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ORIGINAL PAPER

Flexible foraging strategies in a highly pelagic seabird revealed by seasonal isotopic niche variation

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Abstract

Flexibility in foraging strategy is an important mechanism by which seabirds cope with spatiotemporal heterogeneity in food availability and the variable energetic constraints of their annual life cycle. Foraging strategy flexibility was investigated in the grey-faced petrel *Pterodroma gouldi* breeding on Ihumoana Island (36°53′S, 174°26′E) using stable isotope analyses. Intra- and inter-annual variations in stable isotope values, isotopic niches and diet inferred from isotope mixing models were studied by analysing δ^{15}N and δ^{13}C in adult wing feathers and blood, chick down and body feathers, and muscle from spontaneously regurgitated prey, collected during 2013 and 2014 breeding seasons. Grey-faced petrels exhibited variations in stable isotopes, isotopic niches and diet more markedly throughout their annual life cycle than between years. A trophic segregation occurred between adults and chicks presumably from adults feeding inshore and chicks being fed more oceanic prey of higher trophic level. Stable-isotope mixing models revealed that adult diet during the breeding season could consist mainly of ram's horn squids *Spirula spirula* and chick diet of crustaceans, fish and other cephalopods being secondary prey throughout the breeding season. Adult male and female isotopic niches slightly differed. Finally, isotopic niche in adults during non-breeding was similar to that during breeding, suggesting non-breeding foraging areas located off the eastern Australian coast, around the limit between the Tasman and Coral seas. Our results demonstrated plasticity in the foraging strategy of grey-faced petrels in response to the changing nutritional demands of their annual cycle and to changes in oceanographic conditions likely driven by El Niño Southern Oscillation.

Keywords Grey-faced petrel · Stable isotopes · Diet · Foraging habitat · Flexible strategy · Niche segregation

Introduction

Energetic demands vary throughout the annual life cycle in animals and they are particularly high during reproduction because adults must balance their own energy requirements with those of their offspring (Stearns 1992; Bryant 1997; Whittow 2001; Sibly et al. 2012). This is especially the case for long-lived animals which have the potential to reproduce for many years. Striking examples of these long-lived animals are seabirds. In addition, population dynamics of these marine predators are generally driven by the abundance and availability of their prey (bottom-up control, Frederiksen et al. 2006) which are highly dynamic in marine systems. Flexibility in foraging strategy is thus an important mechanism by which seabirds cope with spatiotemporal heterogeneity in food availability (extrinsic factors) and the variable energetic constraints of their annual life cycle (intrinsic factors) (e.g. Kato et al. 2003; Shaffer et al. 2003; Tremblay and Cherel 2003; Peery et al. 2009; Zimmer et al. 2011; Ramos

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et al. 2015; Leal et al. 2017; Thabet et al. 2019). These energetic constraints are particularly high during breeding stages and moult. Optimal foraging theory predicts that animals adopt foraging strategies that provide the most energy for the lowest cost, maximizing net energy gain and thus fitness (MacArthur and Pianka 1966; Schoener 1971). In accordance with this theory, seabirds can adjust their foraging strategies in response to extrinsic and intrinsic factors. They can thus switch their diet to prey that are more accessible (more abundant and/or closer to their nesting grounds), temporally available or more energetic/nutrient-rich (Quillfeldt 2002; Navarro et al. 2009; Machovsky-Capuska et al. 2018). They can also forage at more or less distant and/or large areas (Leal et al. 2017; Ramos et al. 2018; Cerveira et al. 2020), and/or utilise different foraging habitats (Quillfeldt et al. 2005; Navarro et al. 2007; Cherel et al. 2014a; Geary et al. 2020).

