

Linking at-sea mortality of a pelagic shearwater to breeding colonies of origin using biogeochemical markers

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ABSTRACT: An emerging issue in seabird conservation is the ability to link at-sea mortality with observed demographic changes at breeding colonies. Applications of modelling and biochemical markers can be used to assign mortalities of unknown provenance to a colony of origin ensuring conservation actions are targeted at those colonies identified as the most affected. We analysed feathers ($n = 120$) from flesh-footed shearwater *Puffinus carneipes* collected from 5 breeding colonies throughout their range. Using stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) and trace element concentrations (Mn, Ni, Cu, Mo, Ag, Ba, Pb), we assigned birds recovered from fishing vessels off Australia, New Zealand, and the North Pacific to colony of origin, and investigated the rate of correct assignment at 3 spatial scales. Using quadratic discriminant analysis, samples of known origin were correctly assigned to basin, region, and breeding colonies at similar rates (92.3, 81.3, and 88.1%, respectively). Stable isotopes succeeded in assigning individuals among basins (72.8%), performing less well at the region and colony level (52.5 and 36.4%, respectively). In contrast, correct assignment was consistent at all 3 scales using only trace elements (93.2, 95.7, and 96.6%, respectively). Applying our final model based on trace elements to 116 flesh-footed shearwaters taken as bycatch in eastern Australia ($n = 30$), Western Australia ($n = 32$), New Zealand ($n = 16$), eastern North Pacific ($n = 27$) and western North Pacific ($n = 11$), we assigned individuals to colonies in New Zealand (35.3%), Western/South Australia (36.2%), Western Australia (27.6%), and Lord Howe Island (0.9%). Bycatch in fisheries may help explain ongoing declines in flesh-footed shearwater populations across the species' range, highlighting the utility of assignment tools to account for unobservable mortality of wildlife at-sea.

KEY WORDS: Fisheries bycatch · Geographic assignment · Trace elements · Stable isotopes · Flesh-footed shearwater · *Puffinus carneipes*

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INTRODUCTION

For long-lived animals, the mortality of adults and independent young is of particular demographic importance, as these species rely heavily on high

survivorship to maintain populations due to low fecundity and a prolonged immature stage (Hamer et al. 2002). Population trajectories of so-called 'K-selected' species are primarily driven by changes in adult survival; thus small changes in survivorship can

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determine whether a population increases or decreases (Saether & Bakke 2000, Doherty et al. 2004). For many migratory animals, adult mortality occurs away from breeding sites. Since individuals are often of unknown provenance, it can be difficult to relate the source of mortality to observed demographic changes of specific populations.

An unknown, but potentially important portion of seabird mortality occurs at sea as fisheries bycatch, which is difficult to monitor and link to specific populations (Croxall et al. 2012). In a few cases, at-sea mortality has been indirectly linked to observed population declines at breeding colonies through the recovery of small numbers of marked birds (Croxall & Prince 1990, Belda & Sanchez 2001, Ryan et al. 2001). Given the paucity of ring returns in general, a more efficient method for establishing links between the status of populations, and known mortality sources, including bycatch, would provide a critical conservation and management tool.

Biochemical analyses, including stable isotopes, trace elements, and genetic data, have been used to establish the provenance of unmarked individuals (Szép et al. 2003, Kelly et al. 2005, Gómez-Díaz & González-Solís 2007, Opperl & Powell 2008, Hobson et al. 2009, 2012, Sturrock et al. 2012). Birds of unknown provenance are frequently assigned to their moult origins in terrestrial systems using measurements of stable-hydrogen isotope values ($\delta^2\text{H}$) in feathers (Hobson & Wassenaar 2008); however, similar approaches have rarely been used in marine systems due to less *a priori* information on the geospatial variation in potential biochemical markers (Szép et al. 2003, Kelly et al. 2005, Opperl & Powell 2008). Landscape-scale patterns in some markers (e.g. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) have recently been used to study the movements of migratory animals in the ocean (Pantaja et al. 2002, Graham et al. 2010, Jaeger et al. 2010, MacKenzie et al. 2011, Militão et al. 2013), but our understanding of these marine patterns lags behind our knowledge of terrestrial isoscapes.

