IBIS
international journal of avian science

Ibis (2023), **165**, 890–904 doi: 10.1111/ibi.13170

Consistent seasonal foraging niche segregation between critically endangered Whenua Hou Diving Petrels and abundant Common Diving Petrels

GRACE E. TOCKER,[1] JOHANNES H. FISCHER,*[1,2] PACO BUSTAMANTE,[3,4] GAËL GUILLOU,[3]
IGOR DEBSKI,[2] GRAEME A. TAYLOR,[2] PETER A. RITCHIE[1] & HEIKO U. WITTMER[1]
[1]*School of Biological Sciences, Victoria University of Wellington, Wellington, New Zealand*
[2]*Aquatic Unit, Department of Conservation, Wellington, New Zealand*
[3]*Littoral Environnement et Sociétés, UMR 7266 CNRS–La Rochelle Université, La Rochelle, France*
[4]*Institut Universitaire de France, Paris, France*

Investigations into niche dynamics and interspecific interactions are crucial to assess the vulnerability of threatened species to competition and environmental change. The Whenua Hou Diving Petrel *Pelecanoides whenuahouensis* is a critically endangered seabird, specializing in breeding in sand dunes in Aotearoa (New Zealand). The species is at risk from competition for burrow sites with the abundant, habitat-generalist Common Diving Petrel *Pelecanoides urinatrix chathamensis*, among other terrestrial and near-shore threats (storm-induced erosion and vessel-based light pollution). However, Whenua Hou Diving Petrel foraging niches at sea and associated threats are poorly understood. We sampled blood and feathers from both species on Whenua Hou (Codfish Island) during 2017–19 and used stable isotope (δ^{15}N and δ^{13}C) analyses to quantify foraging niche dynamics and interspecific interactions. During incubation periods, when birds are restricted by central place foraging, diving petrels exhibited clear niche segregation. Whenua Hou Diving Petrels were more generalist feeders with wider isotopic niches than Common Diving Petrels, which exhibited restricted isotopic niches and fed in neritic waters. During non-breeding periods, foraging niches expanded, and segregation was reduced, as both species dispersed into the Southern Ocean. These patterns were largely consistent among years, despite varying climatic conditions. However, Common Diving Petrel foraging niches appeared to shrink during El Niño conditions, suggesting environmental sensitivity. In contrast, the consistently stable, generalist foraging niches of Whenua Hou Diving Petrels suggested potential limited sensitivity to competition and impacts of environmental change at sea. Recovery efforts should, therefore, focus on addressing the previously identified terrestrial and near-shore threats.

Keywords: diet, foraging habitat, interspecific interactions, niche overlap, *Pelecanoides*, stable isotope analyses, trophic ecology.

The theory of ecological niche segregation posits that coexisting species partition resources, to reduce competition, in either temporal, spatial or trophic dimensions, which in combination delineate a species' niche (Hutchinson 1959). Niche segregation is important for community stability, particularly in densely populated communities of central place foragers sharing breeding grounds (Croxall & Prince 1980, Navarro *et al.* 2013, 2015). Seabird communities exemplify niche segregation, allowing ecologically similar species to breed in sympatry (Cherel *et al.* 2008, Jones *et al.* 2020, Bedolla-Guzmán *et al.* 2022). These species coexist by breeding in different

---

*Corresponding author.
Email: johannesfischer@live.nl
Twitter: @flying_force

Grace E. Tocker and Johannes H. Fischer are joint first authors.

habitats, at different times of the year, and by foraging at different times of the day, in different parts of the surrounding ocean, at different depths of the water column, or by targeting different prey species (Croxall & Prince 1980, Phalan *et al.* 2007, Masello *et al.* 2010, Navarro *et al.* 2013, 2015, Ravache *et al.* 2020).

For threatened species, it is crucial to investigate niches and interactions with other species to assess vulnerability to competition (Barger & Kitaysky 2012, Ravache *et al.* 2020) and pressures from environmental changes (Grecian *et al.* 2016, Ramirez *et al.* 2021, Rayner *et al.* 2021). Seabirds are among the most threatened species on the planet (Croxall *et al.* 2012, Dias *et al.* 2019) and species exhibiting narrower niches (i.e. specialists) may be more at risk than species with wider niches (i.e. generalists) (Richard *et al.* 2021). Specifically, if a threatened species, already under pressure from various threats, also exhibits a small, inflexible niche, it may be considerably more vulnerable to future changes in the environment, and therefore more at risk of extinction (Barger & Kitaysky 2012). As anthropogenic pressures and impacts continue to accelerate (e.g. climate change or overfishing; Sydeman *et al.* 2012, Gremillet *et al.* 2018), characterizing niches and segregation among species is crucial to understanding the vulnerability of species.

The use of stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) has greatly improved our understanding of foraging niches among different seabird species (Peterson & Fry 1987, Hobson *et al.* 1994, Bearhop *et al.* 2004, Cherel *et al.* 2005, Newsome *et al.* 2007). Carbon isotope ratios reflect foraging location, when carbon isoscapes exist throughout the environment (Kelly 2000, Quillfeldt *et al.* 2005, Jaeger *et al.* 2010). In marine habitats, the heavier ^{13}C isotope is enriched in neritic food webs compared with oceanic food webs. Similarly, in the Southern Ocean, the heavier ^{13}C isotope is enriched at lower latitudes compared with higher latitudes (Peterson & Fry 1987, Cherel & Hobson 2007). Nitrogen isotope ratios increase predictably with the trophic position at a rate of $\delta^{15}N \sim 3–5‰$ per trophic level (Minagawa & Wada 1984, Post 2002). Together, foraging areas, as inferred from carbon isotope ratios, and trophic positions, as inferred from nitrogen isotope ratios, compose a species' foraging niche. As different tissues have different turnover rates, temporal variations in a species' foraging niche can be detected by sampling multiple tissue types (Bearhop *et al.* 2004). For example, whole blood stable isotope ratios are representative of the isotopic ingestion over the previous ~ 30 days (Hobson & Clark 1993), whereas feathers are inert once formed and their isotopic composition reflects isotopic ingestion at the time of feather growth (Nisbet *et al.* 2002, Cherel *et al.* 2006, Gladbach *et al.* 2007). Stable isotope analyses have distinct advantages over other methods investigating trophic positions and foraging areas. Tracking technologies have revolutionized seabird ecology (Bernard *et al.* 2021), but these studies only provide insights into foraging areas and not diet or trophic positions. Traditional methods investigating diet and trophic positions include the sampling of faeces or stomach contents, but these methods are inherently biased to certain species groups (e.g. larger prey items) and can be highly invasive (Cherel *et al.* 2005). DNA analyses, e.g. of faeces or stomach contents, are less biased (McInnes *et al.* 2017), but these methods still cannot provide insights into diet during the non-breeding period when birds are out at sea. In contrast, carbon and nitrogen isotope ratios can provide standardized and year-round insights into foraging areas as well as trophic positioning of species.

The trophic positions and foraging areas of species can be subject to variation within populations and among years, and accounting for these sources of variation is crucial to understanding the underlying patterns of foraging niche dynamics. A common source of intraspecific variation is sex, as different sexes may vary in foraging strategy, habitat or prey species to avoid intraspecific competition (Hobson *et al.* 1993, Bearhop *et al.* 2006, Schultz *et al.* 2021). Many external drivers can also cause variation in trophic positions and foraging areas. Most prominently, oceans are under the influence of various climatic cycles such as the El Niño Southern Oscillations (ENSO), resulting in fluctuations of food availability (Schreiber & Schreiber 1984, Yasunari 1987). Seabirds can adapt to these changing seascapes by flexibly adjusting their foraging habits and feeding areas from year to year (Bourgeois *et al.* 2022). Consequently, to effectively characterize the trophic positions and foraging areas that compose foraging niches, intraspecific and interannual variation should be taken into account (Navarro *et al.* 2013, Ravache *et al.* 2020).