During the breeding period, seabirds need to return to colonies regularly to take incubation shifts or feed their chicks, thus behaving as central place foragers (Orians and Pearson 1979). This adds further constraints to seabirds during the breeding period as their foraging ranges, and likely access to habitats and food resources, are reduced in comparison with the period outside reproduction when they may move continually through vast oceanic areas searching for food. In addition, breeding seabirds have to adapt their foraging strategies according to their breeding duties that vary throughout the stages of the breeding cycle, to the needs of their offspring and to spatiotemporal variation in food availability. This allows them to maximize foraging efficiency and reproductive output (Shaffer et al. 2003; Navarro et al. 2007; Cherel et al. 2014a; Chiaradia et al. 2016; Dehnhard et al. 2016; Leal et al. 2017; Booth et al. 2018). Moreover, to meet the high energetic demands of chick provisioning, some seabird species, or populations of a given species, particularly in Procellariiformes, are known to employ a dual-foraging strategy alternating between frequent, short, chick-provisioning foraging trips punctuated by long self-maintenance trips (Weimerskirch et al. 1994; Ropert-Coudert et al. 2004; Congdon et al. 2005; Steen et al. 2007; Magalhães et al. 2008; Shoji et al. 2015). During the longer trips, seabirds generally target more productive but more distant areas, such as inherently richer deep oceanic waters, seasonally stable sea fronts, marginal sea ice zones or continental shelf edges (Catard et al. 2000; Magalhães et al. 2008; Jakubas et al. 2012; Shoji et al. 2015). This results in the use of different foraging areas by adults for self-feeding and for chick-provisioning as well as in segregated trophic niches between adults and chicks (Catard et al. 2000; Alonso et al. 2012). However, trophic niche segregation between parents and offspring can also be explained by adults provisioning offspring with higher-quality food (prey of higher trophic levels) to facilitate their growth (e.g. Hodum and Hobson 2000; Cherel et al. 2008; González-Medina et al. 2017). Finally, seabird foraging strategies can also differ between sexes (e.g. Forero et al. 2005; Bearhop et al. 2006; Miller et al. 2018; Zango et al. 2020). While this may reflect sexual habitat or dietary specialization or avoidance of competition in sexually dimorphic species, this may result from sexually differing reproductive roles, parental investment, nutritional requirements or from risk partitioning in monomorphic or dimorphic species (Phillips et al. 2011; 2017). Sex-specific foraging strategies of seabirds tend to be more common in species with marked sexual size dimorphism and to be more likely during the pre-laying and later breeding stages than during the non-breeding period.

Stable isotope analysis of various tissues allows investigation of seabird foraging strategy flexibility over different time periods and at different time scales (e.g. whole blood is expected to retain information on diet and foraging habitat used for a period from 3 to 4 weeks previous and feathers for the period when they were grown), since different body tissues incorporate the isotopic values of resources at different rates (Hobson 1993; Hobson and Bond 2012; Cherel et al. 2014a; Thabet et al. 2019). Stable-nitrogen and stable-carbon isotope ratios (δ^{15}N and δ^{13}C, respectively) allow the determination of seabird isotopic niches (i.e. the δ-space they use, defined by an area with isotopic values as coordinates; Newsome et al. 2007). Hence, δ^{15}N reflects seabird trophic position/diet, while δ^{13}C reflects seabird spatial foraging distribution (Hobson et al. 1994; Kelly 2000), mostly in relation to coastal–offshore, benthic–surface and/or latitudinal gradients (Jaeger et al. 2010; Paiva et al. 2010; Roscales et al. 2011).

