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Using Stable Isotopes to Assign Origin of White-Chinned Petrels Killed by Longline Fisheries

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ABSTRACT

Incidental capture (bycatch) of seabirds in longline and trawl fisheries is one of the main threats to many albatrosses and large petrels. The White-chinned Petrel (*Procellaria aequinoctialis*) has a circumpolar distribution and is the seabird species killed most frequently by fisheries in the Southern Ocean. In an attempt to identify provenance, stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) in feathers from White-chinned Petrels killed in longline fisheries off Brazil, South Africa and New Zealand were compared with those from petrels breeding at five major colonies (South Georgia, Prince Edward, Crozet, Kerguelen and Antipodes Islands). Feather $\delta^{15}N$, and to a lesser extent, $\delta^{13}C$ values in feathers differed among breeding birds sampled at South Georgia, Antipodes Islands and the three Indian Ocean colonies. Given that adult feathers are moulted primarily in temperate waters, away from their colonies, this confirms that most adults from these three regions winter in different areas. Discriminant function analysis of stable isotope values indicated that most petrels killed off Brazil and South Africa were from Atlantic and Indian Ocean populations, respectively. Birds killed in New Zealand fisheries in summer were assigned to populations from all three oceans, with few assigned to the Antipodes; however, we lacked stable isotope data from the Auckland Islands, which is the most likely source population. Identifying the origin of bycaught birds is essential for determining which populations are affected by human activities and for prioritising conservation efforts. This includes targeting of mitigation regulations, monitoring of compliance and bycatch rates, and ensuring cooperation between breeding and non-breeding range states to ensure best practices are adopted in national fisheries and in the high seas.

1 | Introduction

Population declines of many albatrosses and large petrels have been attributed predominantly to mortality in fisheries, invasive alien predators and climate change (Dias et al. 2019; Phillips et al. 2016). Most of these species are very wide-ranging and so are at risk of bycatch over large regions during their breeding and non-breeding seasons (Beal et al. 2021; Clay et al. 2019; Delord et al. 2010). In the Southern Ocean, longline and trawl fisheries kill thousands of seabirds each

year, and mortality is under-reported, particularly in high-seas fisheries, which are less easily managed (Anderson et al. 2011; Phillips et al. 2024; Tuck et al. 2011). Bycatch has decreased in some fisheries due to the adoption of bycatch mitigation measures (Collins et al. 2021; Da Rocha et al. 2021; Maree et al. 2014; Phillips et al. 2024). However, actual mortality remains underestimated in longline fisheries because not all birds are retrieved, and those that are captured alive during hauling may die later from their injuries (Brothers et al. 2010; Phillips and Wood 2020). Cryptic mortality is even higher from strikes on trawl warp and net monitoring cables as birds are seldom hauled aboard (Phillips et al. 2024; Sullivan et al. 2006; Watkins et al. 2008).

To assess the severity of fishing mortality and its impact on seabird populations, we need to know which populations are affected and to what degree. This requires estimates of the numbers killed, population sizes and vital rates, and in the case of species that breed at multiple sites, their distribution at sea to determine which are impacted by specific fisheries (Small et al. 2013; Tuck et al. 2011). Linking breeding and wintering areas, that is, understanding migratory connectivity, is crucial for effective conservation because efforts may be required year-round (Hobson 1999; Webster et al. 2002). There are several ways to track or assign birds to their geographical origin. Until the advent of electronic tracking, banding recoveries contributed the most information on bird movements, but recovery rates for pelagic seabirds typically are very low; for example, of more than 15,000 petrels banded at Indian Ocean colonies, only 0.3% were recovered over 31 years (Weimerskirch et al. 1985). Technological advances, such as the development of satellite transmitters, GPS loggers and geolocators (Global Location Sensors or GLS loggers), have vastly improved our knowledge of seabird movements in the last two decades (Clay et al. 2019; Phillips et al. 2006; Péron et al. 2010; Frankish et al. 2021). Although archival GPS loggers are cheap, transmitters for long-term tracking of non-breeding birds are expensive, and their long-term attachment using harnesses can cause mortality (Geen et al. 2019). Furthermore, recovery rates of leg-mounted geolocators from juveniles and immatures are low, largely limiting studies to date, to breeding adults. Moreover, none of these methods can be used to determine the provenance of individual birds killed in fisheries that were not marked previously.