The Whenua Hou Diving Petrel *Pelecanoides whenuahouensis* is a critically endangered seabird in need of an assessment of its foraging niche to inform vulnerability to competition and future environmental change. The Whenua Hou Diving Petrel is restricted to Whenua Hou (Codfish Island), Aotearoa, where the entire world population (~ 200 adults) breeds in fragile foredunes < 20 m from the tideline (Fischer *et al.* 2018a, 2018b, 2020b, 2022b). The species is at risk during the breeding period from terrestrial threats, including storms and storm surges that erode their breeding habitat, and competition for burrow sites with the abundant congeneric Common Diving Petrel *Pelecanoides urinatrix chathamensis* (Fischer *et al.* 2017, 2021c). At-sea threats are poorly understood, but birds are at risk from deck strikes (light-pollution-induced collisions with vessels) near shore during the breeding period (Fischer *et al.* 2021a, 2021b). Competition with Common Diving Petrels at sea and vulnerability to environmental changes, during either the breeding or non-breeding periods, has not been assessed to date. Anecdotal evidence and tracking with geolocators indicated that Whenua Hou Diving Petrels forage south of Rakiura (Stewart Island) near the Snares Shelf and the Subtropical Front during the breeding period (September–January) (Imber & Nilsen 1980, Fischer *et al.* 2021a, 2021c). After the breeding period, birds migrate ~3500 km to the Polar Front southwest of Australia. Although the breeding and non-breeding foraging areas of several Common Diving Petrel subspecies (*P. u. urinatrix* and *P. u. exsul*) are known (Navarro *et al.* 2013, 2015, Rayner *et al.* 2017, Zhang *et al.* 2019, Dunphy *et al.* 2020, Fromant *et al.* 2020, 2022), the foraging areas of the subspecies in Southern Aotearoa (*P. u. chathamensis*) during both breeding (September–February; Richdale 1945) and non-breeding periods remain unknown. Prey composition of both species in Aotearoa also remains largely unknown, but anecdotal evidence suggests that Whenua Hou Diving Petrels feed on euphausiids, small fish and small cephalopods during the breeding period (Imber & Nilsen 1980). Previous studies have shown niche segregation between sympatric populations of diving petrels through diet, tracking and isotopic investigations (Croxall *et al.* 1997, Bocher *et al.* 2000, Navarro *et al.* 2013, 2015, Fromant *et al.* 2020, 2022). However, no study has investigated the foraging niches of diving petrels on Whenua Hou or the vulnerability of the critically endangered Whenua Hou Diving Petrel to at-sea competition with congenerics and future environmental change.

We collected blood and feather samples from Whenua Hou Diving Petrels and Common Diving Petrels over three consecutive years (2017–19) and used stable isotope analyses to quantify foraging niches, investigate intraspecific and interannual variation, infer interspecific competition, and investigate their vulnerability to environmental changes.

METHODS

Study site and species

Whenua Hou (46.8°S, 167.6°E) is a 14-km^2 island free of invasive predators, 3 km west of Rakiura off Aotearoa, with a single small sand dune (~ 0.02 km^2) located in Waikoropupū (Sealers Bay). The sole remaining population of the Critically Endangered Whenua Hou Diving Petrel (~ 200 adults) breeds in this sand dune (Fischer *et al.* 2018a, 2018b, 2020b, 2022b). Approximately 40 adult Common Diving Petrels also breed in the dune. In contrast to Whenua Hou Diving Petrels, Common Diving Petrels are not habitat specialists; they breed in a wide variety of coastal habitats, including forests, and their population numbers in the 100s or 1000s on Whenua Hou and in the 100 000s across southern Aotearoa (Taylor 2000, Fischer *et al.* 2020a).

Sample collection

We captured up to 30 Whenua Hou Diving Petrels and Common Diving Petrels each per year by hand or with custom-made burrow traps for whole blood and primary covert feather sampling in mid- to late November in 2017–19 (Table 1). Whole blood isotope ratios reflect the diet and distribution over the previous ~ 30 days (Hobson & Clark 1993). To provide insights into foraging niches during the incubation period, we collected blood samples late in the incubation period (which lasts from mid-October to early December for both species; Richdale 1945, Fischer *et al.* 2021c). We collected blood samples (~ 0.1 mL) from birds by venepuncture of the metatarsal vein following standard operating procedures (Taylor *et al.* 2010). We then stored blood samples in 0.9 mL of 70% ethanol and subsequently refrigerated them at

Table 1. Number of blood and feather samples collected from Whenua Hou Diving Petrels and Common Diving Petrels on Whenua Hou.

Species	Sample type	2017 *n* (♀; ♂)	2018 *n* (♀; ♂)	2019 *n* (♀; ♂; u[a])	Total *n* (♀; ♂; u[a])
Whenua Hou Diving Petrel	Blood	30 (15; 15)	26 (13; 13)	30 (14; 16)	86 (42; 44)
	Feathers	30 (15; 15)	26 (13; 13)	30 (14; 16)	86 (42; 44)
Common Diving Petrel	Blood	19 (12; 7)	30 (20; 10)	30 (15; 14; 1[a])	79 (47; 31; 1[a])
	Feathers	21 (13; 8)	30 (20; 10)	30 (15; 14; 1[a])	81 (48; 32; 1[a])

[a] The sex of one Common Diving Petrel could not be determined (u, unknown) and it was excluded from analyses.

4°C, which has no known effect on stable isotope ratios (Hobson *et al.* 1993, Bugoni *et al.* 2008). In contrast to whole blood samples, isotope ratios in feathers reflect diet and distribution during feather synthesis and are inert thereafter (Cherel *et al.* 2014a, 2014b). As diving petrels moult during the non-breeding period, feather samples provide insights into foraging niches during the preceding non-breeding periods, and so we sampled the distal 2 cm from the sixth primary coverts of each wing (ensuring consistency). We stored feather samples in zip-lock bags at room temperature. Sampling years were subject to considerable climatic variation due to varying ENSO conditions (Table 2; NOAA 2022). We also sampled four contour feathers from flanks for genetic sex determination (using polymerase chain reaction primers specific to the CHD-W gene; Norris-Caneda & Elliott 1998).

Sample preparation

We dried whole blood samples using an evaporator (Genevac Ltd, Ipswich, UK) until a stable dry weight was reached. Subsequently, we ground dehydrated blood samples into a homogeneous powder and stored this at room temperature. We suspended feathers in chloroform:methanol (2:1 solution) in an ultrasonic bath for 5 min to remove dust and dirt (Cherel *et al.* 2018). We repeated this step using fresh chloroform:methanol to ensure complete removal of surface contaminants. We then passed the samples through a solution of pure methanol and dried samples in an oven at 50°C overnight. Once dry, we cut the feathers into very small fragments to homogenize them, which we stored at room temperature.

Table 2. Oceanic Niño Index (ONI) values for Diving Petrel non-breeding and breeding periods. Data sourced from NOAA (2022).

Year	ONI during incubation period (Oct–Dec)	ONI during non-breeding period (Feb–Aug)
2017	−0.83[a]	0.10
2018	0.83[b]	−0.29
2019	0.43	0.50[b]

[a] ONI values ≤ −0.5 indicate La Niña conditions. [b] ONI values ≥ 0.5 indicate El Niño conditions.

Stable isotope analyses

In 2017 and 2018, we weighed whole blood and feather samples out into ~ 0.8-mg aliquots into tin containers for stable isotope analysis at Isotrace (Otago University, Dunedin, Aotearoa). We determined relative abundance of C and N isotopes using a continuous flow isotope ratio mass spectrometry (CF-IRMS) system consisting of a Carlo Erba NA1500 (Thermo Fisher Scientific, Rodano, Italy) elemental analyser interfaced with a Europa Scientific '20/20 Hydra' (Sercon, Cheshire, UK) mass spectrometer. Two laboratory standards (EDTA-OAS and IAEA MP153) were analysed for every 12 samples to check analytical precision and accuracy and to correct instrumental drift when required. The measurement error was < 0.18‰ for δ^{15}N and < 0.27‰ for δ^{13}C.

In 2019, we weighed whole blood and feather samples into ~ 0.3-mg aliquots into tin containers for stable isotope analysis at the Littoral Environnement et Sociétés laboratory (LIENSs, La Rochelle Université, France). We determined relative abundance of C and N isotopes with a Thermo Scientific Flash EA 1112 (Thermo Scientific, Rodano, Italy) elemental analyser coupled to a Thermo Scientific Delta V Advantage (Thermo Scientific, Dreieich, Germany) continuous-flow mass spectrometer. Two laboratory standards (USGS-61 and USGS-62) were analysed for every 20 samples. The measurement error was < 0.15‰ for both δ^{13}C and δ^{15}N values.

We present results in the δ notation relative to the standard reference materials (Vienna PeeDee Belemnite for C and atmospheric N_2 for N). We express results in δ-notation using:

$$\delta X = \left[\left(\frac{R_{\text{Sample}}}{R_{\text{Standard}}}\right) - 1\right] \times 1000$$

where X is the heavy isotope (^{15}N or ^{13}C), R_{Sample} is the ratio of heavy to light isotope in the sample, and R_{Standard} is the ratio of heavy to light isotope in the reference standard (Peterson & Fry 1987, MacNeil *et al.* 2005). We tested for confounding factors due to the use of two laboratories by reanalysing 10% of the 2018 samples at LIENSs. Results indicated that samples analysed at different institutions with varying protocols produced consistent ratios, allowing comparison of results across all 3 years (paired t-test δ^{13}C: $t = -1.56$, df = 19, $P = 0.13$; δ^{15}N: $t = 0.21$, df = 19, $P = 0.84$).