Using stable isotope analyses, this study investigates foraging strategy flexibility in the grey-faced petrel *Pterodroma gouldi*, a highly pelagic Procellariiform seabird endemic to the northern half of North Island, New Zealand (Greene et al. 2015; Wood et al. 2017). With hundreds of thousands of breeding pairs, the grey-faced petrel is one of the few burrowing seabird species remaining on the main island and in high abundance. As such, it has a vital role replenishing terrestrial areas with marine resources transported from the ocean and feeding grounds. Because of the tight link between grey-faced petrels and the health of marine ecosystems, New Zealand Department of Conservation uses the species as an indicator species for long-term monitoring of changes in the marine environment (Monks et al. 2013; Russell et al. 2017). An understanding of grey-faced petrel trophic ecology and foraging strategy can help identify causes for population declines and provide information about the changes in food web structure or in prey abundance and diversity across its foraging areas. El Niño Southern Oscillation (ENSO) affects New Zealand weather through changes in air pressure, sea temperature, and wind direction. The impact on oceanographic conditions can affect grey-faced petrel prey distribution and abundance. Over two

consecutive years with different Southern Oscillation Indices (SOIs: a measure of ENSO strength), we analysed δ^{15}N and δ^{13}C in adult blood collected at two different breeding stages to characterise incubation and chick rearing. Over the same years, we analysed δ^{15}N and δ^{13}C in chick down and body feathers to characterise two distinct periods of the chick rearing stage, as well as in adult wing feathers to characterise the non-breeding period. Finally, we used δ^{15}N and δ^{13}C values of muscle from spontaneously regurgitated prey to infer petrel diet by stable isotope mixing modelling. We thus examined variations in grey-faced petrel foraging areas and diet throughout their annual life cycle, over consecutive years with different ENSO oceanographic conditions, between adults and chicks and between sexes, using stable isotope analyses. We specifically tested if (1) stable isotope values vary during annual cycle stages and over years, resulting from diet and foraging habitat segregation over time, (2) adults and chicks exhibit different stable isotope values, suggesting that adults have a different diet or habitat when feeding themselves vs their chicks, and (3) adult males and females have different stable isotope values, exploiting different prey or foraging habitats.

We expected to find significant intra- and inter-annual variations in grey-faced petrel stable isotope values, as found in other seabird species including Procellariiformes (e.g. Navarro et al. 2007; Alonso et al. 2012; Cherel et al. 2014a; Thabet et al. 2019), due to changes in nutritional and energy demands throughout the annual life cycle and to potential variation in food availability related to ENSO. We also hypothesized that, in accordance with the dual-foraging strategy which is common in Procellariiformes (Weimerskirch et al. 1994; Catard et al. 2000; Congdon et al. 2005; Magalhães et al. 2008; Shoji et al. 2015), adults feed their chick with more coastal prey than those they feed on for themselves. In addition, adult males and females could exhibit different stable isotope values from different foraging strategies, as observed in some other Procellariiformes with various levels of sexual size dimorphism (Forero et al. 2005; Quillfeldt et al. 2008b; Pinet et al. 2012; Hedd et al. 2014; Jaeger et al. 2014; Danckwerts et al. 2016; Paiva et al. 2018; Zango et al. 2020). Finally, because petrels generally spend their non-breeding period in areas several thousand kilometres away from their foraging areas during the breeding season (e.g. Rayner et al. 2012; Priddel et al. 2014; Ramos et al. 2017), we expected different stable isotope values in grey-faced petrels between these two periods.

Materials and methods

Study site and species

We studied grey-faced petrel on Ihumoana, a 1.7 ha island connected to the mainland at low tide and situated at the northern end of Te Henga (Bethells Beach) on the North Island of New Zealand (36°53′S, 174°26′E). Ihumoana hosts a grey-faced petrel breeding colony of approximately 120 pairs, that has been monitored (burrow occupancy, breeding success, adult and chick ringing) for over 20 years (G.A. Taylor unpubl data). This study was conducted during the breeding seasons of 2013 and 2014 which exhibited different SOIs (June–December: $n=7$, 0.46 ± 0.46 in 2013 and -0.50 ± 0.37 in 2014, paired t test, $t_6=7.4$, $P<0.001$; www.ncdc.noaa.gov/teleconnections/enso/indicators/soi/).