An alternative method to infer seabird movements or provenance is to use intrinsic markers linked to a known geographical area. Plumage and morphological measurements can be used to distinguish similar species or subspecies (Cuthbert et al. 2003; Jiménez et al. 2017), and molecular markers can allow discrimination between populations (Abeyrama et al. 2021; Burg et al. 2017; Ramos et al. 2009). Trace elements provide another set of intrinsic markers, which coupled with stable isotope values can be a powerful tool for assignment (Gómez-Díaz and González-Solis 2007; Reinhold et al. 2022). In marine environments, $\delta^{13}C$ and $\delta^{15}N$ values vary in a predictable way. In general, tissues become more depleted in ^{13}C relative to ^{12}C at high latitudes, with abrupt changes at the boundaries of different water masses (François et al. 1993; Cherel and Hobson 2007; Phillips et al. 2009). In addition, $\delta^{13}C$ is related to primary sources, increasing ~1‰ with each trophic level (Inger and Bearhop 2008) and provides spatial information relative to inshore and benthic foodwebs, which are more enriched in ^{13}C than offshore and pelagic food webs (Hobson et al. 1994; Cherel and Hobson 2007). $\delta^{15}N$ is used as a tracer of trophic level, with consumer tissues typically enriched by 2‰–4‰ relative to their prey (Post 2002). Thus, it is possible to identify marine habitats and regions used during the breeding and non-breeding seasons, as well as to detect diet shifts using the natural variation of stable isotopes in the environment and hence in seabird tissues (Cherel et al. 2000; Gómez-Díaz and González-Solis 2007; Ramos et al. 2009). Given that the turnover rates of isotopes differ among tissues, we can use the isotope values to infer carbon source and trophic level over different periods when the tissues were formed. For example, blood cells provide isotopic information on diet over weeks immediately prior to sample collection, whereas feathers integrate diet over a similar duration but reflect diet at the time of moult because they are metabolically inert after synthesis, which may be for successive periods for flight feathers that are grown sequentially (Bearhop et al. 2002).

The White-chinned Petrel (*Procellaria aequinoctialis*) is the seabird species killed most often by longline fisheries across the Southern Ocean (Delord et al. 2005; Petersen et al. 2009; Phillips et al. 2006). They have a wide breeding range on subantarctic islands in the Atlantic, Indian and Pacific oceans (Brooke 2004), making it hard to assess the provenance of individuals killed in fisheries where populations overlap, which is mainly in their wintering areas. Genetic analyses indicate that birds from the New Zealand subantarctic islands are distinct from those in the Atlantic and Indian oceans (Techow et al. 2009; Rexer-Huber et al. 2019), providing a potential tool for narrowing down the origins of bycaught birds (Techow 2007). Tracking using geolocators indicates that most non-breeding adults from South Georgia, the largest global colony, winter off the coast of South America (Phillips et al. 2006; Frankish et al. 2021). However, body feathers of one of 16 adults sampled in 2001 indicated that it probably wintered in the Benguela Upwelling region (Phillips et al. 2009). Tracking of adults from the Kerguelen Islands, the largest colony in the Indian Ocean, and from Marion and Crozet Islands indicates that they winter off southern Africa (Delord et al. 2013; Péron et al. 2010; Rollinson et al. 2018), and those from Antipodes Islands winter off the west coast of South America (Rexer-Huber 2017). Here we use stable isotope analysis of White-chinned Petrel feathers to assess differences in carbon source (water mass) and trophic level among adults from five populations (island groups) and compare these with stable isotope values in feathers of petrels killed in fisheries off Brazil, South Africa, and New Zealand. By matching isotopic values from breeding populations with those from different fishing regions, we aim to link bycatch hotspots to the populations affected. The results provide insights into relative bycatch risks faced by each population and implications of this mortality for population trends.

2 | Methods

2.1 | Study Sites

The White-chinned Petrel breeds in burrows on subantarctic islands during the austral summer (Marchant and Higgins 1990; Figure 1). Between 2001 and 2011, body feathers from the

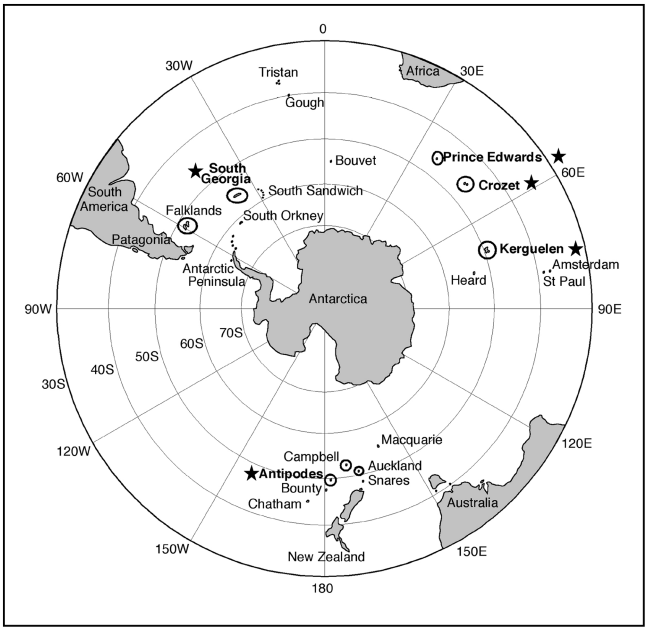

FIGURE 1 | Breeding colonies of White-chinned Petrel (open circles) in the south Atlantic, Indian and Pacific oceans. Colonies where samples were collected are indicated by a star.

chest and belly or the tip of the innermost primary were collected during the breeding season from 247 adult birds incubating eggs from five breeding populations: Bird Island (South Georgia), Marion Island (Prince Edward Islands), Possession Island (Crozet), the Kerguelen Islands and Antipodes Island (New Zealand) (Figure 1). Together, these island groups support more than 60% of the total global population (Birdlife International 2018; Phillips et al. 2016), and the only major breeding location that was not sampled was New Zealand's Auckland Islands.