Data analysis

We aimed to compare the foraging niches of Whenua Hou Diving Petrels and Common Diving Petrels during the incubation and non-breeding periods for each year, while also assessing intraspecific differences between sexes and interannual variation. First, we retrospectively corrected δ^{13}C values from whole blood samples for lipid content using linear models calculating the $\Delta\delta^{13}$C from C:N molar ratios (Post *et al.* 2007). To ensure that results from whole blood and feather samples were comparable, we also corrected δ^{13}C and δ^{15}N from blood samples using linear models to account for the different enrichment factors between the tissues (Cherel *et al.* 2014a, 2014b). We then used δ^{15}N to infer trophic position and δ^{13}C to infer approximate foraging areas (i.e. water masses). For the latter, we used approximate positions of Polar and Subtropical Fronts in the Indian Ocean (Jaeger *et al.* 2010) to delineate water masses. Using a univariate analysis approach, we fitted four generalized linear models (one per incubation/non-breeding period per isotope ratio) with Gaussian error structures and identity link functions to test for effects of species, year and sex, including all two- and three-way interactions on the observed stable isotope ratios. In other words, model structures were fully parameterized and included species, year and sex, as well as all two- and three-way interactions as fixed-effects coefficients (β). No model simplification steps were carried out. For subsequent pairwise comparisons, we used Tukey honest significant difference tests. We removed one extreme outlier using model diagnostics from the R package *performance* (Ludecke *et al.* 2021). In addition, we also applied an unbiased Bayesian bivariate analysis approach to account for the covariance between δ^{15}N and δ^{13}C (Jackson *et al.* 2011). Specifically, we compared the foraging niches of male/female Whenua Hou Diving Petrels and male/female Common Diving Petrels per year during incubation and non-breeding periods by calculating Bayesian Standard Ellipse Areas (SEA_b in ‰^{2}), rescaled to capture 95% of the data, using the R package *SIBER* 2.1.6 (Jackson *et al.* 2011). Through *SIBER*, we called JAGS 4.3.0 (Plummer 2003) to fit vague inverse Wishart priors ($R = 1$, $k = 2$, $\tau_\mu = 0.001$) to the covariance matrix of the isotopic space and simulated 5000 ellipses after a burn-in of 5000 ellipses. We then made pairwise comparisons of SEA_b using the ellipses generated, and if a 95% probability of difference was calculated, we considered this significant. We also calculated the relative pairwise overlap per ellipse iteration using:

$$\text{O}_{i,j} = \frac{A_{i,j}}{A_i + A_j - A_{i,j}},$$

in which $\text{O}_{i,j}$ is the pairwise overlap index, $A_{i,j}$ is the area of overlap in ‰^{2} between SEA_b i and SEA_b j, A_i is the area of SEA_b i, and A_j is the area of SEA_b j. $\text{O}_{i,j}$ is therefore a standardized overlap estimate ranging from 0 (no overlap/complete segregation) to 1 (complete overlap/no segregation), allowing us to assess foraging niche segregation between species and sexes and among years in an unbiased fashion, while taking full account of covariance within the isotopic space. All analyses were conducted in Program R 4.1.0 (R Development Core Team 2021).

RESULTS

During incubation periods (as inferred from blood samples), clear and consistent foraging segregation between Whenua Hou Diving Petrels and Common Diving Petrels was evident (Fig. 1, Table 3; for model summaries, including β coefficients, see Table S1). Whenua Hou Diving Petrels exhibited similar δ^{15}N values but lower δ^{13}C values than Common Diving Petrels ($F_{1,151} = 2.07$, $P = 0.152$

and $F_{1,151} = 99.10$, $P < 0.001$ for species effects in generalized linear models, respectively). Foraging niches of Whenua Hou Diving Petrels were generally larger (mean $\text{SEA}_b = 0.94‰^2$; Fig. 2a) than the foraging niches of Common Diving Petrels ($0.45‰^2$), aside from the 2017 incubation period, a result probably caused by sample sizes. The resulting isotopic overlap during incubation periods was low (mean $O_{i,j} = 0.13$; Fig. 3a), suggesting trophic segregation. These patterns appeared largely consistent across years, as no differences were found for δ^{13}C ($F_{2,151} = 2.13$, $P = 0.123$ for the species*year interaction). Yet, δ^{15}N values showed some variation ($F_{2,151} = 5.57$, $P = 0.004$). Specifically, Whenua Hou Diving Petrels exhibited slightly higher δ^{15}N values during the 2018 El Niño incubation period ($P < 0.05$ in all pairwise comparisons). In contrast, Common Diving Petrels occupied a small isotopic niche during the 2018 El Niño incubation period ($\text{SEA}_b = 0.23‰^2$), resulting in minimal overlap between species ($O_{i,j} = 0.08$).

During non-breeding periods (as inferred from feather samples), segregation between Whenua Hou Diving Petrels and Common Diving Petrels was less pronounced (Fig. 1, Table 3, Table S1). Whenua Hou Diving Petrels exhibited slightly higher δ^{15}N and δ^{13}C values than Common Diving Petrels ($F_{1,152} = 40.16$, $P < 0.001$ and $F_{1,152} = 8.92$, $P = 0.001$, respectively). Isotopic shifts between incubation and non-breeding periods were pronounced for both species; mean trophic shifts equated to −3.1 δ^{15}N ‰ and −4.0 δ^{13}C ‰ for Whenua Hou Diving Petrels and −4.0 δ^{15}N ‰ and −5.1 δ^{13}C ‰ for Common Diving Petrels. Compared with incubation period foraging niches, Whenua Hou Diving Petrel non-breeding period foraging niches were of similar size (mean $\text{SEA}_b = 1.25‰^2$; Fig. 2b), but Common Diving Petrel non-breeding foraging niches increased

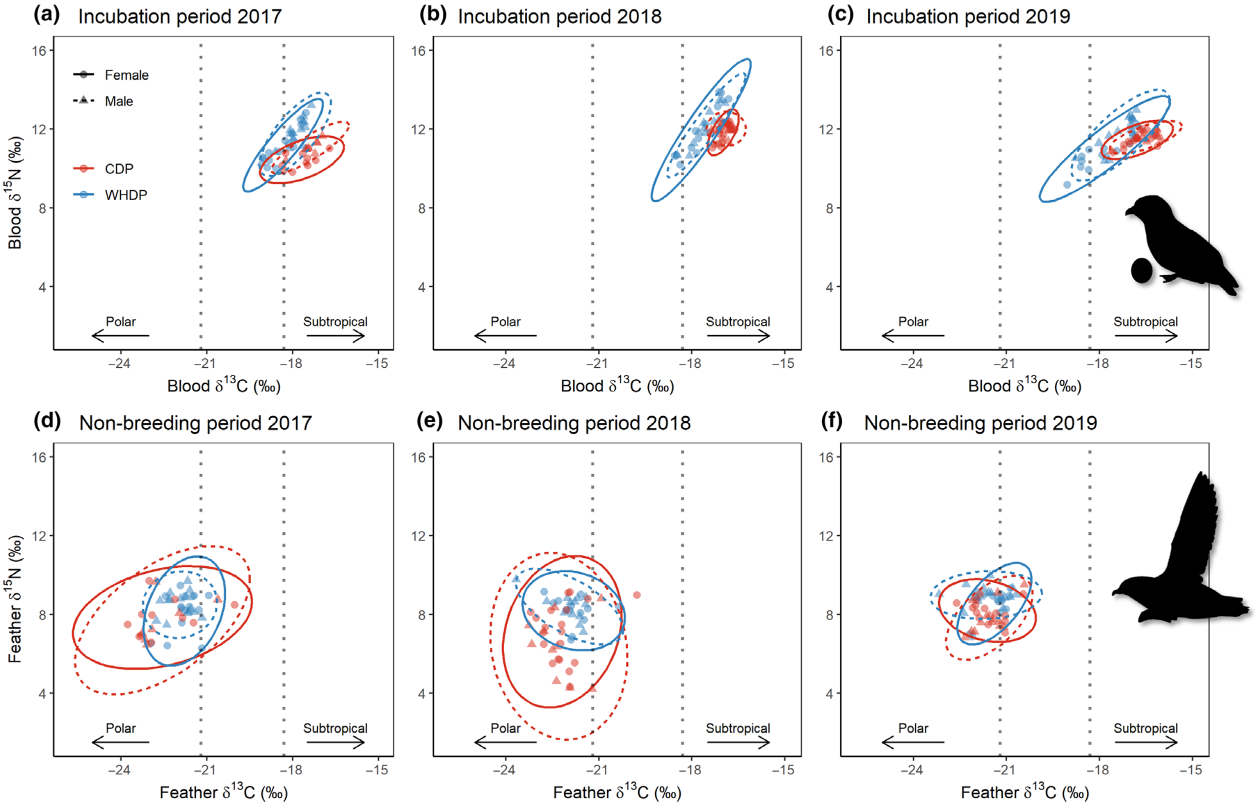

Figure 1. Isotopic (i.e. foraging) niches of Whenua Hou Diving Petrels (WHDP) and Common Diving Petrel (CDP) females and males during incubation periods (Oct–Dec, inferred from blood; a–c) and non-breeding periods (Feb–Aug, inferred from feathers; d–f) illustrated by single 95% standard ellipses (as an example for the iterative Bayesian Standard Ellipses used in analyses). Corrections were applied to account for different enrichment factors between blood and feather tissues (Cherel *et al.* 2014b). Approximate locations of Fronts (dotted lines) based on Jaeger *et al.* (2010). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 3. Stable isotope ratios of Whenua Hou and Common Diving Petrels during incubation (derived from blood samples) and non-breeding periods (derived from feather samples) expressed as means (min; max) and Bayesian Standard Ellipse Areas (SEA_b), rescaled to capture 95% of the data, and overlap ($O_{i,j}$) expressed as means (95% credible intervals). Bold type indicates significance ($P < 0.05$) of pairwise comparisons between species, either through Tukey honest significant difference tests following generalized linear models ($\delta^{15}N$ and $\delta^{13}C$), or through Bayesian probability calculations (SEA_b).