The grey-faced petrel is an austral winter breeder that nests in underground burrows. Potential breeders return to the colony to re-establish pair bonds in April. Females lay a single-egg clutch between late June and late July (Imber 1976). Chicks hatch from mid-August to early-September (26 August ± 8 days in 2013, $n=26$), after both parents share egg incubation for an average of 55 days. Both parents contribute to chick provisioning during an average of 118 days of chick rearing. On Ihumoana, chicks fledge in December-early January (19 December ± 10 days in 2013, $n=23$).

While at sea, adults of the grey-faced petrel forage widely in the southwest Pacific Ocean and the Tasman Sea between 20° and 50°S, feeding over deep pelagic water beyond the continental shelf (Marchant and Higgins 1990; MacLeod et al. 2008). They feed mainly on cephalopods, fish and crustaceans (Imber 1973), that they catch by surface seizing or dipping by night (Harper 1987). Grey-faced petrels thus undertake shallow dives infrequently as their average diving depth is 1.64 ± 0.18 m (average maximal depth: 2.41 ± 0.30 m; Dunphy et al. 2015). The most common prey during the breeding season is the ram's horn squid *Spirula spirula* (small Spirulidae squid) but Histioteuthidae and Cranchiidae cephalopods dominate in terms of mass ingested (Imber 1973). Fish (mainly Myctophidae, the lantern-fishes, and Gonostomatidae) and crustaceans (Decapoda: Caridean prawns, Mysidacea: Lophogastridae, Euphausiacea: Euphausiidae, and Amphipoda: Hyperiidea) are secondary prey. Grey-faced petrels mainly feed on deep-sea prey which undertake diel vertical migration (vertical migration toward the surface at night and in deeper waters during the day). Only a few of their prey are available in daylight at the sea surface. Scavenging of fish and cephalopods supplements their diet.

Sample collection

We captured breeding adults and chicks by hand in burrow nesting chambers by reaching through the entrance for short burrows or, for longer burrows, through access holes, or on the ground close to burrow entrances when adults came back to feed the chick. Feather isotopic values retain information on diet and at-sea foraging habitat used when the feather was grown (Hobson and Clark 1992; Bearhop et al. 2002). We

clipped 2–3 cm of the fourth primary covert from breeding adults ($n = 60$ in 2013 and $n = 27$ in 2014). The fourth primary covert is most likely moulted at the same time as the fourth primary (i.e. during the non-breeding period; Grecian et al. 2016). In order to represent the non-breeding period this feather is thus a safer alternative to primaries, whose collection can impair the birds' flying ability (Jaeger et al. 2009). We sampled blood from breeding adults attending burrows during incubation (August; $n = 26$ in 2013, $n = 20$ in 2014) and chick rearing (November; $n = 16$ in 2013 only). We collected a maximum of 0.4 mL of blood from the tarsal vein. Blood samples were drawn into heparinised 0.5-mL disposable syringes through a 29-gauge needle. We dispensed the blood into two different small plastic vials, one containing 70% ethanol and the other one absolute ethanol. Blood samples stored in 70% ethanol were used for stable isotope analyses (see Hobson et al. 1997) while those stored in absolute ethanol were used for molecular analyses. By using the same brand and batch of ethanol for all sampling groups, we expected to minimize ethanol storage effects on stable isotope values (Bugoni et al. 2008). Whole blood isotopic value is expected to retain information on diet and at-sea foraging habitat used from 3 to 4 weeks prior to the sample collection (Bearhop et al. 2002). Therefore, blood that we collected in August and in November reflects nutrients ingested during incubation and mid-chick rearing, respectively. Adults were uniquely ringed but not systematically repeatedly sampled: some adults were thus sampled only once, while others were sampled several times (mean number of samples per individual ± SD: 1.8 ± 0.8, $n = 85$, range: 1–5). We collected secondary down (mesoptiles; Warham 1996) and 2–4 body (breast) feathers from the same chicks within a year (second half of November; $n = 23$ in 2013 and $n = 22$ in 2014). Secondary down reflects nutrients ingested subsequent to hatching during early chick rearing (Danckwerts et al. 2016) while chick body feathers reflect their period of growth during late chick rearing. Sexing of adults was previously performed molecularly or by cloacal inspection during the laying period, or the sex was deduced when the mate was reliably sexed. We stored all samples at room temperature (20–25 °C) once back in the laboratory.