Three to five body feathers were collected from each bird, except at Crozet and Kerguelen Islands where only one body feather or a single primary tip was collected. Three to five body feathers were collected from White-chinned Petrels killed in longline fisheries operating off Brazil, New Zealand, and South Africa between 2007 and 2010. A sample of the second primary feathers was analysed from birds caught in Brazil, and of the first primary feathers from birds caught off South Africa. The choice of different primaries (P1–P2) is unlikely to bias the analyses, because the three inner primaries grow at the same time (Adekola and Ryan 2025). The bycaught birds from Brazil (27°S–34°S) and South Africa (30°S–38°S) were caught mainly in the austral winter (April–October), whereas birds from New Zealand (31°S–50°S) were mainly caught in austral summer (October–April).

Bycaught birds from Brazil and South Africa were aged from bill characters such as moult scarring and coloration, condition of the gonads, and timing of moult. Breeding adults were easily recognised based on gonad development during the early breeding season (September–December). Outside this period, it is easy to separate juveniles (yearlings) from adults by their greyish, uniformly smooth bills and lack of active moult, but distinguishing immatures from adults (especially males) can be difficult. Different observers aged birds in Brazil, South Africa and New Zealand, with no control to test consistency of scoring, and a large proportion of birds were scored as unknown in Brazil. Birds from New Zealand were all scored as adults, so they were all included in the analyses. Given that young birds are caught more frequently than adults off South Africa (Petersen et al. 2009), two juveniles and 10 immature White-chinned Petrels were also sampled for body and primary feathers ($n = 9$ immature birds for primary feathers only). Stable isotope values in feathers from juvenile and some immature birds were compared with those in feathers collected from pre-fledging chicks sampled on Prince Edward (Barquete 2012). Due to the small number of bycaught juveniles sampled off South Africa, these were grouped with immature birds in the analyses.

Feathers were stored frozen in paper bags. In the lab they were washed, dried and cut into tiny pieces (Knoff et al. 2001). Between 0.6 and 0.7 mg of feather was weighed into tin cups for measurement of stable carbon and nitrogen isotope values. Analysis was carried out at the Archaeology Department of the University of Cape Town by combusting in a Flash EA 1112 series elemental analyser (Thermo Finnigan, Milan, Italy). The gases were passed to a Delta Plus XP IRMS (isotope ratio mass spectrometer—Thermo Electron, Bremen, Germany), via a Conflo III gas control unit (Thermo Finnigan, Bremen, Germany). Precision and accuracy of measurements were $\leq 0.2‰$ for ^{13}C and ^{15}N. Isotope values are expressed as δ values in parts per thousand (‰) according to the equation:

$$\delta X = \left[R_{\text{sample}}/R_{\text{standard}} - 1\right] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ related to standard values. R_{standard} values were based on Vienna Pee Dee Belemnite (VPDB) for ^{13}C and atmospheric nitrogen ^{15}N (Bond and Hobson 2012). Internal laboratory standards used were sucrose from Australian National University (ANU), and DL valine from Sigma and Merck gel from Merck. All the in-house standards have been calibrated against IAEA (International Atomic Energy Agency) standards.

2.2 | Data Analysis

Body feathers and primaries from breeding birds were collected in different years; hence, for the analyses, samples collected in different years were pooled. First, the isotopic values collected at each colony and in each fishing region were tested for normality. Samples from colonies that did not conform to a normal distribution were checked for outliers using visual inspection of boxplots, since the discriminant function analysis is sensitive to outliers (Quinn and Keough 2009). Outliers were identified separately for $\delta^{13}C$ and $\delta^{15}N$ values. These were two outliers from Kerguelen Islands (−21.24, 13.14; −22.23, 11.66) one from Crozet Island (−17.73, 12.41), four from Marion Island (−22.95, 11.57; −19.56, 9.35; −18.63, 14.21; −19.33,9.27), and two from the Antipodes Islands (−16.85, 15.08; −16.88, 13.66), which were therefore excluded from all analyses; the remaining data conformed to normal distributions. Two-way ANOVAs were used to check for differences in $\delta^{13}C$ and $\delta^{15}N$ values between colonies, and between body and flight feathers for each colony and fishing region, followed by Tukey multiple

comparisons of means ($\alpha = 0.05$). Feather $\delta^{13}C$ and $\delta^{15}N$ values were set as response variables, with feather type and colony as explanatory variables and an interaction term between colony and feather type. Because $\delta^{13}C$ and $\delta^{15}N$ values in primary and body feathers differed for some of the breeding populations (see Section 3), these were analysed separately. To assign provenance of bycaught birds, linear discriminant function analyses were performed using the package MASS in the statistical programme 'R' v. 2.13 (R Development Core Team 2011). The leave-one-out cross-validation (LOOCV), where k equals the number of observations was used to evaluate the performance of a model. LOOCV is used for small datasets because it ensures that every observation is used for both training and testing, providing a more robust estimate of the model's performance.

