Climate change alters the trophic niche of a declining apex marine predator

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Abstract

Changes in the world's oceans have altered nutrient flow, and affected the viability of predator populations when prey species become unavailable. These changes are integrated into the tissues of apex predators over space and time and can be quantified using stable isotopes in the inert feathers of historical and contemporary avian specimens. We measured $\delta^{13}C$ and $\delta^{15}N$ values in Flesh-footed Shearwaters (*Puffinus carneipes*) from Western and South Australia from 1936–2011. The Flesh-footed Shearwaters more than doubled their trophic niche (from 3.91 ± 1.37 ‰^{2} to 10.00 ± 1.79 ‰^{2}), and dropped an entire trophic level in 75 years (predicted $\delta^{15}N$ decreased from +16.9 ‰ to + 13.5 ‰, and $\delta^{13}C$ from -16.9 ‰ to -17.9 ‰) – the largest change in $\delta^{15}N$ yet reported in any marine bird, suggesting a relatively rapid shift in the composition of the Indian Ocean food web, or changes in baseline $\delta^{13}C$ and $\delta^{15}N$ values. A stronger El Niño-Southern Oscillation results in a weaker Leeuwin Current in Western Australia, and decreased Flesh-footed Shearwater $\delta^{13}C$ and $\delta^{15}N$. Current climate forecasts predict this trend to continue, leading to increased oceanic 'tropicalization' and potentially competition between Flesh-footed Shearwaters and more tropical sympatric species with expanding ranges. Flesh-footed Shearwater populations are declining, and current conservation measures aimed primarily at bycatch mitigation are not restoring populations. Widespread shifts in foraging, as shown here, may explain some of the reported decline. An improved understanding and ability to mitigate the impacts of global climactic changes is therefore critical to the long-term sustainability of this declining species.

Keywords: El Niño-Southern Oscillation, flesh-footed shearwater, Leeuwin Current, niche width, *Puffinus carneipes*, stable isotopes

Introduction

Anthropogenic effects on marine ecosystems are ubiquitous, and include bycatch of marine animals in fisheries, ocean acidification, warming waters and pollution (Jennings & Kaiser, 1998; Rayner *et al.*, 2003; Votier *et al.*, 2005; Mallory *et al.*, 2010; Cheung *et al.*, 2013; Lavers *et al.*, 2014). These alterations can result in changes to species' distributions, diets and behaviours over ecological time (Reisewitz *et al.*, 2006; Cheung *et al.*, 2013; Hazen *et al.*, 2013). Large-scale climate influences species reproductive success, survival, diet and distributions (Jones *et al.*, 2002; Durant *et al.*, 2004; Péron *et al.*, 2010; Bond *et al.*, 2011, 2012; Surman *et al.*, 2012). Such changes in the marine ecosystem can be tracked using stable isotopes of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) from historical and contemporary specimens, which serve as proxies for foraging location and trophic level, respectively (Peterson & Fry, 1987; Kelly, 2000). These tracers can track changes in ecosystem

nutrient flow, and reflect changes in predators' diets (Shindler *et al.*, 1997; Becker & Beissinger, 2006). In the marine environment, these changes include general reduction of trophic level, restructuring of the food web and changes in fisheries interactions (Pace *et al.*, 1999; Essington *et al.*, 2006; Karpouzi *et al.*, 2007; Cury *et al.*, 2011), all of which can have drastic consequences for high-trophic predators, such as marine birds (Becker & Beissinger, 2006; Jaeger & Cherel, 2011; Wiley *et al.*, 2013). Identifying impacts on marine food webs over time requires historical baselines, which are often sparse, rarely begin prior to 1960, and are generally rare in the domain of oceanic birds: the open ocean (Wiley *et al.*, 2013). An important caveat, however, is that simply measuring a change in predators' isotope values does not necessarily signify that a dietary shift has occurred. Isotope values at lower trophic levels, from the base of the food web to the predators' immediate prey, all influence the $\delta^{13}C$ and $\delta^{15}N$ values in predators' tissues. Food web restructuring could also result in a predator's diet remaining unchanged over time, while $\delta^{13}C$ and $\delta^{15}N$ values change – a baseline shift. Regardless of the mechanism (diet shift or baseline

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shift), changes in δ^{13}C and δ^{15}N values in top predators do reflect changes in nutrient cycling, and are useful in examining ecosystem dynamics (Cabana & Rasmussen, 1994). In most systems, comparable time series of δ^{13}C and δ^{15}N in other lower components of the food web are unavailable, so while changes in stable isotope values are commonly ascribed to a change in predators' diet, this is indistinguishable from changes in nutrient cycling at lower trophic levels.

Flesh-footed Shearwaters (*Puffinus carneipes*) are apex predators in the Indian and Pacific Oceans, whose population has declined significantly in the last 40 years on their Australian & New Zealand breeding grounds (JLL, unpublished data; Priddel *et al.*, 2006; Reid *et al.*, 2013; Waugh *et al.*, 2013). The diet of Flesh-footed Shearwaters is poorly known, but likely consists of a mixture of squid and fish, such as pilchard (*Sardinops sagax*) (Gould *et al.*, 1997; JLL, unpublished data).

We examined evidence of a trophic shift and change in isotopic niche in breeding Flesh-footed Shearwaters from Western and South Australia using measurements of δ^{13}C and δ^{15}N in feathers grown on the breeding grounds during a period of relatively rapid oceanographic change (as indicated by the Southern Oscillation Index; SOI). Our goal was to determine whether there had been any significant changes in shearwaters' foraging patterns over the last 75 years, and use this information to provide insight into likely future impacts faced by this vulnerable species.

Materials and methods

Details of samples collected, and methods used for stable isotope analysis are presented by Lavers *et al.* (2013). Briefly, adult Flesh-footed Shearwaters were caught at breeding sites in Western and South Australia (Fig. 1) during the Austral summer of 2009–2011 and two breast feathers, grown during the breeding season (Onley & Scofield, 2007), were removed for stable isotope analysis. These contemporary samples were supplemented by birds caught as bycatch around Australia and New Zealand, and in the North Pacific Ocean during 1936–2011. Lavers *et al.* (2013) predicted the provenance of these bycatch individuals of unknown provenance using spatially varying trace elements (e.g., Gómez-Díaz & González-Solís, 2007). This resulted in a total of 119 birds originating in Western and South Australia (Table 1). There were insufficient samples from other breeding sites (Lord Howe Island or New Zealand) to examine changes in δ^{13}C and δ^{15}N over time (Lavers *et al.*, 2013).

