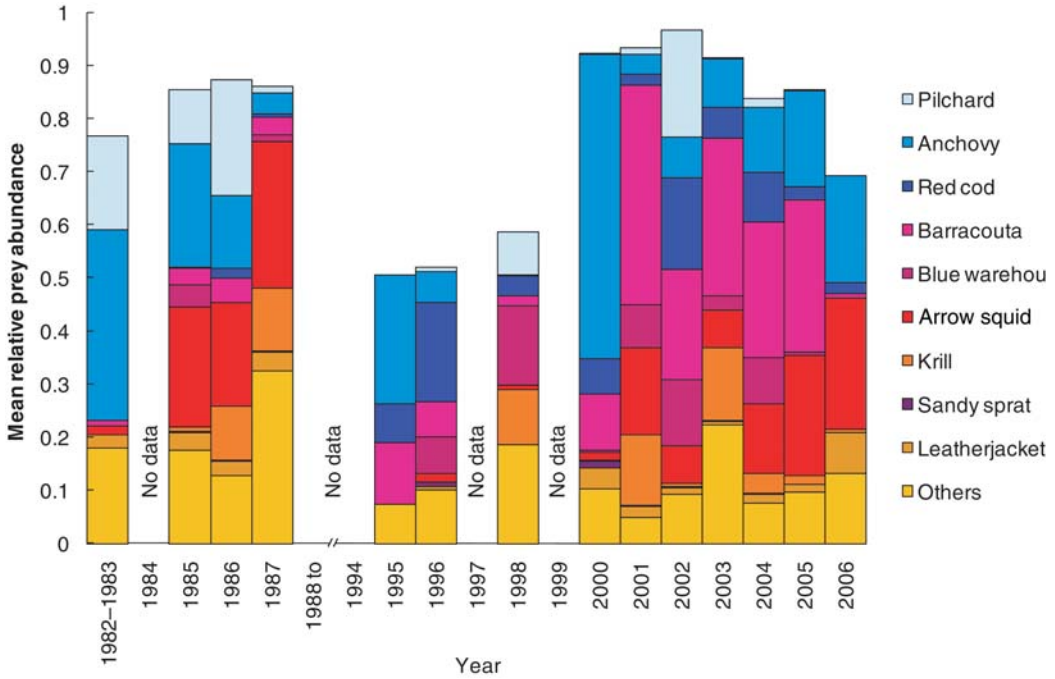

Figure 1. Mean relative prey abundance in the diet of little penguins from 1982 to 2006. Note that diet data are discontinuous and not available for the years 1984, 1988–1994, 1997, and 1999. Data for 1982 and 1983 are grouped, because the values were reconstructed from Montague and Cullen (1988), and data were not separated by years. Relative prey abundance does not add to 100% because zero values from empty stomachs are included (see the text). Therefore, decreased values of relative prey abundance indicate overall low prey abundance in the stomachs, most noticeably in 1995, 1996, and 1998.

Blood and prey sampling

Blood samples were collected from the Parade and Radio-Tracking Bay sites in 2003 and 2004 and from Radio-Tracking Bay only in 2006. At each colony, adults were sampled during the pre-laying, incubation, guard (chicks up to 3 weeks old), and post-guard stages [chicks between 6 and 7 weeks old; details on breeding stage in Chiaradia and Kerry (1999)]. Additionally, young (guard) and old chicks (post-guard) were sampled at each site. About 0.08 ml of blood was extracted from the brachial or tarsal vein (see Hobson *et al.*, 1997). Muscle samples of prey species (Table 1) were from catches of size similar to the penguins' prey (standard length ~14 cm; Cullen *et al.*, 1992), obtained from fishing boats operating inside Port Phillip Bay and in areas of the Bass Strait within 100 km of the study site. Samples of prey and penguin blood were stored in 70% ethanol at room temperature (20–25°C) until isotope analysis.

Stable-isotope analyses

Before stable-isotope analysis, ethanol was removed from the samples by decanting superfluous ethanol, then freeze-drying the balance. Prey tissues were treated for lipid extraction using a 2:1 chloroform:methanol solvent, then dried at 60°C for 24 h to remove residual solvent. The extraction of lipids was considered unnecessary for blood samples, because the lipid component in blood is generally very low (Deuel, 1955). Whole blood was freeze-dried, then powdered. Stable-carbon- and nitrogen-isotope assays were performed on 1-mg subsamples of homogenized materials by loading the material into tin cups and combusting at 1200°C in a Robo-Prep elemental analyser. The resultant carbon dioxide and nitrogen were then analysed using an interfaced Europa 20:20 continuous-flow isotope ratio mass spectrometer, with every five unknowns separated by two (baleen and egg albumen) laboratory standards. Based on replicate measurements on within-run standards, measurement error was estimated to be ± 0.3 and ± 0.1‰ for δ^{15}N and δ^{13}C measurements, respectively.