	Whenua Hou Diving Petrel			Common Diving Petrel			
Incubation period[a]	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	SEA_b (‰^{2})	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	SEA_b (‰^{2})	$O_{i,j}$
2017	**10.6 (9.2; 11.7)**	**−18.1 (−19.1; −17.4)**	0.84 (0.59; 1.21)	**11.5 (10.0; 13.2)**	**−17.6 (18.8; −16.7)**	0.76 (0.48; 1.19)	0.15 (0.04; 0.33)
2018	12.1 (10.2; 13.9)	**−17.6 (−18.6; −16.8)**	**0.85 (0.58; 1.25)**	11.9 (11.1; 12.4)	**−17.0 (−17.4; −16.6)**	**0.23 (0.16; 0.33)**	0.08 (0.00; 0.22)
2019	11.3 (9.2; 13.0)	**−17.6 (−16.7; −19.0)**	**1.21 (0.84; 1.74)**	11.6 (10.8; 12.5)	**−16.7 (−17.6; −16.0)**	**0.36 (0.25; 0.53)**	0.16 (0.07; 0.27)
Non-breeding period							
2017	8.3 (6.3; 9.7)	**−21.9 (−23.0; −20.9)**	**1.33 (0.93; 1.90)**	7.9 (6.5; 9.2)	**−22.5 (−23.8; −20.0)**	**3.1 (2.0; 4.9)**	0.40 (0.23; 0.58)
2018	**8.3 (6.7; 9.8)**	−21.9 (−23.7; −20.4)	**1.26 (0.86; 1.85)**	**6.9 (4.2; 9.1)**	−22.2 (−23.3; −19.8)	**3.6 (2.5; 5.1)**	0.31 (0.31; 0.41)
2019	**8.8 (6.9; 10.0)**	−21.5 (−23.2; −20.7)	1.16 (0.81; 1.67)	**8.0 (6.8; 9.5)**	−21.6 (−22.6; −20.4)	1.2 (0.8; 1.8)	0.50 (0.31; 0.69)

[a]Corrections were applied to account for different enrichment factors between blood and feather tissues (Cherel *et al.* 2014b).

considerably in size ($SEA_b = 2.64‰^2$). Consequently, Whenua Hou Diving Petrel non-breeding foraging niches were generally smaller than Common Diving Petrel non-breeding foraging niches. Despite the slight differences detected in trophic level and foraging areas, the foraging niche overlap between the two species during non-breeding periods was higher than during incubation periods (mean $O_{i,j} = 0.40$; Fig. 3b). These patterns appeared largely consistent across years ($\delta^{13}C$: $F_{2,152} = 2.67$, $P = 0.073$ for the species*year interaction), but some interannual variation was evident in $\delta^{15}N$ values ($F_{2,152} = 3.55$, $P = 0.031$). Specifically, Common Diving Petrels exhibited low $\delta^{15}N$ values during the Niño-neutral 2018 non-breeding season ($P < 0.05$ in all pairwise comparisons). In addition, Common Diving Petrels exhibited a smaller foraging niche during the 2019 El Niño non-breeding season ($SEA_b = 1.22‰^2$).

For both species, sexual segregation was limited during incubation and non-breeding periods (incubation $\delta^{15}N$: $F_{1,151} = 0.81$, $P = 0.368$, incubation $\delta^{13}C$: $F_{1,151} = 0.74$, $P = 0.393$, non-breeding $\delta^{15}N$: $F_{1,152} = 6.40$, $P = 0.012$, non-breeding $\delta^{13}C$: $F_{1,152} = 0.26$, $P = 0.611$ for species*sex interactions in generalized linear models; Fig. 1; Table S2). The sizes of incubation period foraging niches of sexes of both species were comparable and overlap indices between sexes were reasonably high (Fig. 3c,e). These patterns were consistent across incubation periods ($\delta^{15}N$: $F_{2,151} = 0.84$, $P = 0.434$, $\delta^{13}C$: $F_{2,151} = 0.13$, $P = 0.878$ for species*sex*year interactions). The size of non-breeding period foraging niches of sexes of both species remained comparable and overlap indices remained reasonably high (Fig. 3d,f). These patterns were also consistent across non-breeding periods ($\delta^{15}N$: $F_{2,152} = 0.25$, $P = 0.781$, $\delta^{13}C$: $F_{2,151} = 0.34$, $P = 0.711$).

DISCUSSION

Our results showed that during the incubation period, the rare and endangered Whenua Hou Diving Petrel exhibited a larger foraging niche, suggesting the species to be a more generalist forager, when compared with the abundant and non-threatened Common Diving Petrel. Specifically, our stable isotope analyses suggested that Whenua Hou Diving Petrels and Common Diving Petrels foraged at similar average trophic positions, but that Whenua Hou Diving Petrels foraged further

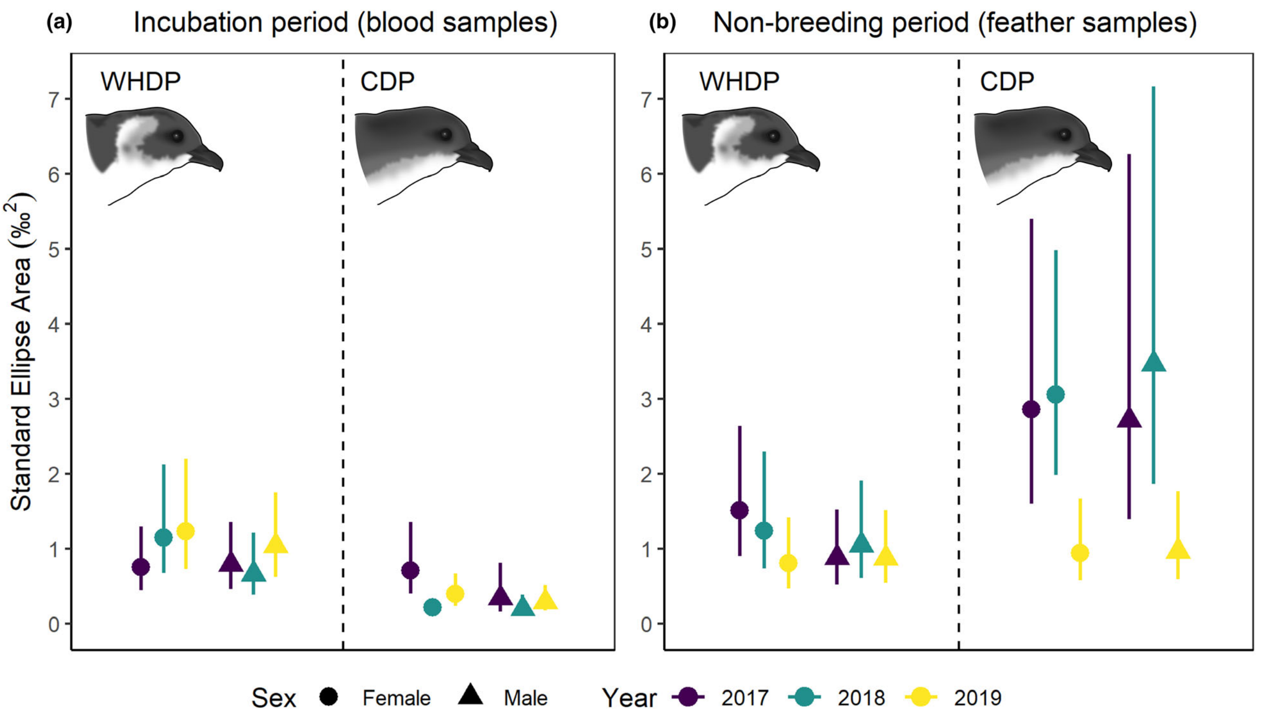

Figure 2. Foraging niche area (‰^{2}) of Whenua Hou Diving Petrel (WHDP) and Common Diving Petrel (CDP) females and males during incubation (a) and non-breeding (b) periods, as estimated with Bayesian 95% Standard Ellipses. Symbols represent posterior means with 95% credible intervals. [Colour figure can be viewed at wileyonlinelibrary.com]

offshore, including in oceanic subantarctic waters, whereas Common Diving Petrels foraged closer to shore, predominantly in subtropical, neritic waters (Kelly 2000, Quillfeldt *et al.* 2005, Jaeger *et al.* 2010). This pattern suggested foraging niche segregation between these two closely related species when they are bound by central place foraging (e.g. Navarro *et al.* 2013, Fromant *et al.* 2022). During the non-breeding period, the foraging niche segregation was reduced, and isotopic niches of both species increased and overlapped considerably (Peterson & Fry 1987, Cherel & Hobson 2007, Jaeger *et al.* 2010). Results further suggested that both during the incubation period and during the non-breeding period, females and males of both species foraged at comparable trophic positions and in similar waters, which was consistent with tracking results from geolocators (Fischer *et al.* 2021a). These patterns were consistent among years, but Common Diving Petrel foraging niches contracted during El Niño conditions, suggesting sensitivity to environmental change.