Table 1 Flesh-footed Shearwaters' δ^{13}C and δ^{15}N stable isotope values in feathers from 1936–2011. Note that summary values may differ slightly from modelled values (see Results). Values are presented as the mean ± S.D

Period	n	δ^{13}C (‰)	δ^{15}N (‰)
Early (1936–1949)	9	−16.0 ± 0.8	+16.9 ± 1.5
Mid (1979–1994)	33	−17.2 ± 1.7	+13.8 ± 2.0
Late (2002–2011)	77	−17.4 ± 1.6	+13.9 ± 1.6

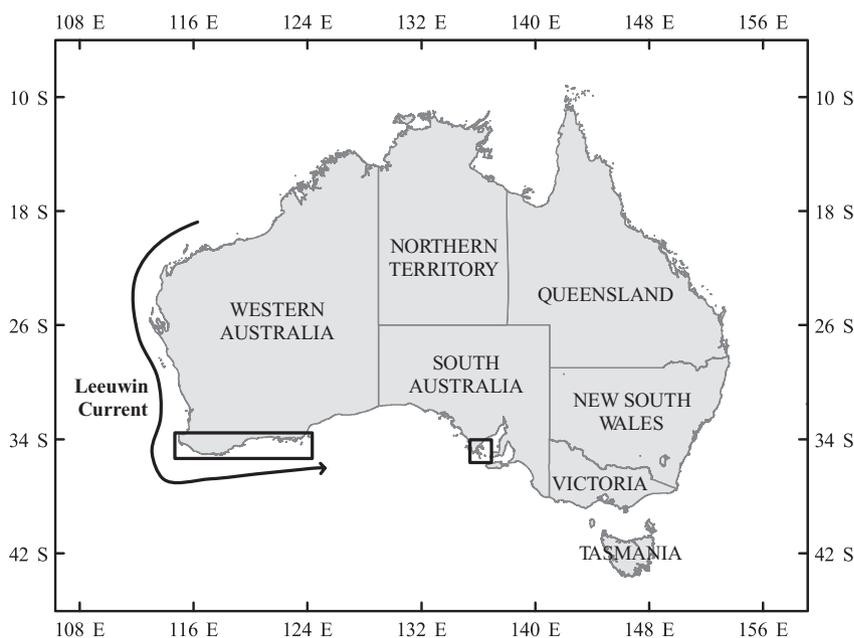**Fig. 1** We measured Flesh-footed Shearwater δ^{13}C and δ^{15}N from Western Australia and South Australia (black boxes; n = 119). The Leeuwin Current is the main oceanographic feature of the region.

Samples were divided into three temporal groups: early (1936–1949), mid (1979–1994) and late (2002–2011) based on availability and existing gaps in historical sampling from museum collections. Values of $\delta^{13}C$ were adjusted for the Suess effect (Suess, 1955):

$$\delta^{13}C_{adjusted} = \begin{cases} \delta^{13}C_{raw} - b_{his} \times (t_i - t_1) & \text{if } t_i \leq 1978 \\ \delta^{13}C_{raw} - b_{his} \times (1978 - t_1) - b_{mod} \times (t_i - 1978) & \text{if } t_i \geq 1978 \end{cases}$$

We used a value of -0.015 ‰ for the modelled annual decline in $\delta^{13}C$ around South and Western Australia after 1978 (b_{mod}), and -0.007 ‰ for the modelled historical decline during 1936–1949 (Gruber *et al.*, 1999; McNeil *et al.*, 2001; Tagliabue & Bopp, 2008). This is a similar estimate to the Suess effect in both global oceanic water and the atmosphere of 0.018 ‰ yr^{-1} (Quay *et al.*, 1992; Keeling *et al.*, 1995; Gruber *et al.*, 1999). Samples were ordered chronologically, where t_1 was the earliest sample, and $i = 1,\ldots,n$ are the remaining ordered samples from 1936 to 2011. The maximum adjustment was 0.5 ‰. $\delta^{13}C$ values are also negatively influenced by higher $CO_{2(aq)}$ (Louanchi & Hoppema, 2000), but the magnitude of change in the southern Indian Ocean is small; Hilton *et al.* (2006) and Jaeger & Cherel (2011) estimated the maximum change in $\delta^{13}C$ to be 0.16 ‰, which is within, or close to, analytical error in stable-isotope analysis (see Lavers *et al.*, 2013), so we did not adjust $\delta^{13}C$ values further.

We used an information theoretic approach to model shearwater isotope values. We constructed a series of biologically relevant models that included the year of collection, and the Southern Oscillation Index (SOI), a measure of the large-scale El Niño-Southern Oscillation (Trenberth, 1984). The SOI is strongly correlated with local oceanographic features that influence seabird ecology (Surman & Nicholson, 2009a; Surman *et al.*, 2012; Feng *et al.*, 2013). Because the SOI is generally increasing over time ($\beta = 0.093 \pm 0.037$, $P = 0.012$ for the years covering our samples), we used the residuals of the linear regression of SOI over time. Our multivariate candidate models predicting $\delta^{13}C$ and $\delta^{15}N$ included the year of collection and SOI (and their interaction) as predictors. Models were ranked using Akaike's Information Criteria (Akaike, 1974), and model weights (w_i) were used in model averaging to generate parameter estimates and their unconditional standard error (Burnham & Anderson, 2002).

To determine shearwaters' niche width during each period, we calculated the standard ellipse area Bayesian techniques (SEA_B) (Jackson *et al.*, 2011). We compared 10 000 posterior Bayesian estimates for each time group using an analysis of variance (ANOVA), and Ryan's Q *post-hoc* test (Ryan, 1960; Day & Quinn, 1989). *P*-values <0.05 were considered significant.

Results

Flesh-footed Shearwater $\delta^{15}N$ values were best explained by a model including year, the SOI, and their interaction ($w_i = 0.62$), but other models also received considerable support (Table S1). Year was the most likely parameter, followed by the SOI when models were averaged; $\delta^{15}N$ was negatively related to year ($\beta = -0.026 \pm 0.014$) and the year × SOI interaction ($\beta = -0.014 \pm 0.014$), and positively associated with the SOI itself ($\beta = 28.038 \pm 28.797$; Table 2).