Analysis of relative prey

Diet composition was calculated by recording the proportional contribution of each species to the total mass of each stomach sample, hereafter referred to as relative prey abundance. The absence of a prey in the sample was recorded as a zero value, including empty stomachs, before the mean percentage value was calculated per prey item per year. As a consequence, the sum of the relative contributions of all species did not reach 100% in all years (Figure 1). Using relative prey abundance, each sample was weighted equally regardless of the mass of stomach contents. This method prevents biases towards the chick-rearing period, when stomach-content mass is several times heavier than at other stages of the penguin life cycle (Montague and Cullen, 1988; Cullen *et al.*, 1992; Chiaradia *et al.*, 2003).

Data analysis

Multivariate analyses were performed separately for adults and chicks to analyse intra-population variability on δ^{15}N and δ^{13}C values. The effect of sex on δ^{15}N and δ^{13}C was also tested for both age classes. The effect of breeding stage and year was tested on stable-isotope values of adults using generalized linear mixed models (GLMMs; Littell *et al.*, 1996). The response variables were the δ^{15}N and δ^{13}C values of blood samples, and the three categorical variables were year (2003, 2004, and 2006), breeding stage (pre-laying, incubation, guard, and post-guard), and sex. Repeated measures from the same adult between years or breeding stages were treated as a random term in the

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Table 1. Diet composition of little penguins during the breeding season from 1982 to 2006 at Phillip Island, Australia.

	Species	1982–1983[a] (321)	1985[b] (24)	1986[b] (164)	1987[b] (160)	1995[c] (6)	1996[c] (69)	1998 (61)	2000 (68)	2001 (95)	2002 (108)	2003 (80)	2004 (50)	2005 (60)	2006 (26)
Fish	**Anchovy (*Engraulis australis*)**	36 (2.1)	23 (7.3)	14 (1.9)	4 (1.0)	24 (12.6)	6 (2.1)	<1	57 (5.0)	4 (1.1)	8 (1.8)	9 (2.4)	12 (3.2)	18 (3.8)	20 (7.3)
	Pilchard (*Sardinops sagax*)	18 (1.6)	10 (5.1)	22 (2.6)	1 (0.4)		<1	8 (3.5)	<1	1 (1.1)	20 (3.5)	<1	2 (1.2)	<1	
	Red Cod (*Pseudophysis bachus*)		<1	2 (0.5)	<1	7 (9.8)	19 (3.7)	4 (2.0)	7 (2.5)	2 (0.7)	17 (2.7)	6 (2.1)	9 (3.0)	2 (1.2)	2 (1.9)
	Barracouta (*Thyrsites atun*)	1 (0.3)	3 (2.0)	4 (1.1)	3 (0.9)	11 (7.5)	7 (2.3)	2 (1.5)	11 (3.0)	41 (4.3)	21 (2.8)	30 (4.0)	26 (4.2)	29 (4.8)	<1
	Blue Warehou (*Seriolella brama*)		4 (3.1)		1 (0.6)		7 (2.6)	15 (4.4)	<1	8 (2.3)	12 (1.7)	3 (1.2)	9 (2.6)	<1	
	Leatherjackets (Monocanthidae)	2 (0.5)	3 (1.7)	3 (0.7)	4 (0.8)		<1		4 (1.1)	2 (0.9)	1 (0.3)	<1	2 (0.8)	1 (0.6)	8 (4.0)
	Seahorses (*Hippocampus* sp.)		<1	2 (0.5)	1 (0.6)	3 (4.1)	4 (1.9)	1 (1.2)	<1	<1	<1	<1	<1	<1	<1
	Sandy Sprat (*Hyperlochus vittatus*)		<1	<1	<1		<1		1 (0.8)	<1	<1	<1	<1		
	Hardyheads (*Atherinason* sp.)		<1		1 (0.8)		<1		<1	1 (1.1)	<1	2 (1.4)			
	Red Bait (*Emmelichthys nitidus*)									<1	3 (1.4)	2 (1.1)			
	Jack Mackerel (*Trachurus declivis*)								<1	<1	<1	5 (1.4)	<1		<1
	Garfish (*Hemiramphus far*)		1 (1.2)	<1	2 (0.6)			2 (1.6)			<1	<1		<1	
	Gurnards (Triglidae)		1 (1.0)	2 (0.7)	3 (0.8)					<1					
	Red Mullet (*Upeneichthys porosus*)					5 (4.4)	<1		<1	<1	<1				
	Pink Ling (*Genypterus blacodes*)						<1				<1		3 (2.1)		
	Silver Warehou (*Seriolella punctata*)								<1		<1		<1		
	Trevallies (Carangidae)		<1	<1	<1				1 (1.5)			<1			
	Fish postlarvae unknown		5 (3.4)	2 (0.9)	5 (1.2)		5 (2.2)	15 (4.1)	7 (2.7)	<1	1 (0.8)	8 (2.5)	1 (1.1)	2 (1.4)	6 (4.2)
Cephalopods	**Arrow squid (*Nototodarus gouldi*)**	2 (0.3)	23 (6.0)	20 (2.2)	28 (2.5)		2 (1.1)	<1	2 (0.6)	16 (3.0)	7 (1.4)	7 (2.0)	13 (3.4)	23 (3.9)	25 (6.7)
	Loliolus noctiluca		2 (1.6)	<1	4 (1.2)				<1			<1			
	Sepioteutis australis		<1	<1	1 (0.7)			<1		<1	<1	<1	<1		
	Argonauta nodosa		2 (1.0)	5 (1.0)	9 (1.6)			<1		2 (1.3)	1 (0.6)	<1	<1	<1	1 (1.0)
	Octopodidae							<1	<1		<1	<1			
	Post Larvae Cephalopod								<1		<1		<1	<1	
	Unknown Cephalopod			<1	2 (0.6)				<1	<1	<1	6 (2.5)		5 (2.3)	5 (3.9)
Crustaceans	Krill (*Nyctiphanes australis*)		<1	10 (2.1)	12 (1.9)			10 (3.4)	<1	13 (3.2)	<1	14 (3.8)	4 (2.5)	2 (1.0)	<1
	Stomatopoda		<1		2 (0.7)			<1	<1	1 (1.1)	2 (0.9)	<1	2 (1.8)	1 (1.0)	<1
	Amphipoda			<1	1 (0.5)			<1	<1	<1	<1	<1	<1	<1	<1
	Brachyura							<1	<1		<1			<1	
	Megalopa		3 (3.0)	<1	1 (0.5)										
	Unknown Crustacea		<1		<1				<1				<1		<1
	Other	18 (1.7)													
	Breeding success (ccp)	–	0.7	0.9	0.5	0.3	1.2	1.0	1.0	0.8	1.3	1.1	0.7	1.3	0.8
	Diversity index	–	1.1	0.8	0.8	0.6	0.5	0.2	0.4	0.4	0.7	0.5	0.6	0.6	0.4