Flesh-footed shearwater *Puffinus carneipes* are frequently affected by fisheries bycatch around their breeding colonies in Australia and New Zealand (Baker & Wise 2005), and during their transequatorial migration to the North Pacific (Gould et al. 1997, Ogi 2008). The population at their largest breeding colony on Lord Howe Island, Australia, has declined by 2.9% yr^{-1} since 2003, following an annual decline of 0.9% between 1978 and 2002 (Priddel et al. 2006, Reid et al. 2013a). The at-sea distribution of this important population overlaps significantly with the Australian Eastern Tuna and Billfish Fishery (ETBF;

see Fig. 1) during the breeding season (Thalmann et al. 2009, Reid et al. 2012) and various North Pacific fisheries during the non-breeding season (DeGange & Day 1991, Ogi 2008, Artukhin et al. 2010, Reid et al. 2013b). Interactions with fisheries (i.e. bycatch) may have reduced the flesh-footed shearwater breeding population in Western Australia, with as many as 60 adult birds taken by individual purse seine vessels in a single trip (DEF 2005, Dunlop 2007, Lavers in press). Recoveries of marked flesh-footed shearwaters are insufficient for identifying factors directly linked with population trends, though fisheries bycatch has been implicated in the observed decline on Lord Howe Island (Priddel et al. 2006, Tuck & Wilcox 2008, Reid et al. 2013b).

Our objective was to ground-truth the variation in biochemical markers (stable isotopes and trace elements) at flesh-footed shearwaters breeding sites, and thereby develop geospatial assignment algorithms at multiple spatial scales to predict the origin of birds caught as bycatch in fisheries around Australia, New Zealand, and in the North Pacific Ocean.

MATERIALS AND METHODS

Study sites and known provenance samples

The flesh-footed shearwater is widely distributed across the southern Indian and south-western Pacific Oceans during the breeding season (Fig. 1, Table 1) with colonies located on L'île Saint-Paul (500 pairs; Roux 1985) in the Indian Ocean, on 41 islands off the south-west coast of Western Australia ($\leq 40\,000$ pairs with the majority breeding in the Recherche Archipelago; Lavers in press), on Smith and Lewis Islands off the Eyre Peninsula in South Australia (~870 pairs; Lavers in press), on Lord Howe Island (16 267 pairs; largest single breeding colony; Reid et al. 2013a), and on 8 islands in northern New Zealand (11 614 pairs; Baker et al. 2010).

Feathers were selected for this study, as they are readily collected from both live and dead birds, are easy to transport and store, and their biochemical and isotopic composition are largely unaffected by preservation techniques after washing (Dauwe et al. 2003, Jaspers et al. 2007). To obtain colony-specific biogeochemical profiles, we sampled breast feathers, which are replaced late in the breeding season (January to March; Onley & Scofield 2007). Therefore, breast feathers sampled from bycatch birds, regardless of the time of year they were recovered, should