The data from birds at breeding colonies were subdivided randomly into equal subsets; one was used to generate the discriminant function (the training model), and the other to validate the model (% of correct assignments). Carbon and nitrogen isotope values were set as response variables and bird provenance as the explanatory variable. The origin was determined at two levels: first, breeding birds were classified by colony (South Georgia, Prince Edward, Crozet, Kerguelen and Antipodes), and second by ocean region. Birds from the Indian Ocean colonies were then compared with birds from the Atlantic Ocean (South Georgia) and Pacific Ocean (Antipodes). The discriminant model was applied to primary feathers and body feathers separately because both feather types were sampled from some individuals, introducing pseudo-replication. The group (colony or ocean region) that had the highest accuracy with the training model was set as the response variable, and then the discriminant model was applied to bycaught birds.

3 | Results

3.1 | Breeding Birds

Body feathers were often more enriched in ^{13}C and ^{15}N than inner primaries at colonies where both feather types were sampled (Table 1). However, the colony had a much greater influence on $\delta^{15}N$ values than feather type (two-way ANOVA, feather type: $F_{1,237} = 24.7$, $p < 0.001$; colony: $F_{4,237} = 205.9$, $p < 0.001$; colony × feather type: $F_{4,237} = 3.5$, $p = 0.152$). Based on post hoc Tukey tests, $\delta^{15}N$ values were highest in feathers of birds breeding at the Antipodes, intermediate at South Georgia and lowest in the Indian Ocean, where values did not differ among Prince Edward, Crozet, and Kerguelen Islands (Figure 2). There was an interaction between colony and feather type on $\delta^{13}C$ values (two-way ANOVA, colony: $F_{4,237} = 26.3$, $p < 0.001$; feather type: $F_{1,237} = 35.2$, $p < 0.001$; colony × feather type: $F_{4,237} = 3.5$, $p = 0.009$), but differences were less marked than for $\delta^{15}N$ values (Figure 2). Based on Tukey tests, petrels from Prince Edward

TABLE 1 | $\delta^{13}C$ and $\delta^{15}N$ values in body and primary feathers (mean ± SD) and sample size (n) of White-chinned Petrels sampled at different breeding colonies or killed by fishing vessels in the Southern Ocean, and the results of the post hoc Tukey tests comparing primary and body feathers. NA: not available.

Colony	Feather (n)	$\delta^{13}C$	p	$\delta^{15}N$	p
South Georgia	Primary (16)	−16.3 ± 1.0	0.045	+17.3 ± 0.8	0.981
	Body (47)	−15.7 ± 0.6		+17.6 ± 1.1	
Marion Island	Primary (16)	−16.1 ± 0.9	0.929	+15.2 ± 1.1	0.982
	Body (24)	−15.8 ± 0.9		+15.5 ± 0.9	
Crozet Islands	Primary (9)	−15.2 ± 0.7	0.037	+15.4 ± 0.6	0.044
	Body (10)	−14.2 ± 0.2		+16.7 ± 0.5	
Kerguelen Islands	Primary (20)	−15.8 ± 0.7	< 0.001	+15.1 ± 0.6	0.028
	Body (27)	−14.9 ± 0.9		16.0 ± 0.8	
Antipodes Islands	Primary (30)	−16.3 ± 0.3	0.974	+10.0 ± 0.7	0.197
	Body (48)	−16.1 ± 0.4		+19.5 ± 0.9	
Fishing region					
Brazil	Primary (19)	−19.20 ± 3.47	0.908	+13.8 ± 3.5	0.997
	Body (21)	−18.65 ± 2.99		+14.2 ± 3.3	
South Africa (adults)	Primary (18)	−15.20 ± 0.64	0.999	+15.9 ± 0.8	0.956
	Body (20)	−15.3 ± 0.6		+16.2 ± 0.7	
South Africa (juvenile/immature)	Primary (11)	−17.1 ± 2.3	0.999	+14.1 ± 2.2	0.956
	Body (12)	−16.5 ± 2.3		+15.2 ± 1.9	
New Zealand	Body (21)	−15.5 ± 0.6	NA	+17.2 ± 1.9	NA