Values are mean (s.e.) of the relative abundance (%) of prey species. For each year, relative prey abundance <1% is represented as <1, and the absence of prey as no entry. Data from 1998 are unpublished (P. Dann, pers. comm.). The yearly sample size is given in parenthesis at the top of each column. The main species in the diet that were used in the stable isotope analysis are in bold. Breeding success is expressed as the number of chicks fledged per pair. Diversity index is a non-unit value based on the Shannon–Weaver index (Shannon and Weaver, 1949).

[a]Relative prey abundance values were reconstructed from Montague and Cullen (1988).

[b]Original data from Cullen *et al.* (1992).

[c]Original data from Chiaradia *et al.* (2003).

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GLMM using the SAS Macro program GLIMMIX (Littell *et al.*, 1996). Changes in δ^{15}N and δ^{13}C values of male and female chicks were examined between guard and post-guard periods, and differences between chicks and their parents at guard and post-guard stages using generalized linear models (GLMs; Littell *et al.*, 1996), applying normal-error and identity-link functions of PROC GENMOD in SAS (Littell *et al.*, 1996).

Segregation among stable-isotope values of prey was analysed by a multivariate analysis of variance (ANOVA) test, and *post hoc* comparisons were tested with Wilks' lambda test. Prey species were classified into different trophic levels based on their δ^{15}N values. Isotope values and stomach-flushed data were combined to infer trophic-level change of penguins from before to after the pilchard mortality. Krill were not included in the analysis because their abundance changed only slightly for the whole period.

Prey were grouped into three trophic-level categories in relation to their δ^{15}N values and classified as low [pilchard and arrow squid (*Nototodarus gouldi*), <13‰], medium [red cod (*Pseudophycis bachus*) and blue warehou (*Seriolella brama*), >13‰ and <15‰], or high [anchovy and barracouta (*Thyrsites atun*), >15‰].

A two-isotope mixing-model analysis (Phillips and Gregg, 2003) was used to determine abundance of prey species in the penguin's isotope mixture, using diet-tissue isotope-discrimination values from Caut *et al.* (2009).

Diversity index

An annual index of diversity was calculated for each stomach sample using the Shannon–Weaver index (Shannon and Weaver, 1949), and it was compared before and after the pilchard mortality in 1995 according to the breeding stage, and between years of below- or above-average breeding success. For the within-year analysis, only data for years post-1995 were used when samples were from penguins of known breeding stage (incubation, guard, post-guard; $n = 9$ years). First, an ANOVA was performed with diversity index as the dependent variable, and the response was the period before and after 1995 (pilchard mortality). Second, the effect of breeding stage (incubation, guard, post-guard) on breeding success was tested with an ANOVA that included the year effect and the interaction between year and stage.

Results

Diet composition

In all, 20 species of fish, 6 of cephalopods, and 6 of crustaceans were identified in the diet of little penguins from 1292 samples (Table 1). The overall composition of fish, crustaceans, and cephalopods was similar to the results of previous studies (Cullen *et al.*, 1992; Chiaradia *et al.*, 2003). As stated above, relative prey abundance did not always add up to 100% because zero values from empty stomachs were included in the analysis. Therefore, low values of relative prey abundance indicated low prey abundance in the stomachs, most noticeably in 1995, 1996, and 1998 (Figure 1).