Many models in the candidate set predicting $\delta^{13}C$ received substantial support; $\delta^{13}C$ as a function of collection year was the top-ranked model ($w_i = 0.36$); year + SOI was also well supported ($\Delta AIC_c = 0.67$; Table S2). The most important model-averaged parameter was year, which was negatively related to $\delta^{13}C$ ($\beta = -0.011 \pm 0.011$), followed by the SOI, which was positively related ($\beta = 1.753 \pm 8.162$; Table 3).

Using model-averaged parameters, the predicted $\delta^{15}N$ decreased from +16.9 ‰ to +13.5 ‰, a difference of 3.4 ‰, or the equivalent of an entire trophic level (Peterson & Fry, 1987; Kelly, 2000). Predicted $\delta^{13}C$ also decreased from −16.9 ‰ to −17.9 ‰, again, the equivalent one trophic level.

Table 2 Flesh-footed Shearwaters' $\delta^{15}N$ was negatively related to the year of collection and the year × Southern Oscillation Index (SOI) interaction, and positively related to the SOI. Parameter estimates are averaged across all candidate models (see Table S1)

Parameter	Parameter likelihood	Weighted estimate	Unconditional SE
Intercept	1.000	65.860	28.566
Year	0.999	−0.026	0.014
SOI	0.943	28.038	28.797
Year × SOI	0.623	−0.014	0.014

Table 3 Flesh-footed Shearwaters' $\delta^{13}C$ was negatively related to the year of collection and the year × Southern Oscillation Index (SOI) interaction, and positively related to the SOI. Parameter estimates are averaged across all candidate models (see Table S2)

Parameter	Parameter likelihood	Weighted estimate	Unconditional SE
Intercept	1.000	4.565	21.006
Year	0.733	−0.011	0.011
SOI	0.482	1.753	8.162
Year × SOI	0.113	−0.001	0.004

Shearwater's isotopic niche size increased significantly from 3.91 ± 1.37 ‰^{2} in early samples, to 7.48 ± 0.86 ‰^{2} in mid-period samples, to 10.00 ± 1.79 ‰^{2} in late samples ($F_{2,29997} = 48521$, $P < 0.0001$, all pairwise comparisons significant; $P < 0.0001$; Fig. 2).

Discussion

We conducted a retrospective study of Flesh-footed Shearwater foraging ecology based on stable-isotope values from samples collected during 1936–2011. Shearwaters' foraging changed significantly between the 1930s and today: $\delta^{15}N$ and $\delta^{13}C$ decreased significantly, and their niche has expanded. The most parsimonious explanation for this change in shearwater isotope values is trophic – the concurrent decline in $\delta^{15}N$ and $\delta^{13}C$ of a magnitude expected with one trophic level. We refrain from making direct dietary links as the shearwaters' trophic position may have decreased, while the composition of their diet may remain unchanged.

Changes in flesh-footed shearwater foraging

Large-scale climatic patterns are frequently related to measures of seabird diet and demography (Stenseth *et al.*, 2003; Durant *et al.*, 2004, 2009; Lavers *et al.*, 2008; Bond *et al.*, 2012), and most likely reflect bottom-up processes by affecting the abundance and availability of prey (Durant *et al.*, 2004, 2007; Hipfner, 2008). The El Niño-Southern Oscillation is known to influence these aspects of seabirds' ecology and behaviour (Barber & Chavez, 1983; Schreiber & Schreiber, 1984; Harding *et al.*, 2003; Stenseth *et al.*, 2003; Surman & Nicholson, 2009a). A negative SOI (related to a decrease in
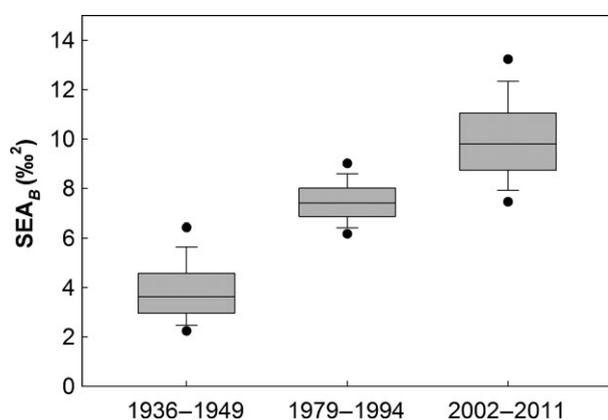
shearwaters' $\delta^{13}C$ and $\delta^{15}N$) indicates El Niño conditions. Around Australia, this is manifested in a weaker Leeuwin Current (the main nutrient transport current in Western Australia and the Great Australia Bight; Cresswell & Domingues, 2009; Feng *et al.*, 2013, 2009; Pattiaratchi & Buchan, 1991; Surman & Nicholson, 2009a), and changes in the vertical and horizontal distribution of shearwaters' prey around breeding colonies (Fletcher, 1992; Caputi *et al.*, 1996; Muhling *et al.*, 2008). Such conditions result in poorer reproductive performance of seabird prey, and more importantly, reduced abundance of these important prey species (Surman & Nicholson, 2009b). This is particularly worrying, as the Leeuwin Current is predicted to weaken under current climate models, and result in decreases in seabird populations through bottom-up mechanisms (Pattiaratchi & Buchan, 1991; Garnaut, 2008; Chambers *et al.*, 2011; Hobday & Lough, 2011). Although there have been large-scale mortality events in pilchards in Western Australia, caused primarily by viral infections (Gaughan *et al.*, 2000), these did not occur during years for which we had samples (1995, 1998), and pilchard stocks recovered quickly (Murray & Gaughan, 2003; Department of Primary Industries, 2009).

There have been few studies of dietary change in marine birds over comparable periods. The 3.4 ‰ shift in shearwaters' $\delta^{15}N$ is equivalent to an annual change of -0.045 ‰ yr^{-1}, and exceeds that reported for other marine birds (Thompson *et al.*, 1995; Becker & Beissinger, 2006; Hilton *et al.*, 2006; Farmer & Leonard, 2011; Jaeger & Cherel, 2011; Wiley *et al.*, 2013). Previous controversial papers have used the trophic level of fisheries landings to demonstrate an overall decrease in the marine system ('fishing down the food web'; Pauly *et al.*, 1997), but the decline in the trophic level of fisheries catch may also be the result of a dilution of the total catch with lower trophic species, or 'fishing through marine food webs' (i.e. not necessarily the replacement of high-trophic catch with that from lower trophic levels; Essington *et al.*, 2006). Unlike these multispecies assessments using fisheries catch, the evidence from seabirds, though from only a few studies, is unequivocal and indicates widespread trophic declines across diverse locations, among multiple foraging guilds, and often in association with the onset or collapse of large-scale fisheries operations.