Procellariiformes have a well described regurgitation response to handling or harassment by potential predators (Carey 2009). We thus collected grey-faced petrel prey items opportunistically whenever individuals regurgitated during handling. Regurgitations were stored frozen once back in the laboratory before a basic analysis isolating prey flesh for stable isotope analysis (SIA) and identifying prey types. Only a few regurgitations contained prey flesh usable for SIA (i.e. from an identifiable prey type and of sufficient size to be analysed). These prey samples for SIA were then stored in 70% ethanol for a few weeks until analysed. We acknowledge the fact that preservation in ethanol increases the prey muscle $\delta^{15}N$ and $\delta^{13}C$ values by about 0.7 ‰ (Kaehler and Pakhomov 2001; Ruiz-Cooley et al. 2011). Nevertheless, lipid extraction eliminates the effect of ethanol (Ruiz-Cooley et al. 2011) and trophic enrichment is in the range of 2–4 ‰ for $\delta^{15}N$ (Cherel et al. 2005b; Williams et al. 2007). The stable isotope values in prey flesh samples were thus used to discuss the likely contributions of each prey type to the seasonal and annual differences in stable isotopic values of grey-faced petrels. We determined the occurrence of the main prey types (i.e. fish, cephalopods and crustaceans) in regurgitations by the presence of hard remains (fish vertebrae and/or otoliths, cephalopod beaks and/or internal shell, crustacean exoskeleton). We then estimated each prey type frequency of occurrence as the percentage of regurgitations containing individual prey types. The minimum number of individuals of each prey type present in each regurgitation was determined from the largest number of similar sized/shaped paired structures or from the number of unpaired remains. We then calculated the numerical frequency of each prey type as the percentage of the total number of individual prey items represented by each prey type. We also calculated the relative percentage occurrence as the percentage of the number of individual prey items represented by each prey type in each regurgitation (Danckwerts et al. 2016).

Stable isotope analysis

Isotopic analyses were performed at the Cornell Isotope Laboratory at Cornell University (http://www.cobsil.com). Prior to SIA, down and feathers were cleaned of surface contaminants using successive rinses in a 2:1 chloroform/ether solution, air-dried and then ground to fine powder in a freezer mill operating at liquid nitrogen temperature. Ethanol was removed from prey samples by successive rinsing in distilled water and freeze-drying. Prey tissues were lipid extracted using a Soxhlet apparatus with chloroform solvent and then dried at 60 °C for 24 h to remove any residual solvent. They were then ground to fine powder before SIA. Whole blood generally has low lipid content and does not require lipid extraction (Cherel et al. 2005c). Blood samples were dried under a fume hood at 50 °C, for approximately 40 h, and then ground into powder.

Stable-carbon and nitrogen isotope assays were performed on 1.1 ± 0.1 mg, $n = 265$, subsamples of homogenized materials by loading into tin cups and combusting at 1800 °C in a Robo-Prep elemental analyser. Resultant CO_2 and N_2 gases were then analysed using a Thermo Delta V isotope ratio mass spectrometer interfaced to a NC2500 elemental analyser with every 10 unknowns separated by laboratory standards routinely calibrated against international reference materials provided by the International Atomic Energy Association. Stable isotope abundances were expressed in

δ notation as the deviation from standards (atmospheric N_2 (air) for ^{15}N and Vienna Pee Dee Belemnite for ^{13}C) in parts per thousand (‰). Replicate measurements of laboratory standards showed the analytical precision (± 1 SD) equalled ± 0.12 ‰ and ± 0.13 ‰ for stable nitrogen and carbon isotope measurements, respectively.