There was an effect of year on the combined proportion of main prey consumed (MANOVA; Wilks' $\lambda = 0.005$, $F_{7,952} = 28\,624$, 98, $p < 0.0001$). The effect of year was also significant for each of the main prey items consumed (ANOVA; all $p < 0.0001$; Figure 1). There was an effect of pilchard mortality on the combined relative abundance of the main prey consumed (Wilks' $\lambda = 0.805$, $F_{7,963} = 33.34$, $p < 0.0001$). The relative abundance of barracouta, anchovy, red cod, and blue warehou increased after the pilchard mortality in 1995 (ANOVA; all $p < 0.0001$). In contrast, pilchard and arrow squid were less frequent in the diet after the pilchard mortality (all $p < 0.0001$). Penguin consumption of krill was unchanged throughout the study period ($F_{1,971} = 1.12$, $p = 0.29$). In 1998, pilchard presence increased slightly in the diet, but another pilchard mortality in southern Australia may have further depleted the stocks (Ward *et al.*, 2001a). Since then, the proportion of pilchard in the diet has been <2%, except for a value of 20% in 2002.

Breeding success

Breeding success varied from 0.07 (1997) to 2 (1981) cpp. Breeding success was below average in the 1980s and recovered to above average in the 1990s until 1995, the year of the pilchard mortality (Figure 2b). Breeding success was very low for 2 years just after the mortality (1995 and 1997), but surprisingly high in 1996, though there was no significant difference in the breeding success before and after the mortality ($t_{37} = 0.47$, $p = 0.64$). However, there was a significantly lower variance in breeding success after the pilchard mortality (0.04 from 1998 to 2006 vs. 0.19 before the mortality, $F_{24} = 5.14$, $p = 0.006$).

Beach counts

The annual mean number of penguins counted crossing the beach showed a pattern similar to that of breeding success (Figure 2c). Small numbers were ashore in the 1980s, followed by an increase in the early 1990s and a drop to below average in the years following the pilchard mortality in 1995. However, there were no differences in the mean or the variance of the numbers of penguins ashore before and after the pilchard mortality ($p > 0.5$).

Diet diversity

Penguins had a more diverse diet before the pilchard mortality (ANOVA; $F_{1,896} = 96.30$, $p < 0.001$). Males and females did not show differences in diet diversity (sex * year: $F_{1,896} = 0.49$, $p = 0.48$). Within years, diet diversity increased as the season progressed from incubation to post-guard stages (ANOVA; breeding stage, $F_{3,529} = 4.03$, $p = 0.02$). There was no difference in diet diversity between years of below- and above-average breeding success (year: $F_{1,529} = 2.35$, $p = 0.13$; year * breeding stage: $F_{2,529} = 0.22$, $p = 0.81$), but the variability in diet diversity was greater in years of poor breeding success (Figure 3). In the 3 years for which stable isotope data were collected (2003, 2004, and 2006), diet diversity was higher in the year of least breeding success (2004; $F_{1,156} = 0.3.14$, $p = 0.05$).

Prey isotope values

There was a significant effect of species on the combined stable isotope values of the main prey of little penguins (MANOVA; Wilks' $\lambda = 0.28$, $F_{10,182} = 16.1$, $p < 0.0001$). As expected, variance was much greater in δ^{15}N (3.6‰) than in δ^{13}C values (0.43‰) from the prey (Table 2). Anchovy and barracouta had the highest and similar δ^{15}N values (Tukey's DHS test, $p = 1.00$) and were segregated from the other few prey species (all $p < 0.02$). There were no significant differences in the δ^{13}C values among the four other dominant prey species (all $p > 0.126$). Arrow squid and barracouta had the highest mean values of δ^{13}C and differed from other prey species (all $p < 0.03$), which had more negative and similar δ^{13}C values (all $p > 0.99$; Figure 4; Table 2).

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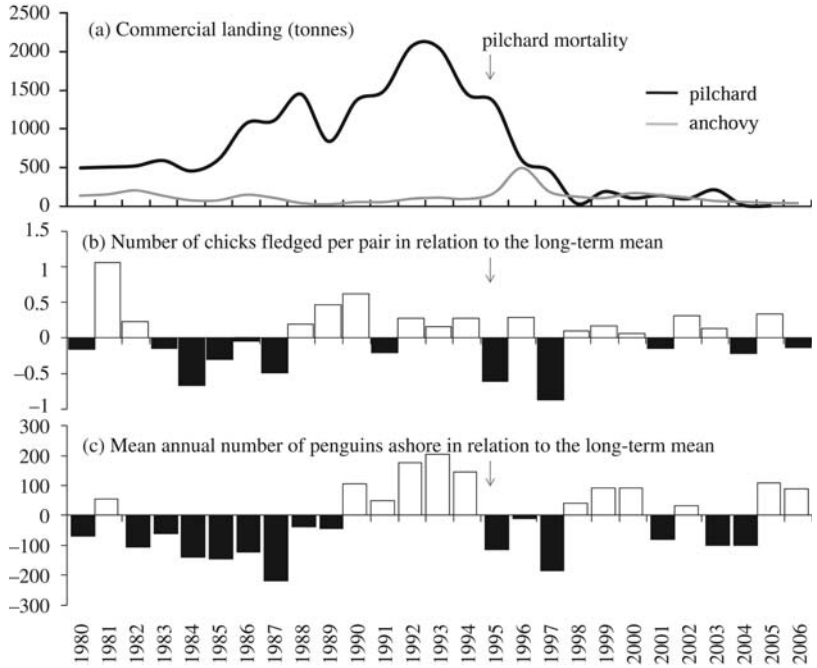