During the incubation period, Whenua Hou Diving Petrels and Common Diving Petrels exhibited foraging niche segregation and avoided at-sea competition when both species were bound by central-place foraging around Whenua Hou. Our results showed that Whenua Hou Diving Petrels are more generalist foragers, using waters further offshore, including oceanic subantarctic waters, when compared with Common Diving Petrels, which appeared to be more specialist foragers that largely used subtropical, neritic waters (Jaeger *et al.* 2010, Fromant *et al.* 2022). These patterns match attendance rates observed at the breeding colony, as Whenua Hou Diving Petrels change incubation shifts every 2–4 days (Fischer *et al.* 2021c), while incubating Common Diving Petrels change over almost every night (Zhang *et al.* 2019, Dunphy *et al.* 2020). Common Diving Petrels therefore appear more restricted by central place foraging than Whenua Hou Diving Petrels, allowing the latter to exploit more oceanic waters (Fischer *et al.* 2021a). These differences in central place foraging restrictions could also cause the apparent trophic restriction in Common Diving Petrels compared with the more generalist Whenua Hou Diving Petrels, which may feed on

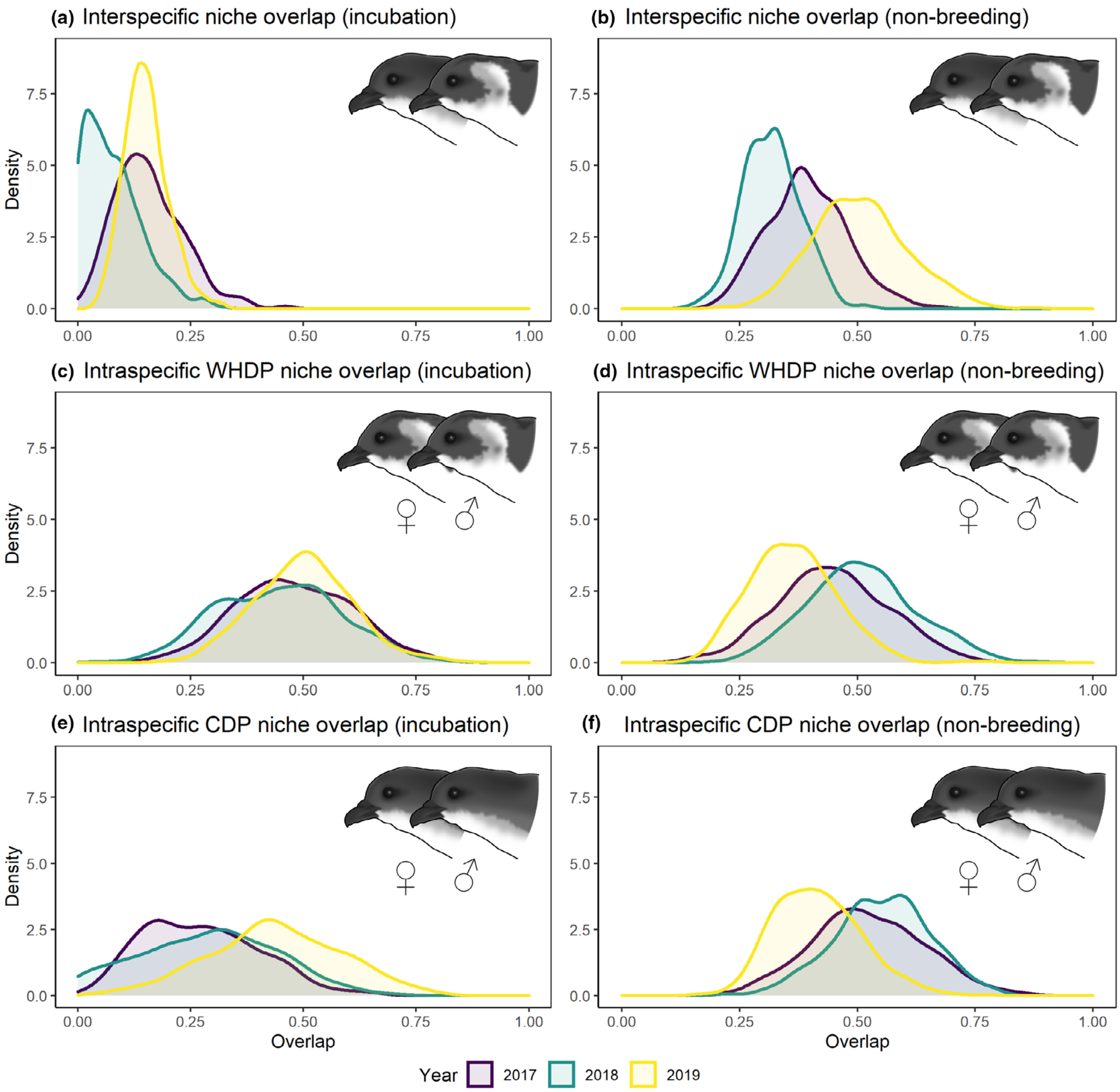

Figure 3. Density plots illustrating interspecific (a, b) and intraspecific (c–f) foraging niche overlap of Whenua Hou Diving Petrel (WHDP) and Common Diving Petrel (CDP) females and males during incubation (a, c, e) and non-breeding (b, d, f) periods, as estimated through pairwise overlap calculations of Bayesian 95% Standard Ellipses. [Colour figure can be viewed at wileyonlinelibrary.com]

euphausiids, small fish and small cephalopods (Imber & Nilsen 1980). The observed foraging niche segregation is unlikely to be explained by the subtle morphological differences between species (Fischer *et al.* 2018a), as both can travel vast distances during the non-breeding period (3000–6500 km for Whenua Hou Diving Petrels, 3000–5000 km for Common Diving Petrels; Rayner *et al.* 2017, Fischer *et al.* 2021a). Our results mirror the diving petrel niche segregation observed in the southern Atlantic and Indian Oceans, where Common Diving Petrels *P. u. exsul* and South Georgian Diving Petrels *P. georgicus* exhibited similar foraging niche segregations (Bocher *et al.* 2000, Navarro *et al.* 2013, Bost *et al.* 2022, Fromant *et al.* 2022). However, GPS tracking results suggested that Common Diving Petrels *P. u. exsul* and South Georgian Diving Petrels forage equally far from their breeding grounds during the incubation periods, and Common Diving Petrels only exhibited restricted neritic foraging during the more energy-demanding chick-rearing period (Navarro *et al.* 2013, Fromant *et al.* 2022). Similar high-resolution GPS tracking of both Common Diving Petrels *P. u. chathamensis* and Whenua Hou Diving Petrels would be required to provide further insights into the use of distinct foraging areas of these species (Bost *et al.* 2022, Fromant *et al.* 2022). Such tracking efforts could also be used to assess the adequacy of the static carbon signatures of ocean fronts, which we used to delineate water masses in this study (Carpenter-Kling *et al.* 2020).

After the breeding period, Whenua Hou Diving Petrels and Common Diving Petrels no longer exhibited foraging niche segregation. Both species leave their breeding grounds in Aotearoa and migrate several thousand kilometres to their non-breeding ranges in the Southern Ocean (Rayner *et al.* 2017, Fischer *et al.* 2021a). During this time, Common Diving Petrels switched from an apparent specialist foraging strategy during the breeding period to a more generalist strategy during the non-breeding period. Fine-scale spatial segregation between Whenua Hou Diving Petrels and Common Diving Petrels in non-breeding areas in the Southern Ocean may still limit competition during this period (Fromant *et al.* 2020, 2022). The non-breeding ranges of Common Diving Petrels of the *chathamensis* subspecies remain unknown and further tracking is required to confirm fine-scale spatial segregation. Additionally, the $\delta^{15}N$ shift between breeding periods suggested that both species fed on a lower trophic level during the non-breeding period (Minagawa & Wada 1984, Cherel *et al.* 2014a). Feeding at higher trophic positions during breeding periods is expected, because seabirds must balance the changing demands of self and offspring provisioning with the constraints imposed by central place foraging (Boersma *et al.* 2015, Booth *et al.* 2018). Similar niche shifts and limited foraging segregation during the non-breeding period were observed between sympatric diving petrels breeding in the Atlantic and Indian Oceans (Bocher *et al.* 2000, Navarro *et al.* 2015, Bost *et al.* 2022, Fromant *et al.* 2022).