Data analysis

We compared grey-faced petrel diet composition between years by using randomisation tests (1000 randomisations) for percent frequencies (frequency of occurrence and numerical frequency; Manly 1997; Bonnaud et al. 2007) and Mann–Whitney *U* tests for relative percentage occurrence. We grouped the prey types into taxonomically and isotopically similar clusters we thus defined as main prey groups. We used a multivariate analysis of variance (MANOVA) with Wilk's lambda statistics using type III sums of squares to simultaneously compare $\delta^{15}N$ and $\delta^{13}C$ values between years and among grey-faced petrel main prey groups. Then, we compared $\delta^{15}N$ and $\delta^{13}C$ values between years and among prey groups using univariate factorial analyses of variance (ANOVAs) followed by post-hoc Bonferroni tests to identify significant differences between prey groups.

In order to compare grey-faced petrel blood and feather isotopic ratios and, consequently, investigate the isotopic niche at different periods of the annual cycle, we needed to take into account the tissue-dependent metabolic routing and enrichment factors (Podlesak and McWilliams 2006; Quillfeldt et al. 2008a). We applied the linear regression equations of Cherel et al. (2014b) to correct blood to feather $\delta^{15}N$ and $\delta^{13}C$ values. Although feathers and whole blood have generally low lipid content and despite prey delipidation, some samples ($n = 4$ feather, 18 down, 7 blood and 3 prey samples) exhibited C:N mass ratios > 3.5, i.e. $\delta^{13}C$ values biased by lipid content (Post et al. 2007). Lipid-associated biases were reduced by mathematically normalising the $\delta^{13}C$ values of these samples using the equation for aquatic animals given by Post et al. (2007). We used a MANOVA with Wilk's lambda statistics to simultaneously compare $\delta^{15}N$ and $\delta^{13}C$ values in adults between years, sexes and among non-breeding period and different breeding stages (incubation and mid-chick rearing), thus testing the effect of year, sex, annual cycle stage and their interactions on stable isotope values. We also included individual identity in this MANOVA to account for repeated observations. Because adult blood during chick rearing was collected only in 2013, we performed a second MANOVA including only data relevant to 2013 chick rearing (adult blood during chick rearing, chick down and body feathers) to test the effect of age (adults vs chicks) on stable isotope values. Upon significant results, we then compared $\delta^{15}N$ and $\delta^{13}C$ values between years, sexes, adults vs chicks and among annual cycle stages (non-breeding, incubation and mid-chick rearing) using univariate factorial ANOVAs followed by post-hoc Bonferroni tests to identify significant differences between groups. Because chick down and body feathers were collected from the same individuals within each year, we performed repeated measures ANOVAs on chick $\delta^{15}N$ and $\delta^{13}C$ values to test the effects of annual cycle stage (early vs late chick rearing, repeated measures), year and their interaction on stable isotope values. We also used post-hoc Bonferroni tests to identify significant differences between groups when there were more than two comparisons.

We used the SIBER package (Stable Isotope Bayesian Ellipses in R; Jackson et al. 2011) to determine grey-faced petrel isotopic niche width and its intra- and inter-annual variation. We estimated isotopic niches during the non-breeding period and the various breeding stages in each year by using the standard ellipse area after small sample size correction (SEAc). SEAc, which is an estimated ellipse encompassing 40% of the data regardless of sample size, facilitated visualization and characterization of isotopic niches, allowing the measurement of the size (area, $‰^2$) and the overlap of the isotopic niches between years and annual cycle stages (Jackson et al. 2011; Parnell et al. 2013). We also calculated the total area (TA) occupied as the area of convex hull that incorporated all individuals, which represents a measure of niche width and reflects the isotopic diversity of each group (Layman et al. 2007; Jackson et al. 2011). For statistical comparison, we calculated Bayesian standard ellipse areas (SEAb) with 95% credible limits of each group using Markov chain Monte Carlo simulation with 10^4 iterations (Jackson et al. 2011). We computed density plots showing the confidence intervals of SEAb to quantify isotopic niche width and measure dietary similarity among groups. This method calculates the probability that the proportion of posterior samples of SEAb differed among groups, allowing a direct probabilistic interpretation of the differences in SEAb.