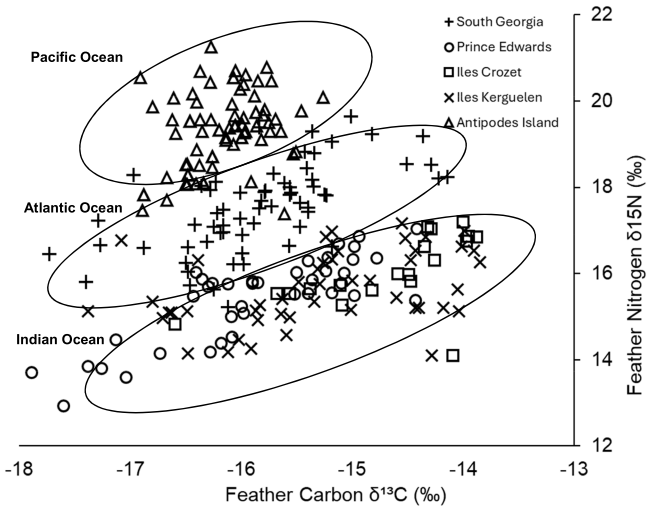

FIGURE 2 | δ^{13}C and δ^{15}N values in body and primary feathers of White-chinned Petrels sampled at five subantarctic colonies. Ellipses represent visual indications of ocean basins of origin.

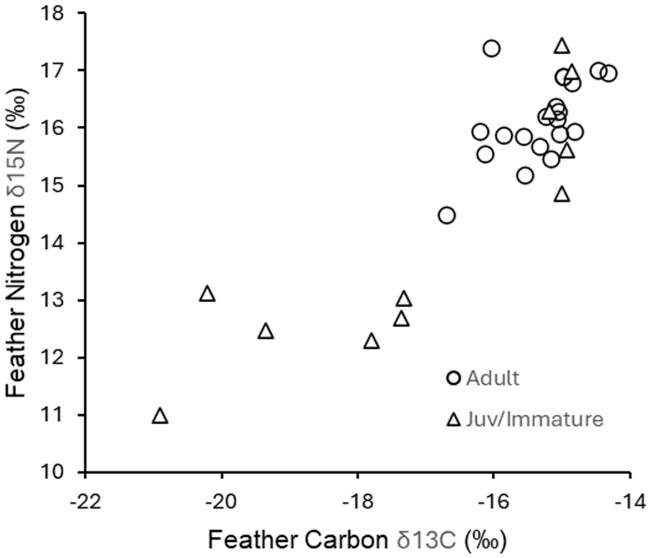

FIGURE 3 | δ^{13}C and δ^{15}N values in the innermost primary feather of young (juvenile and immature; triangles) and adult (circles) White-chinned Petrels killed in longline fisheries off South Africa.

had similar δ^{13}C values to those at South Georgia and the Antipodes.

3.2 | Bycaught Birds

Although primary and body feathers of the 12 young White-chinned Petrels caught off South Africa were on average more depleted in ^{15}N and ^{13}C than those of adults, there was some overlap (Table 1 and Figure 3). Stable isotope values in feathers of White-chinned Petrels caught off Brazil were highly variable, with δ^{13}C values ranging from −22.5‰ to −14.6‰ for body feathers and −23.6‰ to −14.7‰ for primary feathers. Similarly, δ^{15}N values ranged from 9.9‰ to 19.3‰ for body feathers and 10.2‰ to 19.4‰ for primary feathers. The individuals with very low values for δ^{13}C and δ^{15}N were most likely to be juveniles or immatures because the only two birds that were aged in the sample were juveniles and also had low values, comparable to juveniles from South Africa and fledglings sampled at the Prince Edward Islands.

Feather δ^{13}C and δ^{15}N values differed with age (young, adult and unknown) and fishing region (country), but there was no significant effect of feather type (three-way ANOVA, δ^{13}C, colony: $F_{2,115}=32.3$, $p<0.001$; feather type: $F_{1,115}=0.6$, $p=0.45$; age: $F_{2,115}=9.6$, $p<0.001$; colony x feather type: $F_{1,115}=0.5$, $p=0.48$; δ^{15}N, colony: $F_{2,115}=13.4$, $p<0.001$; feather type: $F_{1,115}=0.9$, $p=0.35$; age: $F_{2,115}=7.1$, $p=0.001$; colony × feather type: $F_{1,115}=0.04$, $p=0.84$; Table 1). According to Tukey tests on the bycaught birds of all ages, δ^{13}C values were similar in bycatch from South Africa and New Zealand, but δ^{15}N differed significantly among the three regions. Results for δ^{13}C were similar if adults only were included in analyses, except that there was no significant difference in δ^{15}N between samples from South Africa and New Zealand.