Figure 2. Commercial fishery landing and penguin parameters from 1980 to 2006. (a) Annual commercial catch of pilchard and anchovy near the little penguin colony (2006 not available for pilchard), showing the decline in pilchard landings after the mortality in 1995 and the relatively constant values for anchovy, except 1996 [data from Department of Primary Industries (2008)]. (b) Penguin breeding success expressed as the number of chicks fledged per breeding pair relative to the long-term mean. (c) Annual mean number of penguins crossing the beach daily as an index of penguin population change relative to the long-term mean. Note that zero on the *x*-axis represents the long-term mean value in (b) and (c).

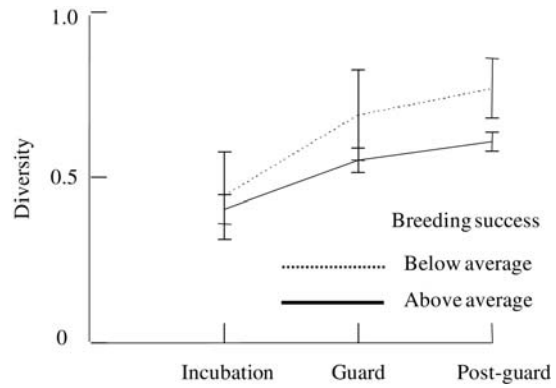

Figure 3. Diversity index of prey (mean ± s.e.) in the diet of little penguins from 1985 to 2006, grouped according to breeding stage and years of below- or above-average breeding success. The diversity index is a non-unit value based on the Shannon–Weaver index (Shannon and Weaver, 1949).

Penguin isotope values

Totals of 350 blood samples from adults and 175 from chicks were collected in 2003, 2004, and 2006 (Table 3). For adults, the GLMMs for δ^{15}N and δ^{13}C included the effects of breeding stage, year, and their interaction, after controlling for the random effect of individual identity (Table 4). Males and females did not differ in stable isotope values. The GLM for δ^{15}N explained a higher percentage (up to 89%) of the variance than δ^{13}C (up to 60%). During incubation and pre-laying, adults showed higher δ^{13}C values than during chick-rearing stages. Adults feeding large chicks at post-guard had the lowest values of δ^{15}N (Figure 5).

Table 2. Mean isotope values of nitrogen (δ^{15}N) and carbon (δ^{13}C) of the dominant prey of little penguins at Phillip Island, Australia, in 2003, 2004, and 2006.

	δ^{15}N(‰)		δ^{13}C (‰)		
Prey species	**Mean**	**s.d.**	**Mean**	**s.d.**	***n*[a]**
Anchovy	15.9	1.5	−19.9	0.5	14
Pilchard	12.8	1.4	−20.0	0.9	16
Barracouta	15.9	1.5	−19.4	0.5	21
Red cod	13.8	0.4	−20.1	0.3	18
Blue warehou	14.1	2.0	−20.0	0.3	10
Arrow squid	12.8	0.9	−19.9	0.4	19

[a]Sample size was the same for both isotopes.

For δ^{15}N and δ^{13}C values for chicks, there was a significant effect of year, age, and their interaction, but the effect of sex was not significant. For any given year of the study, small young chicks showed higher values of δ^{15}N than large older chicks, with 2006 the year with the greatest difference (Figure 5). The mixing-model analyses did not converge (Phillips and Gregg, 2003).

When analysing inter-year variance in stable isotope values and its relationship with diet diversity and breeding success, inverse trends for δ^{15}N and δ^{13}C were found over the 3 years studied. In 2004, when breeding success was lowest (0.7 chicks per pair), variance in δ^{15}N (0.13‰) was the lowest and variance in δ^{13}C (0.31‰) the highest. 2004 also had the highest diversity index

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calculated from regurgitations (0.6). Results for 2006 were opposite, with variance highest in δ^{15}N (1.55‰) and lowest in δ^{13}C (0.15‰), diversity of the diet lowest (0.4), and breeding success higher (0.8 chicks per pair) than in 2004.

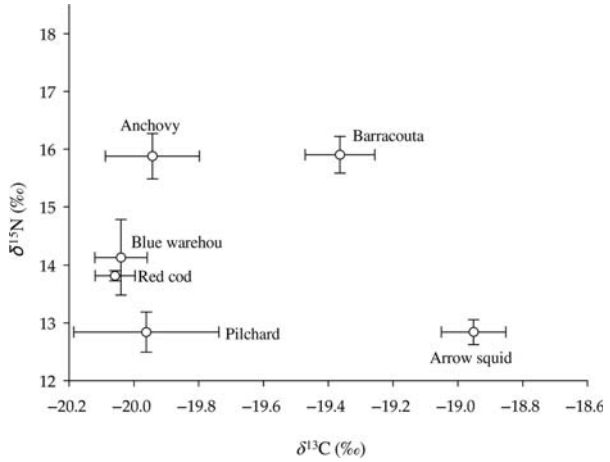

Figure 4. Trophic position (mean ± s.e.) of little penguin prey (open circles).