The observed foraging niche dynamics of Whenua Hou Diving Petrels were largely consistent among years, despite varying climatic conditions, in contrast to Common Diving Petrels, which showed more fluctuations. Varying ENSO conditions have considerable influences on the waters surrounding Aotearoa. El Niño conditions are characterized by cooler waters, whereas La Niña conditions are characterized by warmer waters (Mullan 1995, Russell *et al.* 2022). Common Diving Petrels appeared to be sensitive to ENSO cycles, as both incubation and non-breeding foraging niches shrank during El Niño conditions. Common Diving Petrels in Australia are known to increase foraging effort, show trophic shifts and exhibit extreme nest failures during marine heatwaves, suggesting considerable sensitivity to environmental change (Fromant *et al.* 2021). Yet, in Aotearoa, El Niño conditions are characterized by cooler waters, and as such, further studies are required to disentangle the underlying mechanisms of the observed Common Diving Petrel sensitivity. Further studies might also elucidate the low trophic levels observed in Common Diving Petrels during the Niño-neutral 2018 non-breeding season. In contrast, despite varying ENSO conditions, the foraging niches of Whenua Hou Diving Petrels were largely consistent. Therefore, Whenua Hou Diving Petrels might be more resilient to fluctuating ocean conditions than Common Diving Petrels (Gremillet *et al.* 2012, Peers *et al.* 2014), which is further supported by fairly consistent adult survival, breeding probability and breeding success, despite climate fluctuations (Fischer *et al.* 2022b). Alternatively, Whenua Hou Diving Petrels may compensate for sub-optimal climatic conditions through behavioural plasticity (e.g. increasing foraging intensities; Fischer *et al.* 2021a, 2021c). It should be noted that our stable isotope study only included three sampling years and that neither this investigation nor previous demographic studies (Fischer *et al.* 2022b) accounted for potential time lags of climate-related impacts (e.g. Jenouvrier 2013). Gaining a more in-depth understanding into the impacts of a changing environment therefore requires integrating future demographic and stable isotope studies with more in-depth environmental data over longer time frames.

Our results suggest that the critically endangered Whenua Hou Diving Petrel is a reasonably adaptable generalist feeder, apparently most at risk from concurrent terrestrial and near-shore threats. We showed that alongside the segregation on land between Common Diving Petrels (habitat generalists) and Whenua Hou Diving Petrels (dune specialists; Fischer *et al.* 2018b), the segregation at sea between generalist-feeding Whenua Hou Diving Petrels and specialist-feeding Common Diving Petrels appears to reduce competition between species at sea, facilitating their coexistence. Specialists are more at risk of extinction than generalists and, as such, it would be disadvantageous for a species to be a specialist across multiple ecosystems (Barger & Kitaysky 2012, Richard *et al.* 2021). The limited sensitivity of foraging niches of Whenua Hou Diving Petrel to varying climates suggests the species may be less vulnerable at sea, which is further supported by limited pollutant loads (Tocker 2020). Conservation management of Whenua Hou Diving Petrels should focus on addressing the immediate terrestrial threats (e.g. storm-induced erosion and competition for burrow sites with Common Diving Petrel; Fischer *et al.* 2017, 2018b) and near-shore threats (i.e. deck strikes; Fischer *et al.* 2021b), while continuing to monitor for indirect, pelagic threats. This is encouraging, as terrestrial threats and near-shore threats can be more readily addressed through tested conservation measures, including best practice mitigation of light pollution (Commonwealth of Australia 2020), competition control (Gummer *et al.* 2015) and translocations (Fischer *et al.* 2021c, 2022a, 2022b). Indirect pelagic threats, on the other hand, are notoriously challenging to address.

AUTHOR CONTRIBUTIONS

Grace E. Tocker: Conceptualization; data curation; formal analysis; investigation; methodology; writing – original draft. **Johannes H. Fischer:** Conceptualization; data curation; formal analysis; investigation; methodology; writing – original draft. **Paco Bustamante:** Conceptualization; investigation; methodology; writing – review and editing. **Gaël Guillou:** Investigation; writing – review and editing. **Igor Debski:** Conceptualization; writing – review and editing. **Graeme A. Taylor:** Conceptualization; writing – review and editing. **Peter A. Ritchie:** Conceptualization; supervision; writing – review and editing. **Heiko U. Wittmer:** Conceptualization; supervision; writing – review and editing.

We thank Kāi Tahu, Kaitiaki Rōpū ki Murihiku and the Whenua Hou Komiti for granting access to Whenua Hou and work on these taonga (treasures), several volunteers for their assistance in the field, S. Hinkley from the Ferrier Institute for his help with sample preparation, J. de Hoop and D. Young for the electronic artwork, and R. Nager, M. Frederiksen and two anonymous reviewers for their helpful comments. Open access publishing facilitated by Victoria University of Wellington, as part of the Wiley - Victoria University of Wellington agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

FUNDING

G.E.T. was supported by a Victoria University of Wellington Master's by Thesis Scholarship and the Tu Horomata Scholarship. J.H.F. was supported by a Victoria University of Wellington Doctoral Scholarship. Fieldwork was supported by the National Geographic Society (WW-249C-17), the Ornithological Society of New Zealand (Bird NZ Research Fund 2017, 2019), the Mohamed Bin Zayed Species Conservation Fund (Project 192520234), the Encounter Foundation, Forest and Bird (JS Watson Trust 2017), the Centre for Biodiversity and Restoration Ecology (Student Award 2017), the Royal Society of New Zealand (Hutton Fund 2017) and the Department of Conservation. Stable isotope analyses were supported by Contrat de Projet Etat-Région (CPER), European Regional Development Fund (FEDER) and the Institut Universitaire de France.

ETHICAL NOTE

All work was carried out with permission from Kāi Tahu, Kaitiaki Rōpū ki Murihiku, the Whenua Hou Komiti, and the Department of Conservation (entry permits M1718/01, M1819/01, M1920/02). All methods were approved by the animal ethics committee of Victoria University of Wellington (VUW AEC 23283 and 27621).

Data Availability Statement

As Kāi Tahu exercise rangatiratanga (sovereignty) and express kaitiakitanga (guardianship) over Whenua Hou and both Diving Petrel species, data can only be made available following consultation. The corresponding author can be contacted to facilitate such consultation.

REFERENCES

Barger, C.P. & Kitaysky, A.S. 2012. Isotopic segregation between sympatric seabird species increases with nutritional stress. *Biol. Lett.* **8**: 442–445.

Bearhop, S., Adams, C.E., Waldron, S., Fuller, R.A. & MacLeod, H. 2004. Determining trophic niche width: a novel approach using stable isotope analysis. *J. Anim. Ecol.* **73**: 1007–1012.

Bearhop, S., Phillips, R.A., McGill, R., Cherel, Y., Dawson, D.A. & Croxall, J.P. 2006. Stable isotopes indicate sex specific and long-term individual foraging specialisation in diving seabirds. *Mar. Ecol. Prog. Ser.* **311**: 157–164.

Bedolla-Guzmán, Y., Masello, J.F., Aguirre-Munoz, A., Lavaniegos, B.E., Voigt, C.C., Gomez-Gutierrez, J., Sanchez-Valesco, L., Robinson, C.J. & Quillfeldt, P. 2022. Year-round niche segregation of three sympatric *Hydrobates* storm-petrels from Baja California Peninsula, Mexico, Eastern Pacific. *Mar. Ecol. Prog. Ser.* **664**: 207–225.

Bernard, A., Rodrigues, A.S.L., Cazalis, V. & Gremillet, D. 2021. Toward a global strategy for seabird tracking. *Conserv. Lett.* **14**: e12804.

Bocher, P., Cherel, Y. & Hobson, K.A. 2000. Complete trophic segregation between south Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar. Ecol. Prog. Ser.* **208**: 249–264.

Boersma, P.D., Rebstock, G.A. & Garcia-Borboroglu, P.G. 2015. Marine protection is needed for Magellanic penguins in Argentina based on long-term data. *Biol. Conserv.* **182**: 197–204.

Booth, J.M., Steinfurth, A., Fusi, M., Cuthbert, R.J. & McQuaid, C.D. 2018. Foraging plasticity of breeding northern rockhopper penguins, *Eudyptes moseleyi*, in response to changing energy requirements. *Polar Biol.* **41**: 1815–1826.

Bost, C.A., Delord, K., Cherel, Y., Miskelly, C.M., Carravieri, A., Bustamante, P., Arnould, J.P.Y. & Fromant, A. 2022. Foraging trips and isotopic niche of chick-rearing south Georgian diving petrels from the Kerguelen Islands. *Mar. Ecol. Prog. Ser.* **689**: 169–177.

Bourgeois, K., Welch, J.R., Dromzee, S., Taylor, G.A. & Russell, J.C. 2022. Flexible foraging strategies in a highly pelagic seabird revealed by seasonal isotopic niche variation. *Mar. Biol.* **169**: 28.

Bugoni, L., McGill, R.A.R. & Furness, R.W. 2008. Effects of preservation methods on stable isotope signatures in bird tissues. *Rapid Commun. Mass Spectrom.* **22**: 2457–2462.