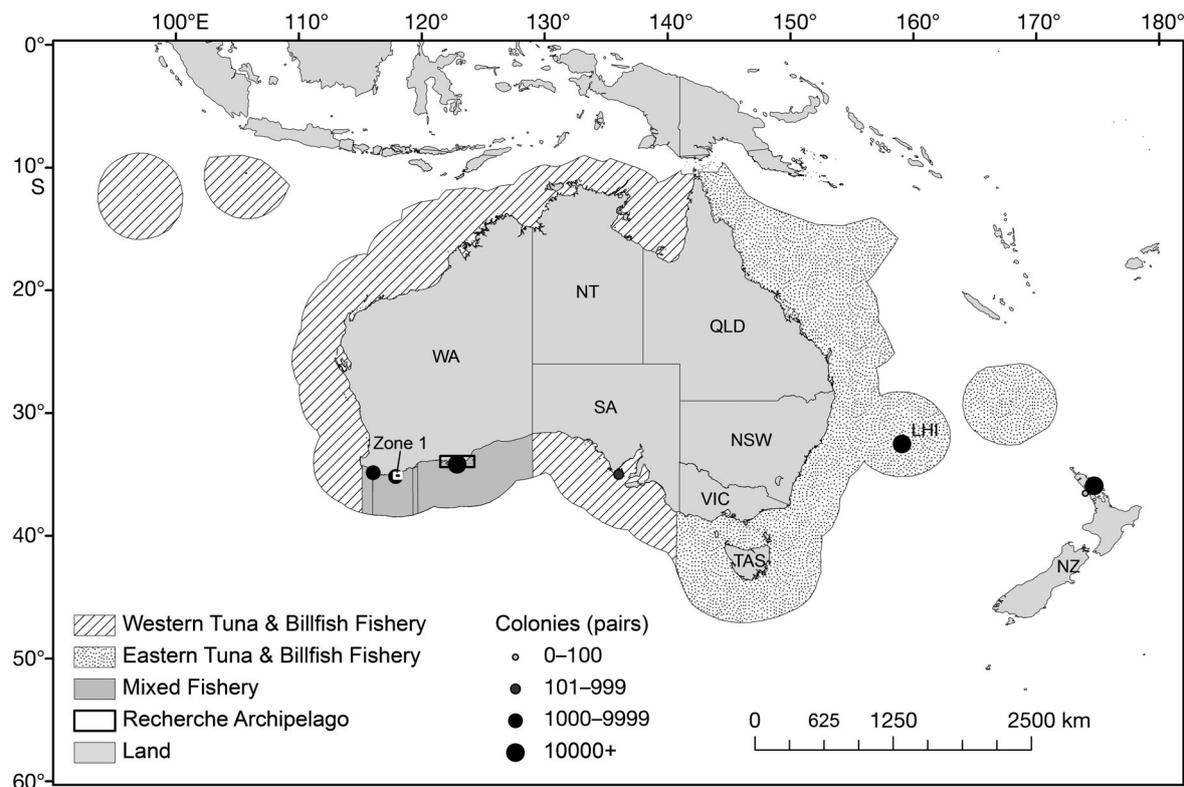


Fig. 1. *Puffinus carneipes*. Flesh-footed shearwater feathers were sampled from breeding colonies in Western Australia (WA; n = 26), South Australia (SA; n = 22), Lord Howe Island (LHI; n = 24), and New Zealand (NZ; n = 48). Key breeding and sampling areas and approximate fishing zones are shown: Western Tuna and Billfish Fishery (hatched), Eastern Tuna and Billfish Fishery (stipples), King George Sound purse seine fishery (Zone 1)

Table 1. *Puffinus carneipes*. Collection date and locations for known provenance flesh-footed shearwater feather samples used to build the quadratic discriminant model. Smith and Sandy Islands could not be statistically distinguished biochemically and were grouped for the colony-level analysis (see 'Materials and methods')

Location	Coordinates	Breeding pairs	Year	No. of birds sampled	
				Live	Museum
Lord Howe Island	32°31'S, 159°4'E	16 267	2008	24	0
New Zealand		11 614			0
Kauwahaia Island	36°32'S, 174°15'E		2009	18	
Lady Alice Islands	35°56'S, 174°44'E		2008	33	
South Australia		~870			0
Smith Island	35°0'S, 136°1'E		2011	20	2
Western Australia		≤40 000			
Sandy Island	34°52'S, 116°3'E		2011	10	0
Woody Island	33°57'S, 122°0'E		1979–2008	3	12

reflect the biogeochemical signature of the colony of origin. By sampling feathers, we were also able to make use of museum collections to increase the sample size of birds from colonies and recover red at sea.

We obtained 120 known-origin breast feather samples from 13 colonies spanning the species' entire

breeding range (Table 1, Fig. 1). We also sampled feathers from L'île Saint-Paul, but the final sample size (n = 7; 1970 to 1971) was insufficient for analysis, and data from these birds were not included.

Unknown provenance samples

Flesh-footed shearwater breast feather samples were obtained from birds recovered off fishing vessels throughout the North Pacific and within Australian and

New Zealand domestic waters. Feather samples were provided by the University of Washington Burke Museum (Seattle, Washington, USA) for 30 birds obtained from Japanese squid driftnet and long line fishing vessels during June to November 1990–2001. The National Institute of Water and

Atmospheric Research (Wellington, New Zealand) provided 15 birds recovered off scampi (*Metaneuprops challengerii*) and john dory (*Zeus* sp.) trawlers from New Zealand during October to April 2006–2009. The Western Australia Department of Environment and Conservation provided 30 birds recovered off purse seine vessels targeting pilchard *Sardinops sagax* in King George Sound in March 2009. The Tasmanian Museum (Hobart, Tasmania, Australia) provided 32 birds recovered off Eastern Tuna and Billfish Fishery (ETBF) long line vessels during October to May 1990–2005. Birds shot off the Goose Island Bank, British Columbia, Canada ($n = 7$; June to August 1947–1949) and taken as bycatch in the eastern North Pacific ($n = 4$; July to August 1990) were provided by the Beaty Biodiversity Museum's Cowan Tetrapod Collection (Vancouver, British Columbia, Canada).