3.3 | Discriminant Function Analyses

Based on stable isotope values in primary feathers, the training models correctly classified 61% of samples to colony, and 94% of samples to ocean basin (Table 2). Applying the latter function to bycaught birds, most (97%) of those killed off South Africa were classified as from Indian Ocean colonies, and (26%) of those killed off Brazil were classified as from South Georgia (Table 3). If young birds were excluded (i.e., those identified as such from South Africa [$n=11$], and any individuals caught off Brazil with δ^{13}C values < −19.0‰ [$n=10$]), the proportion of birds killed off Brazil that were assigned to South Georgia increased to 56%, and 100% of birds killed off South Africa were assigned to Indian Ocean colonies (Table 3).

The training model based on stable isotope values in body feathers was more accurate than that for primary feathers in assigning birds to colony (72% vs. 61%), but less accurate for assigning ocean basin (86% vs. 94%; Table 2). Classification results for bycatch birds using body feathers were similar to those using primary feathers (Table 3). Removing young birds made little or no change to the classification of birds killed off South Africa or New Zealand but increased the proportion of birds killed off Brazil that were assigned to Atlantic Ocean colonies (Table 3). Of birds killed off New Zealand, almost half were assigned to Indian Ocean colonies, a third to South Georgia, and a few to the Antipodes (Table 3). However, caution is needed in interpreting the results from New Zealand, because training data were only available from one of the main breeding colonies in the region.

4 | Discussion

This is one of the first studies to use stable isotopes as a forensic marker to infer the provenance of seabirds killed incidentally by fisheries in the Southern Ocean. Using a discriminant function based on stable isotope values, 88%, 100% and 94% of breeding adult White-chinned Petrels were assigned correctly to their colony or region of origin for birds from South Georgia, the Indian Ocean and Antipodes Island, respectively. Of the bycaught

TABLE 2 | Numbers of birds grouped per ocean region (*N*), number of birds assigned to the correct origin (50% of the original dataset), percent of birds assigned to the correct origin and misclassifications of the training data of discriminant function analysis, based on $\delta^{13}C$ and $\delta^{15}N$ values in the first primary and body feathers of White-chinned Petrels sampled at five breeding colonies.

Breeding colony			Training model		
Feather type	Ocean	*N*	Assigned correctly (number)	Assigned correctly (%)	Misclassified as
Primary					
South Georgia	Atlantic	16	7/8	88	Pacific
Kerguelen, Crozet, Prince Edward	Indian	45	22/22	100	
Antipodes Islands	Pacific	30	17/18	94	Atlantic
Body					
South Georgia	Atlantic	47	14/19	74	Indian, Pacific
Kerguelen, Crozet, Prince Edward	Indian	61	29/29	100	
Antipodes Islands	Pacific	48	25/30	83	Atlantic

TABLE 3 | White-chinned Petrels killed in longline fisheries in three different regions and their provenance based on the discriminant function analysis. * excludes juvenile and immature birds.

Bycatch		% of assignments		
Feather type	*N*	Atlantic Ocean	Indian Ocean	Pacific Ocean
Primary				
Brazil	19	26	63	11
South Africa	29	3	97	0
Brazil *	9	56	22	22
South Africa *	18	0	100	0
Body				
Brazil	21	81	19	0
South Africa	32	9	91	0
New Zealand	21	38	48	14
Brazil *	11	91	9	0
South Africa *	20	10	90	0

birds, most adults (91%) killed off Brazil were assigned to South Georgia based on stable isotope values in body feathers, and 90%–100% of adults killed off South Africa were assigned to colonies in the Indian Ocean based on values in primaries or body feathers. By comparison, only a minority of birds killed off New Zealand during the breeding period were assigned to the colony at the Antipodes Islands. However, as noted in results, caution is needed in interpreting the New Zealand results as data were not available from the main breeding colony in the region, the Auckland Islands, which is a significantly larger colony.

4.1 | Isotopic Variation of Breeding Adults

White-chinned Petrels, like most albatrosses and petrels, do not breed and moult at the same time (Bridge 2006; Adekola and Ryan 2025). Stable isotope analyses indicate that, with the possible exception of the innermost primaries, all flight feathers are replaced in temperate waters north of the Subtropical Front, far from the breeding grounds (Barquete 2012; Adekola and Ryan 2025). The strong differentiation among colonies in isotopic values of feathers of breeding individuals results from their distinct wintering grounds. All adults sampled at Bird Island (South Georgia) had feather isotope values corresponding to subtropical and mixed subtropical-subantarctic water masses along the continental shelf and slope of the southwest Atlantic Ocean and southeast Pacific Ocean, except for a single bird with an isotope value corresponding to the Benguela Upwelling region (Phillips et al. 2009). White-chinned Petrels breeding at Crozet feed across a wide latitudinal range from subtropical waters off South Africa to Antarctic waters while breeding (Weimerskirch et al. 1999), but their feather isotope values correspond to the Subtropical Zone (Jaeger et al. 2010a). Similarly, the isotopic value of White-chinned Petrels breeding on Prince Edward, Kerguelen and Antipodes islands corresponds to the Subtropical Zone (Jaeger et al. 2010a, 2010b).