Carpenter-Kling, T., Pistorius, P., Reisinger, R., Cherel, Y. & Connan, M. 2020. A critical assessment of marine predator isoscapes within the southern Indian Ocean. *Mov. Ecol.* **8**: 29.

Cherel, Y. & Hobson, K.A. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **329**: 281–287.

Cherel, Y., Hobson, K.A. & Weimerskirch, H. 2005. Using stable isotopes to study resource acquisition and allocation in Procellariiform seabirds. *Oecologia* **145**: 533–540.

Cherel, Y., Phillips, R.A., Hobson, K.A. & McGill, R. 2006. Stable isotope evidence of diverse species-specific and individual wintering strategies in seabirds. *Biol. Lett.* **2**: 301–303.

Cherel, Y., Le Corre, M., Jaquemet, S., Menard, F., Richard, P. & Weimerskirch, H. 2008. Resource partitioning within a tropical seabird community: new information from stable isotopes. *Mar. Ecol. Prog. Ser.* **366**: 281–291.

Cherel, Y., Connan, M., Jaeger, A. & Richard, P. 2014a. Seabird year-round and historical feeding ecology: blood and feather δ^{13}C and δ^{15}N values document foraging plasticity of small sympatric petrels. *Mar. Ecol. Prog. Ser.* **505**: 267–280.

Cherel, Y., Jaquemet, S., Maglio, A. & Jaeger, A. 2014b. Differences in δ^{13}C and δ^{15}N values between feathers and blood of seabird chicks: implications for non-invasive isotopic investigations. *Mar. Biol.* **161**: 229–237.

Cherel, Y., Barbraud, C., Lahournat, M., Jaeger, A., Jaquemet, S., Wanless, R.M., Phillips, R.A., Thompson, D.R. & Bustamante, P. 2018. Accumulate or eliminate? Seasonal mercury dynamics in albatrosses, the most contaminated family of birds. *Environ. Pollut.* **241**: 124–135.

Commonwealth of Australia 2020. *National Light Pollution Guidelines for Wildlife Including Marine Turtles, Seabirds and Migratory Shorebirds*. Canberra, Australia: Commonwealth of Australia.

Croxall, J.P. & Prince, P.A. 1980. Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol. J. Linn. Soc.* **14**: 103–131.

Croxall, J.P., Prince, P.A. & Reid, K. 1997. Dietary segregation of krill-eating South Georgia seabirds. *J. Zool.* **242**: 531–556.

Croxall, J.P., Butchart, S.H.M., Lascelles, B., Stattersfield, A.J., Sullivan, B., Symes, A. & Taylor, P. 2012. Seabird conservation status, threats and priority actions: a global assessment. *Bird Conserv. Int.* **22**: 1–34.

Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G. & Croxall, J.P. 2019. Threats to seabirds: a global assessment. *Biol. Conserv.* **237**: 525–537.

Dunphy, B.J., Vickers, S.I., Zhang, J., Sager, R.L., Landers, T.J., Bury, S.J., Hickey, A.J.R. & Rayner, M.J. 2020. Seabirds as environmental indicators: foraging behaviour and ecophysiology of common diving petrels (*Pelecanoides urinatrix*) reflect local-scale differences in prey availability. *Mar. Biol.* **167**: 53.

Fischer, J.H., Debski, I., Taylor, G.T. & Wittmer, H.U. 2017. Assessing the suitability of non-invasive methods to monitor interspecific interactions and breeding biology of the south Georgian diving petrel (*Pelecanoides georgicus*). *Notornis* **64**: 13–20.

Fischer, J.H., Debski, I., Miskelly, C.M., Bost, C.A., Fromant, A., Tennyson, A.J.D., Tessler, J., Cole, R., Hiscock, J.H., Taylor, G.A. & Wittmer, H.U. 2018a. Analyses of phenotypic differentiations among south Georgian diving petrel (*Pelecanoides georgicus*) populations reveal an undescribed and highly endangered species from New Zealand. *PLoS One* **13**: e0197766.

Fischer, J.H., Debski, I., Taylor, G.A. & Wittmer, H.U. 2018b. Nest-site selection of South Georgia diving-petrels on Codfish Island (Whenua Hou), New Zealand: implications for conservation management. *Bird Conserv. Int.* **28**: 216–227.

Fischer, J.H., Taylor, G.A., Debski, I. & Wittmer, H.U. 2020a. Acoustic attraction system draws in competing seabird species. *Notornis* **67**: 568–572.

Fischer, J.H., Taylor, G.A., Cole, R., Debski, I., Armstrong, D.P. & Wittmer, H.U. 2020b. Population growth estimates of a threatened seabird indicate necessity for additional management following invasive predator eradications. *Anim. Conserv.* **23**: 94–103.

Fischer, J.H., Debski, I., Spitz, D.B., Taylor, G.A. & Wittmer, H.U. 2021a. Year-round offshore distribution, behaviour, and overlap with commercial fisheries of a critically endangered small petrel. *Mar. Ecol. Progr. Ser.* **660**: 171–187.

Fischer, J.H., Debski, I., Taylor, G.A. & Wittmer, H.U. 2021b. Consistent artificial light at night near the last breeding colony of a critically endangered seabird. *Conserv. Sci. Pract.* **3**: e481.

Fischer, J.H., Wittmer, H.U., Taylor, G.A., Debski, I. & Armstrong, D.P. 2021c. Preparing for translocations of a critically endangered petrel through targeted monitoring of nest survival and breeding biology. *Oryx* **55**: 564–572.

Fischer, J.H., Parker, K.A., Kenup, C.F., Taylor, G.A., Debski, I. & Ewen, J.G. 2022a. *A Structured Decision-Making Approach for the Recovery of Kuaka/Whenua Hou Diving Petrel (Pelecanoides whenuahouensis)*. Wellington: Department of Conservation.

Fischer, J.H., Wittmer, H.U., Kenup, C.F., Parker, K.A., Cole, R., Debski, I., Taylor, G.A., Ewen, J.G. & Armstrong, D.P. 2022b. Predicting harvest impact and establishment success when translocating highly mobile and endangered species. *J. Appl. Ecol.* **59**: 2071–2083.

Fromant, A., Bost, C.A., Bustamante, P., Carravieri, A., Cherel, Y., Delord, K., Eizenberg, Y.H., Miskelly, C.M. & Arnould, J.P.Y. 2020. Temporal and spatial differences in the post-breeding behaviour of a ubiquitous southern hemisphere seabird, the common diving petrel. *R. Soc. Open Sci.* **7**: 200670.

Fromant, A., Delord, K., Bost, C.A., Eizenberg, Y.H., Botha, J.A., Cherel, Y., Bustamante, P., Gardner, B.R., Brault-Favrou, M., Lec'hvien, A. & JPY, A. 2021. Impacts of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving seabird, the common diving petrel. *Prog. Oceanogr.* **198**: 102676.

Fromant, A., Arnould, J.P.Y., Delord, K., Sutton, G.J., Carravieri, A., Bustamante, P., Miskelly, C.M., Kato, A., Brault-Favrou, M., Cherel, Y. & Bost, C.A. 2022. Stage-dependent niche segregation: insights from a multi-dimensional approach of two sympatric sibling seabirds. *Oecologia* **199**: 537–548.

Gladbach, A., McGill, R.A.R. & Quillfeldt, P. 2007. Foraging areas of Wilson's storm petrel *Oceanites oceanicus* in the breeding and inter-breeding period determined by stable isotope analysis. *Polar Biol.* **30**: 1005–1012.

Grecian, J.W., Taylor, G.A., Loh, G., McGill, R.A.R., Miskelly, C.M., Phillips, R.A., Thompson, D.R. & Furness, R.W. 2016. Contrasting migratory responses of two closely related seabirds to long-term climate change. *Mar. Ecol. Prog. Ser.* **559**: 231–242.

Gremillet, D., Welker, J., Karnovsky, N.J., Walkusz, W., Hall, M.E., Fort, J., Brown, Z.W., Speakman, J.R. & Harding, A.M.A. 2012. Little auks buffer the impact of current Arctic climate change. *Mar. Ecol. Prog. Ser.* **454**: 197–206.

Gremillet, D., Ponchon, A., Paleczny, M., Palomares, M.L.D., Karpouzi, V. & Pauli, D. 2018. Persisting worldwide seabird–fisheries competition despite seabird community decline. *Curr. Biol.* **28**: 4009–4013.

Gummer, H., Taylor, G., Wilson, K.J. & Rayner, M.J. 2015. Recovery of the endangered Chatham petrel (*Pterodroma axillaris*): a review of conservation management techniques from 1990 to 2010. *Glob. Ecol. Conserv.* **3**: 310–323.

Hobson, K.A. & Clark, R. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for non-destructive sampling in avian dietary studies. *Auk* **110**: 638–641.

Hobson, K.A., Alisauskas, R.T. & Clark, R.G. 1993. Stable-nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress: implications for isotopic analyses of diet. *Condor* **95**: 388–394.