Stable-isotope analysis

Feathers were washed in 0.25 M NaOH and rinsed thoroughly in grade 3 deionized water, or washed in a 2:1 chloroform:methanol solution to remove external contamination (Bearhop et al. 2000, Bond & Diamond 2009, Paritte & Kelly 2009). Approximately 0.25 mg per sample were placed in a tin capsule, crushed, and combusted in a Carlo Erba NA1500 Series II elemental analyzer for continuous-flow analysis of compounds for isotope ratios. The resultant gases were analyzed by a Delta V Plus isotope ratio mass spectrometer through a continuous-flow interface (CF-IRMS). Isotope values were calibrated using blanks and secondary isotopic reference materials that together cover the range of isotopic values in our samples and give precision (SD of replicates within and among runs) of 0.1‰ for $\delta^{15}\text{N}$ and 0.2‰ for $\delta^{13}\text{C}$ (Table S1 in the Supplement at www.int-res.com/articles/suppl/m491p265_supp.pdf). $\delta^{13}\text{C}$ values are presented relative to Vienna Pee Dee Belemnite, and $\delta^{15}\text{N}$ values relative to atmospheric N_2 (air) following Bond & Hobson (2012).

Trace element analysis

We weighed and washed (as per stable-isotope analysis) 2 feathers per bird (~15 to 25 mg per sample), and placed samples into clean Savillex 15 ml Teflon screw-cap vessels. We analysed 2 feathers per sample, as individual feathers can be highly variable in metal concentrations (Bond & Diamond 2008). We

added ~1 ml of 8 M HNO_3 (Fisher Scientific, 16 M, distilled in-house using Teflon stills) to the vessels, and capped and heated them on a hotplate at 70°C for 60 min. After 60 min, an additional 1 ml of 8 M HNO_3 was added and the feathers were pushed down with clean disposable plastic pipettes until fully submerged in the acid, and were capped and heated for 24 h. After 24 h, the hotplate was cooled to 50°C, the vessels were uncapped, and 1 ml of H_2O_2 (Fisher Scientific, 30% certified, American Chemical Society) was added. When the feathers had completely digested, the vessels were recapped and left on the hotplate for 3 h more at 70°C. We then diluted the sample 500× with distilled deionized water in clean, sealed containers. For inductively coupled plasma mass spectrometry (ICP-MS) analysis, 1 ml of the sample solution was pipetted into clean 10 ml tubes, and 4 ml of distilled, deionised water were added to make a final tube dilution of ~2500×.

Trace element concentrations were measured in a PerkinElmer ELAN DRCII ICP-MS (Rf power: 1200 W; ICP-MS plasma gas flow: 15 l min^{-1} ; auxiliary gas flow: 1 l min^{-1} ; nebulizer gas flow: 1 l min^{-1} ; sample uptake rate: 3.055 ml min^{-1}). Data acquisition was at peak-hopping mode (where the instrument software calculates concentrations at certain peaks, corresponding to certain elements), and each analyte mass was measured for 6 s based on protocols established by Friel et al. (1990). Procedural blanks and secondary reference materials were included every 15 to 20 samples. The secondary materials used are certified human hair samples 6H-09 and 7H-09 from the Centre de Toxicologie du Québec, Institut National de Santé Publique du Québec. Secondary reference materials were certified for concentrations of ^9Be , ^{27}Al , ^{51}V , ^{53}Cr , ^{55}Mn , ^{59}Co , ^{60}Ni , ^{63}Cu , ^{66}Zn , ^{75}As , ^{77}Se , ^{98}Mo , ^{107}Ag , ^{111}Cd , ^{118}Sn , ^{121}Sb , ^{137}Ba , ^{201}Hg , ^{205}Tl , ^{208}Pb , and ^{238}U , and we restricted our statistical analysis to those elements that could be analysed reliably as assessed by the recovery of reference materials. We therefore excluded Be, Cr, Se, and Sn from our analysis. We also excluded As and Hg from our statistical analysis, as museum preservation techniques can significantly affect concentrations in feathers (Marte et al. 2006, Vo et al. 2011). Recovery of the secondary reference material ranged from 85 to 129% among all runs. Values were corrected for background levels (e.g. atmospheric elemental concentrations not attributed to the analytical sample) using procedural blanks. For each element, we used the keratin reference material with the same magnitude of concentration as the unknowns to correct for recovery. Approximately 12% of samples