Although breeding adults moult away from their breeding grounds, stable carbon and nitrogen isotopes in their feathers were sufficiently distinct to differentiate most individuals from different ocean basins, but not to discriminate birds from the three colonies within the Indian Ocean. Tracking using geolocators similarly indicates that adults from different ocean basins have discrete wintering areas (Phillips et al. 2006; Péron et al. 2010; Rexer-Huber 2017), which matches with population

genetic structure (Techow et al. 2016; Rexer-Huber et al. 2019). White-chinned Petrels from Bird Island, South Georgia, migrate to South America, mainly to the Patagonian Shelf and the shelf break north to Brazil, but 20% of birds venture around Cape Horn into the eastern Pacific Ocean, reaching southern Chile (Frankish et al. 2021; Phillips et al. 2006). White-chinned Petrels breeding at all three Indian Ocean Islands migrate to the Benguela Upwelling region (Delord et al. 2013; Péron et al. 2010; Rollinson et al. 2018). Spear et al. (2005) inferred that most New Zealand White-chinned Petrels winter off Chile in the productive Humboldt Current, which has been confirmed by geolocator tracks of adults from the Antipodes Islands (Rexer-Huber 2017). The $\delta^{13}C$ values of breeding adult White-chinned Petrels from South Georgia, Prince Edward, Crozet, Kerguelen and Antipodes islands fit well with the $\delta^{13}C$ isoscape proposed for the Southern Ocean (Jaeger et al. 2010b).

4.2 | Geographic Assignment of Breeding Birds—Training Model

Feather isotope values were used to assign adults with high accuracy to ocean basins, but accuracy was lower in terms of assignment to the correct colony within the Indian Ocean. The model based on isotope values in primary feathers gave the best results, which is to be expected given that birds moult their flight feathers annually after leaving their breeding grounds (Adekola and Ryan 2025), whereas body feather moult is more protracted and not all feathers are necessarily replaced each year (Marchant and Higgins 1990; Warham 1996; Adekola and Ryan 2025). Misclassification rates were highest for birds sampled at South Georgia, which might indicate variable timing of moult, or minority migration strategies that have not yet been detected in the birds tracked to date; the latter would explain the bird with an isotopic value typical of the Benguela Upwelling (Phillips et al. 2009). Further evidence of individual variability in moult and movement patterns comes from the outliers excluded from our analyses. This included birds with very low isotopic values for the inner primaries ($\delta^{13}C < -19‰$), typical of the Antarctic region (Phillips et al. 2009; Jaeger et al. 2010b). These birds could have deferred breeding the previous season or failed early and regrown a primary in the summer while still feeding south of the Antarctic Polar Front, which is the main foraging region used by chick-rearing adults (Phillips et al. 2006).

Isotopic segregation of feathers from adult White-chinned Petrels was more evident for $\delta^{15}N$ than $\delta^{13}C$, suggesting that $\delta^{15}N$ varied with longitude. This concurs with longitudinal variation in $\delta^{15}N$ in feathers of Cory's Shearwater (*Calonectris diomedea*) (Gómez-Díaz and González-Solis 2007). Such differences may be linked to regional differences in hydrography and sea surface temperature (Laakmann and Auel 2010) or in biological processes such as nitrification that influence the movement of nitrogen in marine ecosystems (Montoya 2007). It is noted that a limitation of this study is that birds from different regions were collected in different years (2001–2011) and stable isotope baselines in areas may vary interannually, and annual baselines were not collected in each area. However, given the known significant differences in isotope baselines between ocean basins, this was not considered to deter from this research at the ocean basin level. Diet is an important source of variation in $\delta^{15}N$, and White-chinned Petrels at Crozet Islands take different prey during chick rearing from those at South Georgia (Croxall et al. 1995; Berrow and Croxall 1999; Catard et al. 2000; Connan et al. 2007). For example, as well as Antarctic krill *Euphausia superba*, birds in the southwest Atlantic feed extensively on Short-finned Squid (*Illex argentinus*) and *Histioteuthis* spp. (Berrow and Croxall 1999; Bugoni et al. 2010; Jiménez et al. 2017), whereas those in the Indian or southeast Atlantic Oceans consume more *Todarodes* spp. (Delord et al. 2010). These squid species differ in distribution and $\delta^{15}N$ values (Cherel et al. 2000; Bugoni et al. 2010). White-chinned Petrels wintering in the Benguela feed on a variety of prey, particularly fish offal such as Hake (*Merluccius* spp.) and Rat-tail (*Coelorhynchus fasciatus*) (Jackson 1988).

4.3 | Geographic Assignment of Bycatch

The assignment of bycaught birds was confounded to some extent by the inability to reliably age birds in some samples. Young White-chinned Petrels have very different stable isotope values from adults, and including the data in models greatly increased the likelihood of misassignment. In the sample from South African fisheries, which were all aged, allocation using the discriminant function matched well with expectations. These data also suggest that stable isotope values of immature birds have wide variance, although some values are similar to adults. This is probably because immature birds moult earlier in the year (Adekola and Ryan 2025), and not necessarily in the same areas as adults.