Penguin trophic position from stomach-flushed data

Trophic diet was reconstructed using the relative abundance of prey from 1985 to 2006 for the prey grouped in the three trophic-level categories in relation to low, medium, or high δ^{15}N values. Combined proportions of consumed prey of different trophic levels varied over the study period (MANOVA; Wilks' $\lambda = 0.054$, $F_{36,2787} = 18.18$, $p < 0.0001$), and this year effect was significant for each trophic-level category (ANOVA; all $p < 0.001$). After the pilchard mortality in 1995, little penguins' trophic position rose, as they consumed more prey from medium and high trophic levels and less from low trophic levels (Wilks' $\lambda = 0.812$, $F_{3,954} = 73.68$, $p < 0.001$; Figure 6).

Discussion

There was a massive mortality of pilchard in 1995 in southern Australia which led to a greatly reduced biomass of this key marine prey species (Jones *et al.*, 1997; Gaughan *et al.*, 2000; Gaughan, 2002; Murray and Gaughan, 2003). The effect of the mortality was immediate on little penguins at Phillip Island. In the first 2 years (1995 and 1996), their diet changed to similar proportions of barracouta, red cod, anchovy, and blue warehou, with pilchard completely absent (Chiaradia *et al.*, 2003), followed by a high mortality of penguins in winter 1995 (Dann *et al.*, 2000) and 2 years of very poor breeding success in 1995 and 1997 (the latter is

Table 3. Mean (and s.d.) isotope values of nitrogen (δ^{15}N) and carbon (δ^{13}C) from the blood of little penguin adults and chicks in 2003, 2004, and 2006.

	2003		2004		2005	
Parameter	**Adults**	**Chicks**	**Adults**	**Chicks**	**Adults**	**Chicks**
δ^{15}N(‰)	15.2 (0.7)	14.7 (0.3)	14.8 (0.4)	14.6 (0.3)	15.9 (1.3)	14.9 (0.6)
δ^{13}C(‰)	−19.6 (0.4)	−20.0 (0.2)	−19.4 (0.6)	−20.0 (0.3)	−20.0 (0.4)	−20.3 (0.2)
n	234	119	68	44	48	12

Table 4. GLMMs for the effect of year, season, and age on stable isotope signatures from the blood of little penguins at Phillip Island, Australia, in 2003, 2004, and 2006.

Response variable	GLM	Variables	Statistic	*p*-value	Explained deviance (%)
δ^{15}N	Adults	Individual identity	$Z = 6.03$	<0.0001	89
		Breeding stage	$F_{3,74} = 45.45$	<0.0001	
		Year	$F_{2,74} = 44.63$	<0.0001	
		Breeding stage * year	$F_{6,74} = 4.67$	0.0004	
	Chicks	Age	$\chi^2_1 = 38.36$	<0.0001	34
		Year	$\chi^2_2 = 11.86$	0.0027	
		Age * year	$\chi^2_2 = 22.44$	<0.0001	
	Small chick-adult segregation	Year	$\chi^2_1 = 86.88$	<0.0001	64
		Age	$\chi^2_2 = 79.05$	<0.0001	
	Large chick-adult segregation	Year * age*	$\chi^2_2 = 10.42$	0.005	10
δ^{13}C	Adults	Individual identity	$Z = 0.42$	0.34	60
		Breeding stage	$F_{3,74} = 35.05$	<0.0001	
		Year	$F_{2,74} = 45.71$	<0.0001	
		Breeding stage * year	$F_{6,74} = 14.39$	<0.0001	
	Chicks	Year	$\chi^2_2 = 18.97$	<0.001	22
		Age	$\chi^2_1 = 14.86$	0.0001	
		Year * age	$\chi^2_2 = 9{,}88$	0.007	
	Small chick-adult segregation	Age	$\chi^2_1 = 68.46$	<0.0001	49
		Year	$\chi^2_2 = 30.37$	<0.0001	
		Age * year	$\chi^2_2 = 17.50$	0.0002	
	Large chick-adult segregation	Year	$\chi^2_2 = 23.79$	<0.001	19
		Age	$\chi^2_1 = 5.00$	0.02	
		Year * age	$\chi^2_2 = 7.92$	0.02	