were run in duplicate, and residual SD of duplicates was within expected levels (range: 0.001 to 8.871; Table S2 in the Supplement). Comprehensive quality assurance and quality control details are provided in Table S3 in the Supplement.

Statistical methods

Prior to analysis, $\delta^{13}\text{C}$ values were adjusted for the Suess effect (Suess 1955): the result of increased combustion of fossil fuels that are depleted in ^{13}C altering $\delta^{13}\text{C}$ in terrestrial and marine systems. We used a 2-step adjustment following Eq. (2) in Farmer & Leonard (2011), where:

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

We used values of 0.007‰ for b_{his} , the modelled historical annual decline in $\delta^{13}\text{C}$ (Tagliabue & Bopp 2008), and 0.015‰ for b_{mod} , the modelled annual decline in $\delta^{13}\text{C}$ in the sub-Antarctic Zone around Australia and New Zealand from 1978 to 1998 (McNeil et al. 2001), and in the central tropical Pacific Ocean (Gruber et al. 1999). This estimate is also similar to the global estimate of 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). When samples were ordered chronologically, t_1 was the earliest sample, and $i = 1, \dots, n$ are the remaining ordered samples from 1936 to 2011. The maximum adjustment was 0.5‰.

We had no *a priori* hypotheses about the spatial scale of variation in our markers (stable isotopes or trace elements); we therefore performed our analyses at 3 spatial scales. At the coarsest spatial resolution (basins, Level 1), we defined 2 source populations: east (New Zealand and Lord Howe Island; ~159° to 175° E), and west (South and Western Australia; ~115° to 136° E). At an intermediate resolution (regions, Level 2), we defined 4 sources: New Zealand (36° S, 175° E), Lord Howe Island (31° S, 159° E), South Australia (34° S, 136° E), and Western Australia (34° S, 115° E to 34° S, 123° E). Our most precise spatial resolution was at the individual colony level (colonies, Level 3; Fig. 1). Preliminary analyses and data exploration suggested that Smith Island (South Australia) and Sandy Island (Western

Australia) could not be statistically distinguished based upon stable isotope values and elemental concentrations. We therefore grouped these 2 colonies together for our colony-level analysis ($n = 6$ colonies; Fig. S1 in the Supplement).

We removed cobalt (Co), cadmium (Cd), antimony (Sb), and thallium (Tl) from our analysis, as concentrations in our feather samples were frequently below detection limits. The concentration of remaining elements (Al, Mn, Ni, Cu, Zn, Mo, Ag, Ba, Pb, U) and isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) were $\ln(x + 0.01)$ -transformed to improve normality. Because our feathers were collected from 1936 to 2011, we used the residuals from linear regressions when there was a significant trend over time (all elements and isotopes except Zn, Mo, and U; Table S4 in the Supplement). The resulting variables were used as predictor variables in a quadratic discriminant analysis (QDA) in the MASS package in R 2.15.1 (Ripley et al. 2012). We used QDA over a linear discriminant analysis (LDA), as QDA relaxes the assumptions of homogeneity of covariances by fitting separate covariance matrices to each group of interest. Using known-origin birds with complete elemental and isotopic data ($n = 120$), we used backward stepwise variable selection with a 10-fold cross-validation to simultaneously reduce the number of predictors while attempting to maximize the separation of populations using trace elements, stable isotopes, and a combination of both. This was implemented using the klaR package (Roever et al. 2012). We removed the least informative variable until the improvement in correct classification was < 5%, and calculated the final rate of correct classification. The same final suite of variables was used in a leave-one-out cross-validation procedure, where we also calculated the proportion of birds correctly classified to origin.