The birds bycaught off New Zealand were assigned mainly to Indian and Atlantic Ocean populations. However, this may be an artefact of inadequate sampling of New Zealand colonies, which was limited to the Antipodes Islands, given that genetic analyses of bycaught birds caught off New Zealand suggested that most, if not all, were from the New Zealand subspecies *P. a. steadi* (Techow 2007). The breeding population at the Auckland Islands (~186,000 pairs) is much larger than at the Antipodes Islands (Rexer-Huber 2017). Based on our results, these birds must be largely distinct in terms of isotope values from the population at the Antipodes Islands, presumably because of spatial segregation during the winter. Future research could target the Auckland Islands to collect stable isotope samples from these colonies, and additional analysis such as sulphur isotope ($\delta^{34}S$) analysis or SIBER analysis could be undertaken to further investigate these differences.

4.4 | Implications for Conservation

White-chinned Petrels are well known for scavenging behind fishing vessels, and given they migrate to highly productive upwelling systems, a high overlap with fisheries is inevitable (Phillips et al. 2006). White-chinned Petrel bycatch in the Brazilian pelagic longline fishery is highest during winter (0.059 per 1000 hooks; Bugoni et al. 2008). The pelagic longline fishery in South Africa also mainly operates in winter, and prior to 2008, White-chinned Petrels were captured at a rate of 0.25 birds per 1000 hooks, approximately four times higher than in the Brazilian fishery (Rollinson et al. 2018). Encouragingly, bycatch rates have fallen in recent years in the South African fishery (averaging <0.05 birds per 1000 hooks, BirdLife Albatross

Task Force, unpublished data). The pelagic longline fishery in New Zealand has the lowest capture rate of the three fisheries sampled in this study (0.004 per thousand hooks; Abraham and Thompson 2011). However, an assessment of the impacts of different fisheries on specific White-chinned Petrel populations requires information on total effort and bycatch rates throughout its breeding and nonbreeding range.

Mitigation measures are available that greatly reduce bycatch of White-chinned Petrels in pelagic and demersal longline and trawl fisheries (Collins et al. 2021; Jiménez et al. 2020; Phillips et al. 2016, 2024). These include managing discard to reduce the attractiveness of vessels to birds when bycatch risk is greatest (setting and hauling), setting longlines at night (although this is less effective for White-chinned Petrels which are adept at nocturnal foraging; Mackley et al. 2011), the use of bird-scaring (streamer or tori) lines and heavier weighting of branch lines to maximise line sink rates (in both demersal and pelagic fishing) (Agreement on the Conservation of Albatrosses and Petrels Bycatch Mitigation Review and Advice https://www.acap.aq/resources/bycatch-mitigation/mitigation-advice). Although most fisheries do not follow best-practice advice, the use of the three measures (managing discards, using bird-scaring lines and heavier weighting of branch lines) should be required, monitored and enforced where certain populations are at particular risk (Phillips et al. 2006; Petersen et al. 2009).

5 | Conclusions

Our study shows that stable isotope values in feathers could be used for the geographical assignment of bycaught White-chinned Petrels to ocean basins, but requires more sampling to be effective across the entire Southern Ocean. The accuracy of the discriminant analysis was higher than 80% for both body and inner primaries, but the use of the latter is recommended. Since young birds differ from adults in their isotopic values, caution is needed when inferring their origin, underlining the importance of ageing correctly. Identifying the origin of bycaught birds is essential for assessing the impact of human activities on specific populations. The breeding populations of White-chinned Petrels in the Indian Ocean are much smaller than in the Atlantic Ocean (Barbraud et al. 2008; Barbraud et al. 2009; Dilley et al. 2019; Martin et al. 2009), but this research shows the Indian Ocean population is affected by multiple fisheries including the large demersal trawl fleet in South Africa (Maree et al. 2014; Rollinson et al. 2018). To continue to conserve all White-chinned Petrel populations, stricter mitigation regulations, monitoring of compliance and bycatch rates and cooperation between breeding and non-breeding range states are needed.

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Ethics Statement

Fieldwork was approved by the Conseil des Programmes Scientifiques et Technologies Polaires of the Institut Polaire Français Paul Emile Victor (IPEV), and procedures were approved by the Animal Ethics Committee of IPEV. Fieldwork at Bird Island was approved by the British Antarctic Survey animal ethics review body and carried out under permit from the Government of South Georgia and the South Sandwich Islands.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The datasets analysed during the current study are available from V.B. on reasonable request. As data was collected over multiple countries, including from fisheries bycatch, there may be legal restrictions on some of the data so they cannot be made publicly available without specific request and permission.

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No material has been reproduced from other sources.

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