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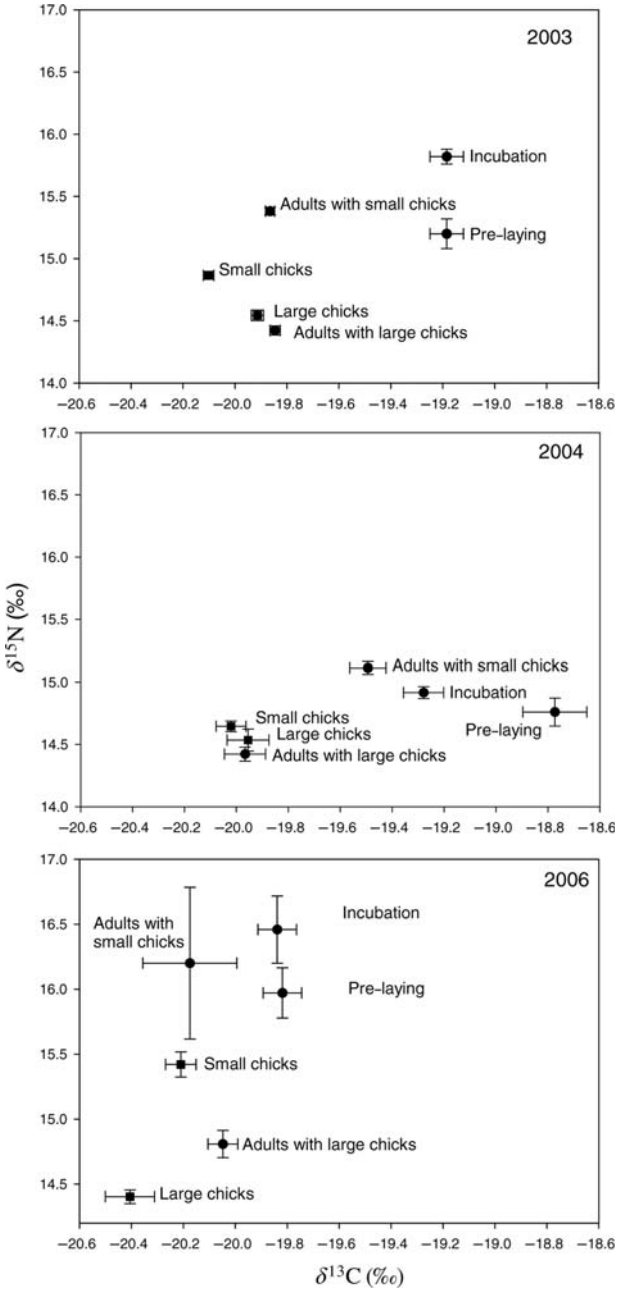

Figure 5. Stable isotope values (mean ± s.e.) for little penguin chicks (squares) and adults (dots) during different breeding stages and years, 2003, 2004, and 2006.

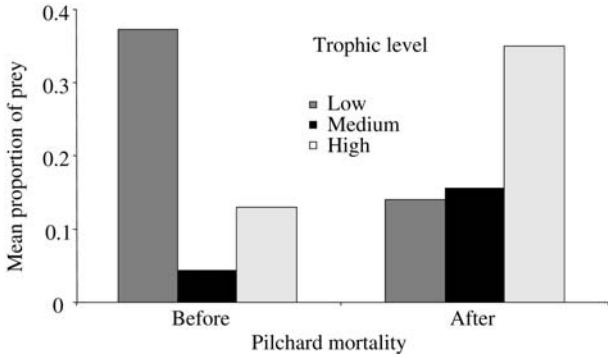

Figure 6. Mean proportion of prey of each trophic level consumed by little penguins before and after the pilchard mortality in 1995.

the lowest ever recorded). The breeding success in 1996 was above average, but the penguins showed high diet diversity and produce lighter chicks (Chiaradia and Nisbet, 2006), an indicator of poor food availability. Also from 1995 to 1997, considerably fewer penguins were counted coming ashore than in the years 1992–94. Overall, it seemed that food was scarce from 1995 to 1997 and that the penguins' low food supply and small chick size (Chiaradia and Nisbet, 2006) reflected this shortage. Then, in 1998, the situation for penguins seemed to improve. Breeding success re-attained average levels and the numbers of penguins coming ashore increased, likely because there was some improvement in feeding conditions after a 2–3-year scarcity; there was probably increased abundance of prey other than pilchard. However, the sudden removal of pilchard from the penguin diet caused a long-term increase in the trophic position of little penguins, coinciding with a less-diversified diet within a simpler foodweb, but with little long-term effect on breeding output and population parameters.

Little penguins, like all seabirds, obtain all their food at sea, but they must return to land to breed. This life strategy poses constraints both on land and at sea. In the 1980s, the breeding success of little penguins was below average and the population was in decline, partly because of an overall shortage of food at sea (Dann and Cullen, 1990; Cullen *et al.*, 1992; Dann, 1992). These declining patterns started to reverse at the start of the 1990s (Figure 2b and c). As decreases in breeding success were partially attributed to low availability of pilchard and anchovy (Cullen *et al.*, 1992; Hobday, 1992), the massive pilchard mortality in 1995 was expected to trigger a negative effect on food supply and breeding output similar to the years when pilchard were absent from the penguin diet in the 1980s.

Pilchard was probably unavailable to the penguins, as suggested by the crash in the commercial catch at Port Phillip Bay, Victoria, from 1339 t in 1995 to virtually zero in 2006 (Figure 2a; Department of Primary Industries, 2008), where the fishery operates within the foraging zone of penguins. Pilchard did not recover to pre-mortality levels in the penguin diet during the 10 years after the mortality in 1995 (with two exceptions, in 1998 and 2002), and the post-mortality absence of pilchard agrees with models simulating its recovery rate, which showed that it would take 15 years for pilchard to recover following the mortality (Murray and Gaughan, 2003).