Our final QDA algorithm (above) was then used to assign birds from the bycatch sample to their origin depending upon the spatial scale of analysis. We report the number of birds assigned to each colony according to their site of collection (west: east Australia, Western Australia, New Zealand, Pacific Ocean; and east: Pacific Ocean; Fig. 1)

RESULTS

The mean \pm SD concentrations of trace elements from known provenance birds used to construct the QDA model are reported in Table 2. Some elements showed significant temporal trends; therefore the residuals from linear regressions of \ln -transformed

Table 2. *Puffinus carneipes*. Mean \pm SD ln-transformed elemental concentrations from known-origin birds used to construct a quadratic discriminant function. *Elements with significant temporal trends (Table S4 in the Supplement at www.int-res.com/articles/suppl/m491p265_supp.pdf); we therefore used the residuals from linear regressions of ln-transformed concentrations over time. Is.: Island

Location	Elements						
	Mn*	Ni*	Cu*	Mo	Ag*	Ba*	Pb*
Kauwahaia Is.	1.599 \pm 0.516	0.916 \pm 0.327	-0.034 \pm 0.248	-1.494 \pm 0.461	-0.514 \pm 0.380	0.634 \pm 0.540	-0.781 \pm 0.399
Lady Alice Is.	-0.283 \pm 0.458	0.140 \pm 0.619	-0.129 \pm 0.216	-1.229 \pm 0.513	-0.512 \pm 0.794	0.179 \pm 0.714	-0.554 \pm 0.944
Lord Howe Is.	0.112 \pm 0.555	-0.276 \pm 1.018	-0.348 \pm 0.294	-1.315 \pm 0.405	0.456 \pm 0.945	-1.590 \pm 1.185	-0.553 \pm 1.021
Sandy/Smith Is.	-2.775 \pm 2.304	-2.085 \pm 2.317	-0.188 \pm 0.499	-1.677 \pm 0.749	-0.833 \pm 1.250	-2.562 \pm 2.104	-1.085 \pm 1.638
Woody Is.	0.127 \pm 0.521	0.520 \pm 0.886	0.402 \pm 0.430	-1.272 \pm 0.430	0.724 \pm 1.151	0.397 \pm 0.461	-0.262 \pm 0.628

concentrations were used in the QDA analysis (Table 2, Table S4 in the Supplement).

While correct classification was consistent across basin, region, and colony using only trace elements (93.2, 95.7, and 96.6%, respectively; Table 3), stable isotopes ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) mainly succeeded in classifying individuals among basins (72.8%), performing less well at the region and colony level (52.5 and 36.4%, respectively). Given the relative similarity in overall rates of correct classification and spatial resolution, the final QDA model was conducted at the colony spatial resolution using trace elements only (Table 3).

The final QDA model (Table 3, in bold) used to assign birds taken as bycatch to their colony of origin was built on 120 flesh-footed shearwaters of known origin using trace elements (Mn, Ni, Cu, Mo, Ag, Ba, Pb). Cross-validation suggested that the model was robust to sampling variance with classification accuracies of 92.3, 81.3, and 88.1% among basins, regions and colonies respectively.

Our final QDA model predicted that 30 flesh-footed shearwaters caught by ETBF vessels operating in eastern Australia came mainly from breeding colonies in South/Western Australia (53.3%) and the Lady Alice Islands (43.3%), with smaller numbers reported from Woody Island (3.3%; Table 4, Fig. 1). Bycatch in purse seine nets operating in King George Sound in south-western Western Australia (n = 32) originated primarily from Woody Island in the Recherche Archipelago (81.3%) with a few birds from Sandy/Smith Islands (9.4%), the Lady Alice Islands (6.3%), and Lord Howe Island (3.1%). Birds taken by Japanese vessels operating in the eastern North Pacific Ocean (n = 4) and shot off the west coast of Canada (n = 7) origi-

nated primarily from Sandy/Smith Islands (48.1%) and New Zealand (48.1%). Birds taken by Japanese vessels operating in the western North Pacific Ocean (n = 11) originated primarily from Sandy/Smith Islands (54.5%) and Woody Island (36.4%). Birds taken as bycatch in New Zealand fisheries (n = 16) were assigned to New Zealand (75.0%) and Sandy/Smith Islands (25.0%).