Furthermore, we demonstrate not only a trophic decline, but a rapid shift in niche size. Without concurrent data on shearwaters' prey composition, and the isotope values of those prey species, we can only speculate as to the cause of the shearwaters' niche expansion. It is possible that shearwater diet was historically more conservative, and less diverse, but the increase in industrial fishing or changing ocean conditions have removed key species from the food web and altered the

Fig. 2 Flesh-footed Shearwaters' isotopic niche increased over time ($F_{2,29997} = 48521$, $P < 0.0001$; all pairwise comparisons significant, $P < 0.0001$). Niches are represented by 10 000 Bayesian iterations of the standard ellipse area (SEA$_B$). Lines indicate the median, boxes represent 1st and 3rd quartiles, whiskers are 95% credible intervals and dots are final outliers.

trophic relationships such that shearwaters' formerly preferred prey is no longer as abundant (Fletcher, 1992). This could result in shearwaters feeding on more diverse, but lower quality species (a 'take what you can get' strategy), as has been observed in other seabird species (Harris *et al.*, 2007; Lavers & Jones, 2007). Also possible is that shearwaters and large pelagic fish competed for similar prey (perhaps forage fish or squid), and the removal of tunas and other predatory fish released shearwaters from this competition causing their niche to expand (Bolnick *et al.*, 2009). Shearwaters and their prey may also be responding differently to changing conditions, resulting in a spatial mismatch (Hazen *et al.*, 2013). Opportunistic use of discards from fishing vessels by the birds have not likely contributed to a broader diet, as at-sea discards in Western and South Australian fisheries are rare (e.g., Division of Primary Industries & Resources, 2011). Regardless of the mechanism, the rapid doubling of shearwaters' trophic niche is a signal of considerable change in the marine environment of the eastern Indian Ocean.

The decrease in $\delta^{13}C$ by 1.4 ‰ has four possible explanations. First, Schell (2000) proposed that a decrease in $\delta^{13}C$ was a reflection of a reduction in primary production, based on the relationship between phytoplankton cellular growth rates and $\delta^{13}C$, even after accounting for the Suess effect (Cullen *et al.*, 2001; Schell, 2001). Consequently, Hilton *et al.* (2006), and Jaeger & Cherel (2011) interpreted the synchronous decline in $\delta^{13}C$ among multiple penguin species over a large area as a decline in the primary production (and therefore carrying capacity) of the southern oceans.

Second, changes in the concentration of aqueous CO_2 could have shifted phytoplankton $\delta^{13}C$ (i.e. the baseline $\delta^{13}C$ value in the system) over time, in addition to the Suess effect caused by anthropogenic CO_2 (Rau *et al.*, 1992; Louanchi & Hoppema, 2000). There are no data for Australian phytoplankton over the timescale in which we are interested, but we believe that any directional change in $\delta^{13}C$ would be accounted for in our correction for the Suess effect (Gruber *et al.*, 1999; McNeil *et al.*, 2001), and any adjustment for dissolved CO_2 would be small (Hilton *et al.*, 2006; Jaeger & Cherel, 2011).

Third, the foraging distribution of Flesh-footed Shearwaters could have changed over time from areas of lower $\delta^{13}C$ and $\delta^{15}N$. There can be considerable spatial variation in stable isotope values at landscape scales (Graham *et al.*, 2010; McMahon *et al.*, 2013), as well as smaller scales near the transition between benthic and pelagic systems (Hobson *et al.*, 1994; Dorresteijn *et al.*, 2012). While climate change is expected to alter the distributions of marine predators (Hazen *et al.*, 2013), we have no evidence that this has yet occurred in Flesh-footed Shearwaters.

And fourth, the change in shearwaters' $\delta^{13}C$ could result from a diet shift (either in the shearwaters or their prey) to food sources with lower $\delta^{13}C$. The concurrent decrease in $\delta^{15}N$ and rapid trophic niche expansion supports the idea that shearwaters' diet has changed over time, and so we believe this to be the most parsimonious explanation. A decrease of 0.5 ‰ is expected with a drop in trophic level (McCutchan *et al.*, 2003). Again, this change could occur at any level of the food web (i.e. shearwaters' diet may not have changed, but the food web certainly has).

Flesh-footed Shearwaters' $\delta^{15}N$, an indicator of trophic position, declined from +16.9 ‰ to +13.5 ‰, representing a decrease in approximately one trophic level (Kelly, 2000). As with the change in $\delta^{13}C$, this could be explained by a shift in baseline isotopic values, or a change in shearwaters' foraging distribution. More likely, although, is that the length of the food web culminating in Flesh-footed Shearwaters has shortened (Cabana & Rasmussen, 1994; Vander Zanden & Rasmussen, 1999; Becker & Beissinger, 2006). This trophic restructuring can have significant effects on predators' contaminant exposure (Lavoie *et al.*, 2013), physiology (Kouwenburg *et al.*, 2013) and demography (Durant *et al.*, 2003).

Changes to trophic structure in the marine environment

The marine environment in Western and South Australia is undergoing rapid changes, and increased 'tropicalization' (Cheung *et al.*, 2012). This coincides with changes in local oceanography (Pattiaratchi & Buchan, 1991; Garnaut, 2008; Cresswell & Domingues, 2009; Feng *et al.*, 2009; Kendrick *et al.*, 2009; Lenanton *et al.*, 2009), significant population declines in Flesh-footed Shearwaters (JLL, unpublished data) and wide-ranging distributional, demographic, dietary and ecological effects on better-studied seabird species (Chambers *et al.*, 2011). These environmental changes are compounded by threats from fisheries bycatch, invasive species, plastic pollution and increased competition for nest sites with Wedge-tailed Shearwaters (*Puffinus pacificus*), a more tropical congener now expanding its range (Chambers *et al.*, 2011; Croxall *et al.*, 2012; Fullagar *et al.*, 1990; R. Johnstone, personnel communication; JLL, unpublished data). Increasing air temperature associated with ENSO events and global climate change will also put pressure on shearwater populations as thermal stress and heavy rainfall have been linked to nest abandonment and breeding failure in seabirds (Howell & Bartholomew, 1961; Whittow, 1979; Whittow *et al.*, 1987; Thompson & Furness, 1991; Ludwig *et al.*, 1993; Tiller *et al.*, 2013).