Since 2000, little penguins have fed mainly on three species: barracouta, anchovy, and arrow squid. They may target pilchard as one of the optimal prey but, in their absence, they may target the next-most-profitable prey and can still breed successfully, as shown here. Therefore, the abundance of prey rather than the presence/absence of a particular prey species may be most important to the breeding success of little penguins.

Stable-isotope analyses during the 3 years of study (2003, 2004, and 2006) provided further detail of foraging behaviour and complemented the long-term stomach-flush data. Isotope values showed a noticeable shift within and between breeding seasons. Inter-year variability in stable-isotope values was high over the 3 years of intensive study. During pre-laying and incubation, adults had higher values of δ^{15}N and δ^{13}C, coinciding with

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inshore feeding within Port Phillip Bay (Collins *et al.*, 1999). Stable isotopes also showed that the two main prey items of penguins, barracouta and anchovy, have the highest values of δ^{15}N among the prey species.

Initially, it was thought that anchovy could increase in penguin diet to occupy the ecological niche left after the pilchard mortality. A decrease in pilchard abundance is usually followed by an increase in anchovy abundance in productive temperate ecosystems (Chavez *et al.*, 2003). However, anchovy schools behave differently (Barange *et al.*, 2009), feed on larger sizes of zooplankton (Espinoza *et al.*, 2009), and exploit a slightly higher trophic level than pilchard (van der Lingen, 1994; van der Lingen *et al.*, 2009). In this study, however, anchovy had δ^{15}N values as high as predators such as barracouta, but this could be explained if anchovy diet was dominated by fish eggs or larvae, placing them in the same trophic level of piscivorous species as anchovy off South Africa's east coast (Mketsu, 2008). This high trophic position of anchovy off Australia suggests that they are less abundant in the foodweb than pilchard. The local commercial landings support this notion, showing that there has not been a substantial increase in the anchovy fishery following the pilchard mortality (Figure 2a).

The relative abundance of arrow squid in the diet of penguins was similar before and after the pilchard mortality. In the absence of pilchard, arrow squid became the only key prey at low trophic position in the penguins' diet. Therefore, it could potentially be a low trophic and abundant substitute in the absence of pilchard. However, it has a much lower nutritional value than pilchard (Kailola *et al.*, 1993), and although squid species constitute main food resources for several species of seabird (Shealer, 2001), its dominance in the diet of little penguins has been related to poor breeding success (Cullen *et al.*, 1992).

Lower diversity in seabird diet is often associated with a decrease in breeding performance (Österblom *et al.*, 2006; Ainley and Blight, 2009), but in some cases, low diversity is related to an abundance of prey (Croxall *et al.*, 1999). In our study, high diet diversity coincided with negative outcomes for little penguin foraging. Diet diversity increased towards the end of the breeding season when foraging conditions usually deteriorate (Chiaradia and Nisbet, 2006). At that time, penguins would increase their diving effort, diving deeper owing to a decrease in the rate of prey encounter (I. Zimmer, pers. comm.). In years of poor breeding success, diet diversity was significantly higher. Previously, little penguins made longer trips to deliver the same amount of food to their chicks in years of low breeding success (Chiaradia and Nisbet, 2006). Therefore, they may have taken a greater diversity of species to compensate for the poor availability of food overall. This hypothesis is supported by greater variance in penguin blood δ^{13}C values during 2004 and lower values in 2006, the years of poorer breeding success than 2003. However, the lowest variance in penguin blood δ^{15}N values for 2004 suggests that penguins fed at the same trophic position even if the diversity of prey species was greater. Notably, diet diversity was less after the pilchard mortality, indicating a greater abundance of fewer prey species. This suggests that generalist birds such as little penguins can be more specialized when prey density is greater (Krebs *et al.*, 1977; Woo *et al.*, 2008).

The large change in biomass and spatial scale of the pilchard mortality could have triggered an ecological regime shift in the southern Australian marine ecosystem, as seen elsewhere (Österblom *et al.*, 2006, 2007). Although the mortality facilitated the expansion of other species off southern Australia (Ward *et al.*, 2001a), it does not seem to have prompted a pilchard/anchovy regime shift (Lluch-Belda *et al.*, 1989; Shannon *et al.*, 2004). However, no long-term studies have been conducted to determine the ecological impact of the mortality event in the marine foodweb of southern Australia, and more research is needed to understand the system better, such as in studies of predator–prey interactions in the Baltic Sea, southern Benguela, North Atlantic, California Current, and Southern Ocean (Christensen *et al.*, 2003; Shannon *et al.*, 2004; Österblom *et al.*, 2006, 2007; Ainley and Blight, 2009; Baum and Worm, 2009). In this context, an increase in the trophic position of little penguin prey reported here, probably a consequence of the pilchard mortality, is one of only a few studies on a predator response to that unique event (see Bunce and Norman, 2000; Ward *et al.*, 2001a; Taylor and Roe, 2004). Fishing up the foodweb would decrease prey abundance of the order of tenfold per trophic level (Christensen, 2000), but such a shift seems to have buffered, if not had a positive impact on, little penguins. However, the simpler foodweb and a less-flexible penguin diet (Srivastava and Bell, 2009) may make little penguins ultimately more vulnerable to further changes in their foodweb.

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