Hobson, K.A., Piatt, J.F. & Pitocchelli, J. 1994. Using stable isotopes to determine seabird trophic relationships. *J. Anim. Ecol.* **63**: 786–798.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *Am. Nat.* **93**: 145–159.

Imber, M.J. & Nilsen, R.J. 1980. South Georgian diving petrels (*Pelecanoides georgicus*) breeding on Codfish Island. *Notornis* **27**: 325–330.

Jackson, A.L., Inger, R., Parnell, A.C. & Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER-Stable Isoptope Bayesian Ellipses in R. *J. Anim. Ecol.* **80**: 595–602.

Jaeger, A., Lecomte, V.J., Weimerskirch, H., Richard, P. & Cherel, Y. 2010. Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators foraging areas in the Southern Ocean. *Rapid Commun. Mass Spectrom.* **24**: 3456–3460.

Jenouvrier, S. 2013. Impacts of climate change on avian populations. *Glob. Change Biol.* **19**: 2036–2057.

Jones, C.W., Phillips, R.A., Grecian, W.J. & Ryan, P.G. 2020. Ecological segregation of two superabundant, morphologically similar, sister seabird taxa breeding in sympatry. *Mar. Biol.* **167**: 45.

Kelly, J.F. 2000. Stable isotopes of carbon and in the study of avian and mammalian trophic ecology. *Can. J. Zool.* **78**: 1–27.

Ludecke, D., Ben-Sachar, M.S., Patil, I., Waggoner, P. & Makowski, D. 2021. Performance: an R package for assessment, comparison and testing of statistical models. *J. Open Source Softw.* **6**: 3139.

MacNeil, M.A., Skomal, G.B. & At, F. 2005. Stable isotopes from multiple tissues reveal diet switching in sharks. *Mar. Ecol. Prog. Ser.* **302**: 199–206.

Masello, J.F., Mundry, R., Poisbleau, M., Demongin, L., Voigt, C.C., Wikelski, M. & Quilllfeldt, P. 2010. Diving seabirds share foraging space and time within and among species. *Ecosphere* **1**: 19.

McInnes, J.C., Jarman, A.N., Lea, M.A., Raymond, B., Deagle, B.E., Phillips, R.A., Catry, P., Stanworth, A., Weimerskirch, H., Kusch, A., Grass, M., Cherel, Y., Maschette, D. & Alderman, R. 2017. DNA metabarcoding as a marine conservation and management tool: a circumpolar examination of fishery discards in the diet of threatened albatrosses. *Front. Mar. Sci.* **4**: 277.

Minagawa, M. & Wada, E. 1984. Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between δ^{15}N and animal age. *Geochim. Cosmochim. Acta* **48**: 1135–1140.

Mullan, A.B. 1995. On the linearity and stability of southern oscillation-climate relationships for New Zealand. *Int. J. Climat.* **15**: 1365–1386.

Navarro, J., Votier, S.C., Aguzzi, J., Chiesa, J.J., Forero, M.G. & Phillips, R.A. 2013. Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS One* **8**: e62897.

Navarro, J., Cardador, L., Brown, R. & Phillips, R.A. 2015. Spatial distribution and ecological niches of non-breeding planktivorous petrels. *Sci. Rep.* **5**: 12164.

Newsome, S.D., del Rio, C.M., Bearhop, S. & Phillips, D.L. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.* **5**: 429–436.

Nisbet, I.C.T., Montoya, J.P., Burger, J. & Hatch, J.J. 2002. Use of stable isotopes to investigate individual differences in diets and mercury exposures among common terns *Sterna hirundo* in breeding and wintering grounds. *Mar. Ecol. Prog. Ser.* **242**: 267–274.

NOAA. 2022. *National Oceanic and Atmospheric Administration Climate Prediction Database Repository*. Available at: https://origin.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_v5.php. (accessed 22 February 2022)

Norris-Caneda, K.H. & Elliott, J.D. 1998. Sex identification in raptors using PCR. *J. Raptor Res.* **32**: 278–280.

Peers, M.J.L., Wehtje, M., Thornton, D.H. & Murray, D.L. 2014. Prey switching as a means of enhancing persistence in predators at the trailing southern edge. *Glob. Change Biol.* **20**: 1126–1135.

Peterson, B.J. & Fry, B. 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* **18**: 293–320.

Phalan, B., Phillips, R.A., Silk, J.R.D., Afanasyev, V., Fukuda, A., Fox, J., Catry, P., Higuchi, H. & Croxall, J.P. 2007. Foraging behaviour of four albatross species by night and day. *Mar. Ecol. Prog. Ser.* **340**: 271–286.

Plummer, M. 2003. A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd International Workshop on Distributed Statistical Computing* **124**: 125.10.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* **83**: 703–718.

Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J. & Montana, C.G. 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* **152**: 179–189.

Quillfeldt, P., McGill, R.A.R. & Furness, R.W. 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. *Mar. Ecol. Prog. Ser.* **295**: 295–304.

R Development Core Team. 2021. *R: A Language and Environment for Statistical Computing (R version 4.0.3)*. Vienna, Austria: R Foundation for Statistical Computing.

Ramirez, F., Vicente-Sastre, D., Afan, I., Igual, J.M., Oro, D. & Forero, M.G. 2021. Stable isotopes in seabirds reflect changes in marine productivity patterns. *Mar. Ecol. Prog. Ser.* **662**: 169–180.

Ravache, A., Bourgeois, K., Weimerskirch, H., Pagenaud, A., de Grissac, S., Miller, M., Dromzee, S., Lorrain, V., Bustamante, P., Bylemans, J., Gleeson, D., Letourneur, Y. & Vidal, E. 2020. Behavioural and trophic segregations help the Tahiti petrel to cope with the abundance of wedge-tailed shearwater when foraging in oligotrophic tropical waters. *Sci. Rep.* **10**: 15129.

Rayner, M.J., Taylor, G.A., Gaskin, C.P. & Dunphy, B.J. 2017. Seasonal activity and unpredicted polar front migration of northern New Zealand common diving petrels. *Emu* **117**: 290–298.

Rayner, M.J., Dunphy, B.J., Lukies, K., Adams, N., Berg, M., Kozmian-Leward, L., Pinkerton, M.H. & Bury, S.J. 2021. Stable isotope record from a resident New Zealand seabird community suggests changes in distribution but not trophic position since 1878. *Mar. Ecol. Prog. Ser.* **678**: 171–182.

Richard, C., Cooke, R.S.C. & Bates, A.E. 2021. Biological traits of seabirds predict extinction risk and vulnerability to anthropogenic threats. *Glob. Ecol. Biogeogr.* **30**: 973–986.

Richdale, L.E. 1945. Supplementary notes on the diving petrel. *Trans. R. Soc. N. Z.* **75**: 42–53.

Russell, J.C., Welch, J.R., Bourgeois, K., Dromzee, S., Dunn, R., Friesen, M.R. & Rayner, M.J. 2022. Climatic effects on Grey-faced petrel (*Pterodroma gouldi*) chick growth and survival. *Birds* **3**: 138–148.

Schreiber, R.W. & Schreiber, E.A. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983. *Science* **225**: 713–716.

Schultz, H., Chang, K., Bury, S.J., Gaskett, A.C., Dennis, T.E., Ismar-Rebitz, S.M.H., Southey, I., Hohnhold, R.J. & Millar, C.D. 2021. Sex-specific foraging of an apex predator puts females at risk of human–wildlife conflict. *J. Anim. Ecol.* **90**: 1776–1786.

Sydeman, W.J., Thompson, S.A. & Kitaysky, A. 2012. Seabirds and climate change: a roadmap for the future. *Mar. Ecol. Prog. Ser.* **454**: 107–117.

Taylor, G.A. 2000. *Action Plan for Seabird Conservation in New Zealand Part B: Non-threatened Seabirds*. Wellington: Department of Conservation.

Taylor, G.A., Jakob-Hoff, R. & Gummer, H. 2010. *Sampling Avian Blood and Feathers, and Reptilian Tissue: Standard Operating Procedure*. Wellington: Department of Conservation.

Tocker, G.A. 2020. *Characterising the Foraging Ecology and Mercury Exposure of the Nationally Critical Whenua Hou Diving Petrel*. MSc Thesis. Wellington: Victoria University of Wellington.

Yasunari, T. 1987. Global structure of the El Niño/southern oscillation part II. Time evolution. *J. Meteorol. Soc. Jpn* **65**: 81–102.

Zhang, J., Rayner, M., Vicker, S., Landers, T., Sagar, S., Stewart, J. & Dunphy, B. 2019. GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of common diving petrels. *Emu* **119**: 126–137.

Received 16 March 2022;
Revision 22 November 2022;
revision accepted 4 December 2022.
Associate Editor: Morten Frederiksen.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Model summaries of univariate models explaining variation in $\delta^{15}N$ and $\delta^{13}C$.

Table S2. Descriptive statistics of stable isotope ratios of female and male Whenua Hou and Common Diving Petrels during incubation and non-breeding periods in each of the three study years.