As seabirds' diet (and distribution) shifted globally over the last 50–150 years, competition between seabirds and fisheries for an ever-decreasing biomass of

fish, squid and other invertebrates also changed, intensifying in some areas, and decreasing in others as new fisheries open and others close (Green *et al.*, 1998; Brooke, 2004; Karpouzi *et al.*, 2007; Cury *et al.*, 2011; Hazen *et al.*, 2013). There was minimal resource overlap between seabirds and fisheries in Western and South Australia in the 1990s (Karpouzi *et al.*, 2007). Pilchards are both a key prey species for shearwaters in Western Australia, and a commercial stock, although current competition between seabirds and harvesting is classified as low to moderate risk (Nardi *et al.*, 2006; Department of Fisheries, 2008; Fletcher & Santoro, 2011). Flesh-footed Shearwaters increasing niche size may increase their competition with fisheries, as they exploit novel prey resources (Jennings & Kaiser, 1998), or may be the result of a mesopredator release as higher-trophic marine species are removed (Crooks & Soulé, 1999; Bergstrom *et al.*, 2009).

The decline in Flesh-footed Shearwater populations has been largely attributed to direct anthropogenic threats such as plastic pollution, and fisheries bycatch (Baker & Wise, 2005; Priddel *et al.*, 2006; Lavers *et al.*, 2014). However, our results indicate changes or reductions in the prey base for this species through large-scale climatic and oceanographic processes has likely contributed to the serious reduction in the Flesh-footed Shearwaters' trophic position, and niche expansion. This could be a serious, but previously unknown, threat to this declining species, and may partially explain why conservation actions (e.g., fisheries bycatch mitigation) have not resulted in population recovery (Reid *et al.*, 2013; JLL, unpublished data).

Time series of museum specimens can be used to reconstruct historical (and prehistorical) marine trophic dynamics in relation to population change and demographics (Hobson *et al.*, 2004; Newsome *et al.*, 2007; Norris *et al.*, 2007; Wiley *et al.*, 2013). With a changing climate, these reconstructions of historic and prehistoric foraging provide a much needed baseline with which to assess changes in nutrient flow and population dynamics of marine predators. Our results suggest that the food web in the eastern Indian Ocean has changed drastically; it is also predicted to worsen in coming years and that will have implications for other apex predators (Garnaut, 2008). Crucial baseline data on the factors influencing the diet and demography of predators and their prey are sorely lacking; our retrospective analysis provides a starting point and offers several new lines of inquiry into the causes of trophic shifts in Leeuwin Current predators.

Additional research into shearwater diet, and historical changes in the ecology of other Indian Ocean predators would provide much needed insight into the scale of change to marine food webs in the region, and further our understanding of how this complex system has changed in ecological time.

Acknowledgements

References

Akaike H (1974) A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, **19**, 716–723.

Baker GB, Wise BS (2005) The impact of pelagic longline fishing on the flesh-footed shearwater *Puffinus carneipes* in eastern Australia. *Biological Conservation*, **126**, 306–316.

Barber RT, Chavez FP (1983) Biological consequences of El Niño. *Science*, **222**, 1203–1210.

Becker BH, Beissinger SR (2006) Centennial decline in the trophic level of an endangered seabird after fisheries decline. *Conservation Biology*, **20**, 470–479.

Bergstrom DM, Lucieer A, Kiefer K, Wasley J, Belbin L, Pedersen TK, Chown SL (2009) Indirect effects of invasive species removal devastate world heritage island. *Journal of Applied Ecology*, **46**, 73–81.

Bolnick DI, Ingram T, Stutz WE, Snowberg LK, Lau OL, Paull JD (2009) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proceedings of the Royal Society of London B Biological Sciences*, **277**, 1789–1797.

Bond AL, Jones IL, Sydeman WJ, Minobe S, Major HL, Williams JC, Byrd GV (2011) Reproductive success of planktivorous seabirds in the north Pacific is related to ocean climate on decadal scales. *Marine Ecology Progress Series*, **424**, 205–218.

Bond AL, Jones IL, Williams JC, Byrd GV (2012) Diet of auklet chicks in the Aleutian islands, Alaska: similarity among islands, interspecies overlap, and relationships to ocean climate. *Journal of Ornithology*, **153**, 115–129.

Brooke MdL (2004) The food consumption of the world's seabirds. *Proceedings of the Royal Society of London B Biological Sciences* (Supplement), **271**, S246–S248.

Burnham KP, Anderson DR (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.

Cabana G, Rasmussen JB (1994) Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature*, **372**, 255–257.

Caputi N, Fletcher WJ, Pearce AF, Chubb CF (1996) Effect of the Leeuwin Current on the recruitment of fish and invertebrates along the Western Australian coast. *Marine and Freshwater Research*, **47**, 147–155.

Chambers LE, Devney CA, Congden BC, Dunlop N, Woehler EJ, Dann P (2011) Observed and predicted effects of climate on Australian seabirds. *Emu*, **111**, 235–251.

Cheung WWL, Meeuwig JJ, Feng M *et al.* (2012) Climate-change induced tropicalisation of marine communities in Western Australia. *Marine and Freshwater Research*, **63**, 415–427.

Cheung WWL, Sarmiento JL, Dunne J *et al.* (2013) Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change*, **3**, 254–258.

Cresswell GR, Domingues CM (2009) The Leeuwin Current south of Western Australia. *Journal of the Royal Society of Western Australia*, **92**, 83–100.

Crooks KR, Soulé ME (1999) Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, **400**, 563–566.

Croxall JP, Butchart SHM, Lascelles B, Stattersfield AJ, Sullivan B, Symes A, Taylor P (2012) Seabird conservation status, threats and priority actions: a global assessment. *Bird Conservation International*, **22**, 1–34.

Cullen JT, Rosenthal Y, Falkowski PG (2001) The effect of anthropogenic CO_2 on the carbon isotope composition of marine phytoplankton. *Limnology and Oceanography*, **46**, 996–998.

Cury PM, Boyd IL, Bonhommeau S *et al.* (2011) Global seabird response to forage fish depletion—one-third for the birds. *Science*, **334**, 1703–1706.

Day RW, Quinn GP (1989) Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs*, **59**, 433–463.