Table 3. *Puffinus carneipes*. Rates of cross validation and correct classification for each scale of the analysis for assignment of flesh-footed shearwater bycatch to colony of origin based on trace elements and stable isotopes. Final model is in bold

	Isotopes	Elements	Isotopes and elements
Cross validation			
Level 1 (basin)	71.1	92.3	91.5
Level 2 (region)	51.6	81.3	85.6
Level 3 (colony)	36.5	88.1	87.2
Analysis			
Level 1 (basin)	72.8	93.2	93.2
Level 2 (region)	52.5	95.7	94.9
Level 3 (colony)	36.4	96.6	96.6

Table 4. *Puffinus carneipes*. Results of the quadratic discriminant analysis based on the final model using trace elements and colony scale resolution indicate the majority of flesh-footed shearwaters taken as bycatch in fisheries originated in South/Western Australia. In parentheses: number of birds. Is.: Island

Bycatch location	Assigned origin				
	Kauwahaia Is.	Lady Alice Is.	Lord Howe Is.	Sandy/Smith Is.	Woody Is.
East Australia		43.3 (13)		53.3 (16)	3.3 (1)
Western Australia		6.3 (2)	3.1 (1)	9.4 (3)	81.3 (26)
North Pacific: west	11.1 (3)	37.0 (10)		48.1 (13)	3.7 (1)
North Pacific: east		9.1 (1)		54.5 (6)	36.4 (4)
New Zealand	43.8 (7)	31.3 (5)		25.0 (4)	

DISCUSSION

Close to 40% of all seabird species are affected by fisheries bycatch (Croxall et al. 2012), and to date, the only way to link individuals in the bycatch to breeding populations was through direct ring returns. The rate of ring returns, even in harvested seabird species, generally does not exceed 1 to 2% (Baillie 1995, Bakken & Mehlum 2005, Gaston et al. 2008), meaning that significant ringing effort is required to obtain reliable estimates of site-specific mortality. Fishers may also be reluctant to turn in rings for fear of prosecution (Camphuysen 2001, Österblom et al. 2002, Lavers et al. 2009), or ringed birds may be specifically targeted (Moore & Battam 2000). In contrast, a significant amount of information on the origin of bycatch can be obtained from feathers from a small number of recovered birds without the potential biases in recovery rates inherent in ringing data.

Here we predicted the origins of flesh-footed shearwaters of unknown provenance using trace elements in breast feathers. Of all flesh-footed shearwaters taken as bycatch (or shot) in Western Australia, Eastern Australia, and the North Pacific, only a small proportion (0.9%; Table 4) of the birds were assigned to Lord Howe Island, suggesting the long-term decline in flesh-footed shearwaters at their largest colony has likely not been as heavily influenced by fisheries as previously thought (Baker & Wise 2005, Thalmann et al. 2009). Recent tracking data suggests fisheries in China and elsewhere in Southeast Asia likely catch an unknown, but potentially significant number of flesh-footed shearwaters originating from Lord Howe Island (Reid et al. 2013b). However, observer data and tissue samples were not available for any of these fisheries. In Western Australia, purse seine fisheries in King George Sound may account for up to 80% of flesh-footed shearwater bycatch mortalities and may be driving population declines on some islands in the region (Lavers in press). The relatively high proportion of bycatch assigned to New Zealand (35.3%) suggests this population remains at risk from bycatch despite local fisheries reporting few recoveries due to the adoption of mitigation techniques (Baird 2004).

Mortality of small numbers of breeding adults can significantly impact the sustainability of long-lived species such as seabirds and sea turtles (Crouse et al. 1987, Hamer et al. 2002). Consequently, determining the origin of individuals killed away from breeding sites is important for

any attempt to assess the potential impact of human activities, such as oil spills and long line fishing, responsible for an increase in mortality of marine species. For the flesh-footed shearwater, adult mortality due to the ETBF has been reduced significantly since 2002 (from up to 4500 birds yr^{-1} to <20; Baker & Wise 2005, Tuck & Wilcox 2008) as the fishery moved further north (Reid et al. 2012). Therefore, the steeper post-2002 decline in the Lord Howe Island breeding population (2.9% yr^{-1}) is likely not solely attributable to bycatch in Australian fisheries, and other hypotheses must be investigated (e.g. plastic ingestion, toxins, and bycatch on the wintering grounds; Hutton et al. 2008, Bond & Lavers 2011, Reid et al. 2013a,b). In contrast, bycatch in Western Australian fisheries and the ETBF may partially explain the population declines reported in Western Australia since the 1970s (Table 4; Lavers in press). These results are concerning given >50% of the world's population breeds in Western Australia and no population monitoring is in place.