Department of Fisheries (2008) *Application to the Department of the Environment, Heritage, Water and the Arts on the West Coast Purse Seine Managed Fishery and the South Coast Purse Seine Managed Fishery*. Department of Fisheries, Perth, Western Australia.

Department of Primary Industries (2009) *Status of fisheries resources in NSW, 2008/09. Australian sardine (Sardinops sagax)*. Wild Fisheries Research Program, Department of Primary Industries of New South Wales, Sydney.

Division of Primary Industries and Resources (2011) Ecological Assessment of the South Australian Marine Scalefish Fishery Reassessment Report. Adelaide, South Australia, Prepared for the Department of Sustainability, Environment, Water, Population and Communities by the Fisheries and Aquaculture Division of Primary Industries and Resources South Australia.

Dorresteijn I, Kitaysky AS, Barger C, Benowitz-Fredericks ZM, Byrd GV, Shultz MT, Young R (2012) Climate affects food availability to planktivorous Least Auklets *Aethia pusilla* through physical processes in the southeastern Bering Sea. *Marine Ecology Progress Series*, **454**, 207–220.

Durant JM, Anker-Nilssen T, Stenseth NC (2003) Trophic interactions under climate fluctuations: the Atlantic puffin as an example. *Proceedings of the Royal Society of London B Biological Sciences*, **270**, 1461–1466.

Durant JM, Anker-Nilssen T, Hjermann DØ, Stenseth NC (2004) Regime shifts in the breeding of an Atlantic puffin population. *Ecology Letters*, **7**, 388–394.

Durant JM, Hjermann DØ, Ottersen G, Stenseth NC (2007) Climate and the match or mismatch between predator requirements and resource availability. *Climate Research*, **33**, 271–283.

Durant JM, Hjermann DØ, Frederiksen M *et al.* (2009) Pros and cons of using seabirds as ecological indicators. *Climate Research*, **39**, 115–129.

Essington TE, Beaudreau AH, Weidenmann J (2006) Fishing through marine food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 3171–3175.

Farmer RG, Leonard ML (2011) Long-term feeding ecology of great black-backed gulls (*Larus marinus*) in the northwest Atlantic: 110 years of feather isotope data. *Canadian Journal of Zoology*, **89**, 123–133.

Feng M, Waite AM, Thompson PA (2009) Climate variability and ocean production in the Leeuwin Current system off the west coast of Western Australia. *Journal of the Royal Society of Western Australia*, **92**, 67–81.

Feng M, McPhaden MJ, Xie S-P, Hafner J (2013) La Niña forces unprecedented Leeuwin Current warming in 2011. *Scientific Reports*, **3**, 1277.

Fletcher WJ (1992) Use of a spatial model to provide initial estimates of stock size for a purse seine fishery on pilchards (*Sardinops sagax neopilchardus*) in Western Australia. *Fisheries Research (Amsterdam)*, **14**, 41–57.

Fletcher WJ, Santoro K(eds) (2011) *State of the Fisheries and Aquatic Resources Report 2010/11*. Government of Western Australia, Department of Fisheries, Perth.

Fullagar PJ, Davey CC, van Tets GF, Heyligers PC (1990) Is the short-tailed shearwater colonizing New South Wales? A long-term study on Montagu Island. *Nature in Eubodalla*, **5**, 51–56.

Garnaut R (2008) Projecting Australian climate change. In: *The Garnaut Climate Change Review-Final Report* (ed. Garnaut R), pp. 105–120. Cambridge University Press, Cambridge.

Gaughan DJ, Mitchell RW, Blight SJ (2000) Impact of mortality, possibly due to herpesvirus, on pilchard *Sardinops sagax* stocks along the south coast of Western Australia in 1998–99. *Marine and Freshwater Research*, **51**, 601–612.

Gómez-Díaz E, González-Solís J (2007) Geographic assignment of seabirds to their origin: combining morphologic, genetic and biochemical analyses. *Ecological Applications*, **17**, 1484–1498.

Gould P, Ostrom P, Walker W (1997) Food of flesh-footed shearwaters *Puffinus carneipes* associated with high-seas driftnets in the central north Pacific Ocean. *Emu*, **97**, 168–173.

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: *Isoscapes: Understanding Movement, Pattern, and Process on Earth through Isotope Mapping* (eds West JB, Bowen GJ, Dawson TE, Tu KP), pp. 299–318. Springer, New York.

Green K, Slip DJ, Moore GJ (1998) The take of fish species by seabirds and marine mammals in the Australian fisheries zone around Heard Island: the potential for competition with a commercial fishery. *Polar Biology*, **20**, 273–280.

Gruber N, Keeling CD, Bacastow RB *et al.* (1999) Spatiotemporal patterns of carbon-13 in the global surface oceans and the oceanic Suess effect. *Global Biogeochemical Cycles*, **13**, 307–335.

Harding AMA, Piatt JF, Hamer KC (2003) Breeding ecology of Horned Puffins (*Fratercula corniculata*) in Alaska: annual variation and effects of El Niño. *Canadian Journal of Zoology*, **81**, 1004–1013.

Harris MP, Beare D, Toresen R *et al.* (2007) A major increase in snake pipefish (*Entelurus aequoreus*) in northern European seas since 2003: potential implications for seabird breeding success. *Marine Biology*, **151**, 973–983.

Hazen EL, Jorgensen SJ, Rykaczewski RR *et al.* (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change*, **3**, 234–238.

Hilton GM, Thompson DR, Sagar PM, Cuthbert RJ, Cherel Y, Bury SJ (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.

Hipfner JM (2008) Matches and mismatches: ocean climate, prey phenology and breeding success in a zooplanktivorous seabird. *Marine Ecology Progress Series*, **368**, 295–304.

Hobday AJ, Lough JM (2011) Projected climate change in Australian marine and freshwater environments. *Marine and Freshwater Research*, **62**, 1000–1014.

Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *Journal of Animal Ecology*, **63**, 786–798.

Hobson KA, Sinclair EH, York AE, Thomason JR, Merrick RE (2004) Retrospective isotopic evidence of steller sea lion tooth annuli and seabird feathers: a cross-taxa approach to investigating regime and dietary shifts in the Gulf of Alaska. *Marine Mammal Science*, **20**, 621–638.

Howell TR, Bartholomew GA (1961) Temperature regulation in ensting Bonin Island petrels, wedge-tailed shearwaters, and Christmas Island shearwaters. *Auk*, **78**, 343–354.

Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER – stable isotope Bayesian ellipses in R. *Journal of Animal Ecology*, **80**, 595–602.

Jaeger A, Cherel Y (2011) Isotopic investigation of contemporary and historic changes in penguin trophic niches and carrying capacity of the southern Indian Ocean. *PLoS ONE*, **6**, e16484.

Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology*, **34**, 201–352.

Jones IL, Hunter FM, Robertson GJ (2002) Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the north Pacific Ocean. *Oecologia*, **133**, 38–44.

Karpouzi VS, Watson R, Pauly D (2007) Modelling and mapping resource overlap between seabirds and fisheries on a global scale: a preliminary assessment. *Marine Ecology Progress Series*, **343**, 87–99.

Keeling CD, Whorf TP, Wahlen M, van der Plicht J (1995) Interannual extremes in the rate of rise of atmospheric carbon dioxide since 1980. *Nature*, **375**, 666–670.

Kelly JF (2000) Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology*, **78**, 1–27.

Kendrick GA, Goldberg NA, Harvey ES, McDonald J (2009) Historical and contemporary influence of the Leeuwin Current on the marine biota of the southwestern Australian continental shelf and the Recherche Archipelago. *Journal of the Royal Society of Western Australia*, **92**, 211–219.

Kouwenburg A-L, Hipfner JM, McKay DW, Storey AE (2013) Corticosterone and stable isotopes in feathers predict egg size in Atlantic puffins *Fratercula arctica*. *Ibis*, **155**, 413–418.

Lavers JL, Jones IL (2007) Impacts of intraspecific kleptoparasitism and diet shifts on Razorbill *Alca torda* productivity at the Gannet islands, labrador. *Marine Ornithology*, **35**, 1–7.

Lavers JL, Jones IL, Diamond AW, Robertson GJ (2008) Annual survival of North American Razorbills (*Alca torda*) varies with ocean climate indices. *Canadian Journal of Zoology*, **86**, 51–61.

Lavers JL, Bond AL, Van Wilgenburg SL, Hobson KA (2013) Linking at-sea mortality of a pelagic shearwater to breeding colonies of origin using biogeochemical markers. *Marine Ecology Progress Series*, **491**, 265–275.

Lavers JL, Bond AL, Hutton I (2014) Plastic ingestion by flesh-footed shearwaters (*Puffinus carneipes*): implications for fledgling body condition and the accumulation of plastic-derived chemicals. *Environmental Pollution*, **187**, 124–129.

Lavoie RA, Jardine TD, Chumchal MM, Kidd KA, Campbell LM (2013) Biomagnification of mercury in aquatic food webs: a worldwide meta-analysis. *Environmental Science & Technology*, **47**, 13385–13394.

Lenanton RC, Caputi N, Kangas M, Craine M (2009) The ongoing influence of the Leeuwin Current on economically important fish and invertebrates off temperate Western Australia – has it changed? *Journal of the Royal Society of Western Australia*, **92**, 111–127.

Louanchi F, Hoppema M (2000) Interannual variations of the Antarctic ocean CO_2 uptake from 1986–1994. *Marine Chemistry*, **72**, 103–114.

Ludwig JP, Auman HJ, Kurita H *et al.* (1993) Caspian Tern reproduction in the Saginaw Bay ecosystem following a 100-year flood event. *Journal of Great Lakes Research*, **19**, 96–108.

Mallory ML, Robinson SA, Hebert CE, Forbes MR (2010) Seabirds as indicators of aquatic ecosystem conditions: a case for gathering multiple proxies of seabird health. *Marine Pollution Bulletin*, **60**, 7–12.

McCutchan JH Jr, Lewis WM Jr, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen and sulfur. *Oikos*, **102**, 378–390.

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. *Limnology and Oceanography*, **58**, 697–714.

McNeil BI, Matear RJ, Tilbrook B (2001) Does carbon 13 track anthropogenic CO_2 in the southern ocean? *Global Biogeochemical Cycles*, **15**, 597–613.

Muhling BA, Beckley LE, Koslow JA, Pearce AF (2008) Larval fish assemblages and water mass structure off the oligotrophic south-western Australian coast. *Fisheries Oceanography*, **17**, 16–31.

Murray AG, Gaughan DJ (2003) Using an age-structured model to simulate the recovery of the Australian pilchard (*Sardinops sagax*) population following epidemic mass mortality. *Fisheries Research* (Amsterdam), **60**, 415–426.

Nardi A, Gaughan D, Lenanton RC, Newman SJ (2006) *South Coast Purse Seine Managed Fishery Status Report*. Western Australia, Department of Fisheries, Albany.

Newsome SD, Etnier MA, Kurle CM, Waldbauer JR, Chamberlain CP, Koch PL (2007) Historic decline in primary productivity in western Gulf of Alaska and eastern Bering sea: isotopic analysis of northern fur sea teeth. *Marine Ecology Progress Series*, **332**, 211–224.

Norris DR, Arcese P, Preikshot D, Bertram DF, Kyser TK (2007) Diet reconstruction and historic population dynamics in a threatened seabird. *Journal of Applied Ecology*, **44**, 875–884.

Onley D, Scofield P (2007) *Albatrosses, Petrels, and Shearwaters of the World*. Princeton University Press, Princeton, USA.

Pace ML, Cole JJ, Carpenter SR, Kitchell JF (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution*, **14**, 483–488.

Pattiaratchi CB, Buchan SJ (1991) Implications of long-term climate change for the Leeuwin Current. *Journal of the Royal Society of Western Australia*, **74**, 133–140.

Pauly D, Christensen V, Dalsgaard J, Froese R, Torres F Jr (1997) Fishing down marine food webs. *Science*, **279**, 860–863.

Péron C, Authier M, Barbraud C, Delord K, Besson D, Weimerskirch H (2010) Interdecadal changes in at-sea distribution and abundance of subantarctic seabirds along a latitudinal gradient in the southern Indian Ocean. *Global Change Biology*, **16**, 1895–1909.

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics*, **18**, 293–320.

Priddel D, Carlile N, Fullagar P, Hutton I, O'Neil L (2006) Decline in the distribution and abundance of flesh-footed shearwaters (*Puffinus carneipes*) on Lord Howe Island, Australia. *Biological Conservation*, **128**, 412–424.

Quay PD, Tilbrook B, Wong CS (1992) Oceanic uptake of fossil fuel CO_2: carbon-13 evidence. *Science*, **256**, 74–79.