Our results, based on interactions with fisheries, provide the first insights into the movement patterns of flesh-footed shearwaters from South Australia. These birds appear to follow a similar route as those from Lord Howe Island, moving northeast into the Tasman Sea before heading to the North Pacific Ocean where they were found to interact with Japanese long line fishing vessels (Table 4). Post-breeding movements of Western Australian birds to the northern Indian Ocean is supported by limited tracking data ($n = 5$ tags transmitting for 6 to 15 d; Powell 2009). However, observations of flesh-footed shearwaters in the northern Indian Ocean comprise mainly older (1960 to 1980s) records of single birds (Hill & Burn 1945, Bailey 1966, 1971, Jensen & Jensen 1967, Shuntov 1968, Pocklington 1979, Wijesingher 1985, Karunaratne 1994). Our QDA results suggest an unknown, but potentially significant number of Western Australian birds may move east through the Bass Strait (between Australia and Tasmania) and on to the North Pacific Ocean where they overlap with high seas fisheries (Table 4). Tracking data from adult flesh-footed shearwaters from western New Zealand ($n = 3$; Rayner et al. 2011) and our assignment of North Pacific Ocean bycatch to New Zealand suggest the majority of birds are predicted to overlap with fisheries in the north-eastern Tasman Sea (e.g. ETBF; 43.3%) and North Pacific Ocean (>50%; Table 4).

Previous assignment studies have highlighted the benefits of using multiple markers (e.g. stable iso-

topes, trace elements, microsattellites, and morphometrics; Royle & Rubenstein 2004, Gómez-Díaz & González-Solís 2007, Sellick et al. 2009, Chabot et al. 2012). However, given funding limitations for most conservation projects, the potentially high analytical costs, and limitations of different methods, some may not be suitable. Morphometrics have been successfully used to differentiate some populations (Gómez-Díaz & González-Solís 2007, Delingat et al. 2011), but they can vary within and among measurers (Camphuysen 2005, Perkta & Gosler 2010), are not always available for bycatch, and precise descriptions of the metrics are often omitted. Microsatellites are expensive to develop, and DNA extraction from feathers can be difficult, leading to a high proportion of samples failing to amplify, especially from museum or bycatch samples (>50%; A. L. Bond & J. L. Lavers pers. obs.). While changes in patterns of some stable isotopes and trace metals in the marine environment over time are poorly understood (Lares et al. 2002, Graham et al. 2010), lab methods are well established, analyses are highly repeatable, and instruments are widely available and relatively inexpensive. Stable-isotope analysis is less expensive than ICP-MS analysis (often by a factor of 2 to 4×), so researchers applying multiple biogeochemical markers to questions of assignment must balance the trade-off between analytical cost and the degree of accuracy and precision required. For flesh-footed shearwaters, there was no appreciable decrease in the accuracy of classification using trace elements alone compared with the combination of stable isotopes and trace elements (Table 3). Gómez-Díaz & González-Solís (2007) also found a greater discriminatory power using elements over isotopes, though we were able to achieve greater rates of correct classification in our study.

Recent advances in characterizing isotopic distributions in the marine landscape, and pairing stable-isotope analyses with telemetric studies have improved our understanding of isoscapes in the marine environment (Graham et al. 2010, Jaeger et al. 2010, MacKenzie et al. 2011). Other intrinsic markers such as genetics or trace elements often lack *a priori* knowledge of spatial patterns, and require more extensive characterization of source populations. Overall, the selection of markers in assignment studies will depend on the degree of spatial resolution desired and budget. Knowledge of temporal variation in isotope values, and especially trace element concentrations, within study systems is limited and should be the focus of future research.

CONCLUSIONS

The successful management of highly migratory animals requires the cooperation of multiple jurisdictions, especially in the case of transequatorial migrants like flesh-footed shearwaters. In this circumstance, the demography of breeding populations can be influenced by mortality occurring thousands of km away and/or in the immediate vicinity of breeding colonies. By linking at-sea mortality to observed population trends on the breeding grounds, we can identify affected colonies and target conservation efforts for declining and threatened populations.

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