Rau GH, Takahashi T, Des Marais DJ, Repeta DJ, Martin JH (1992) The relationship between $\delta^{13}C$ of organic matter and $[CO_2(aq)]$ in ocean surface water: data from a JGOFS site in the northeast Atlantic Ocean and a model. *Geochimica et Cosmochimica Acta*, **56**, 1413–1419.

Rayner NA, Parker DE, Horton EB *et al.* (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research*, **108**, 4407.

Reid T, Hindell MA, Lavers JL, Wilcox C (2013) Re-examining mortality sources and population trends in a declining seabird: using Bayesian methods to incorporate existing information and new data. *PLoS ONE*, **8**, e58230.

Reisewitz SE, Estes JA, Simenstad CA (2006) Indirect food web interactions: sea otters and kelp forest fishes in the Aleutian archipelago. *Oecologia*, **146**, 623–631.

Ryan TA (1960) Significance tests for multiple comparison of proportions, variances and other statistics. *Psychological Bulletin*, **57**, 318–328.

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

Schell DM (2001) Carbon isotope ratio variations in Bering Sea biota: the role of anthropogenic carbon dioxide. *Limnology and Oceanography*, **46**, 999–1000.

Schreiber RW, Schreiber EA (1984) Central Pacific seabirds and the El Niño-Southern Oscillation: 1982 to 1983 perspectives. *Science*, **225**, 713–716.

Shindler DE, Carpenter SR, Cole JJ, Kitchell JF, Pace ML (1997) Influence of food web structure on carbon exchange between lakes and the atmosphere. *Science*, **277**, 248–251.

Stenseth NC, Otterse G, Hurrell JW *et al.* (2003) Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño-Southern Oscillation and beyond. *Proceedings of the Royal Society of London B Biological Sciences*, **270**, 2087–2096.

Suess HE (1955) Radiocarbon concentration in modern wood. *Science*, **122**, 415–417.

Surman CA, Nicholson LW (2009a) El Niño-Southern Oscillation and the Leeuwin Current influence on seabird reproductive performance and diet at the Houtman Abrolhos. *Journal of the Royal Society of Western Australia*, **92**, 155–163.

Surman CA, Nicholson LW (2009b) The good, the bad and the ugly: ENSO driven oceanographic variability and its influence on seabird diet and reproductive performance at the Houtman Abrolhos, eastern Indian Ocean. *Marine Ornithology*, **37**, 129–138.

Surman CA, Nicholson LW, Santora JA (2012) Effects of climate variability on breeding phenology and performance of tropical seabirds in the eastern Indian Ocean. *Marine Ecology Progress Series*, **454**, 147–157.

Tagliabue A, Bopp L (2008) Towards understanding global variability in ocean carbon-13. *Global Biogeochemical Cycles*, **22**, GB1025.

Thompson KR, Furness RW (1991) The influence of rainfall and nest-site quality on the population dynamics of the manx shearwater *Puffinus puffinus* on Rhum. *Journal of Zoology* (London), **225**, 427–437.

Thompson DR, Furness RW, Lewis SA (1995) Diets and long-term changes in $\delta^{15}N$ and $\delta^{13}C$ values in Northern Fulmars *Fulmarus glacialis* from two northeast Atlantic colonies. *Marine Ecology Progress Series*, **125**, 3–11.

Tiller CJ, Klomp NI, Fullagar PJ, Heyligers PC (2013) Catastrophic breeding failure caused by heavy rainfall in a shearwater colony. *Marine Ornithology*, **41**, 97–99.

Trenberth KE (1984) Signal vs. noise in the Southern Oscillation. *Monthly Weather Review*, **112**, 326–332.

Vander Zanden MJ, Rasmussen JB (1999) Primary consumer $\delta^{13}C$ and $\delta^{15}N$ and the trophic position of aquatic consumers. *Ecology*, **80**, 1395–1404.

Votier SC, Hatchwell BJ, Beckerman AP *et al.* (2005) Oil pollution and climate have wide-scale impacts on seabird demographics. *Ecology Letters*, **8**, 1157–1164.

Waugh SM, Tennyson AJD, Taylor GA, Wilson K-J (2013) Population sizes of shearwaters (*Puffinus* spp.) breeding in New Zealand, with recommendations for monitoring. *Tuhinga*, **24**, 159–204.

Whittow GC (1979) The effects of heavy rain on nesling wedge-tailed shearwaters (Rabbit island). *'Elepaio*, **39**, 138–139.

Whittow GC, Pettit TN, Ackerman RA, Paganelli CV (1987) Temperature regulation in a burrow-nesting tropical seabird, the wedge-tailed shearwater (*Puffinus pacificus*). *Journal of Comparative Physiology B Biochemical Systemic and Environmental Physiology*, **157**, 607–614.

Wiley AE, Ostrom PH, Welch AJ *et al.* (2013) Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, **110**, 8972–8977.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. The model set for predicting flesh-footed shearwaters' $\delta^{15}N$ values from 1936–2011. N: number of samples, K: number of parameters, AIC_c: Akaike's Information Criteria adjusted for small sample size, w_i: Akaike weight.

Table S2. The model set for predicting flesh-footed shearwaters' $\delta^{15}N$ values from 1936–2011. Abbreviation as in Table S1.

SUPPLEMENTAL MATERIAL

Table S1 – The model set for predicting Flesh-footed Shearwaters' $\delta^{15}N$ values from 1936-2011. N: number of samples, K: number of parameters, AIC_c: Akaike's Information Criteria adjusted for small sample size, w_i: Akaike weight.

Model	N	K	AIC_c	ΔAIC_c	w_i
Year + SOI + Year×SOI	119	4	138.00	0.00	0.623
Year + SOI	119	3	139.33	1.33	0.320
Year	119	2	142.77	4.77	0.057
SOI	119	2	152.25	14.26	0.000
Intercept Only	119	1	155.09	17.09	0.000

Table S2 – The model set for predicting Flesh-footed Shearwaters' $\delta^{15}N$ values from 1936-2011. Abbreviation as in Table S1.

Model	N	K	AIC_c	ΔAIC_c	w_i
Year	119	2	108.21	0.00	0.362
Year + SOI	119	3	108.89	0.67	0.258
Intercept Only	119	1	109.89	1.68	0.156
Year + SOI + Year×SOI	119	4	110.54	2.33	0.113
SOI	119	2	110.57	2.36	0.111