Mixing models can be used to estimate the relative proportion of different dietary sources. We used Bayesian multisource stable isotope mixing models (SIAR: Stable Isotope Analyses in R; Parnell et al. 2010) to estimate ranges of probable contributions of each prey (or group of prey) to the diet of grey-faced petrels during the various breeding stages in each year. We used the main prey groups that we earlier identified as taxonomically and isotopically distinct. We included in the models a non-informative Dirichlet prior distribution, with zero concentration dependencies, and default SIAR MCMC estimation (iterations = 5×10^5, burning = 5×10^4, thinning = 15). We applied to the mixing models an isotopic mean ± SD diet-feather discrimination factor of 3.42 ± 0.35 ‰ for $\delta^{15}N$ and 1.38 ± 0.48 ‰ for $\delta^{13}C$ (mean values from studies on seabirds and lipid-extracted marine prey muscle, $n = 12$: Becker et al. 2007; Ramos et al.

2009) and an isotopic diet-blood discrimination factor of 2.55 ± 0.39 ‰ for δ^{15}N and 0.11 ± 0.62 ‰ for δ^{13}C (mean values from studies on seabirds and lipid-extracted marine prey muscle, $n = 7$: Bearhop et al. 2002; Cherel et al. 2005b; Williams et al. 2007; Paiva et al. 2010; Dehnhard et al. 2011; Chiaradia et al. 2014). We then assessed proportion densities for each prey group and displayed them with 50%, 75% and 95% credibility intervals in figures. This method allows a direct probabilistic interpretation of the differences in proportions.

Mann–Whitney tests, MANOVAs and ANOVAs, randomisation tests, and SIBER and SIAR analyses were performed using Statistica 6.0 or R software, version 3.5.0 (R Development Core Team 2018). Presented values are means ± SD, and statistical significance was assumed at $P < 0.05$.

Results

Prey types and stable isotope ratios

A total of 307 individual prey items were identified in 62 spontaneous regurgitations of grey-faced petrels mainly obtained from chicks (93.5%). Cephalopods were the most common prey type in the diet as they were present in more than 84% of the regurgitations analysed (frequency of occurrence) and their items accounted for more than two thirds of all prey items found in all regurgitations (numerical frequency) and on average for more than 50% of all prey items found in a regurgitation (relative percentage of occurrence; Table 1). Typical internal shell remains of ram's horn squids *Spirula spirula* were found in particularly high abundance. Their frequency of occurrence was 58.1% in 2013 and 68.4% in 2014 while their relative percentage occurrence was 24.6 ± 30.0%, $n = 43$, and 25.8 ± 26.6%, $n = 19$, respectively, and their numerical frequency was 19.4% and 22.5%, respectively. Hard parts from crustaceans were also common (frequency of occurrence > 72%) whereas their abundance was moderate (20–30% of items). Fish were the least common (frequency of occurrence ~ 50%) and least abundant (11–16% of items) prey. Grey-faced petrel diet composition (mainly of chicks) did not differ significantly between 2013 and 2014 (frequency of occurrence: observation = 0.004, $P = 0.831$ and all observed percentage differences < 0.070, $P > 0.396$; relative percentage occurrence: all adjusted $Z < 1.3$ and all $P > 0.209$; numerical frequency: observation = 0.013, $P = 0.498$ and all observed percentage differences < 0.047, $P > 0.193$).

Cephalopods could be separated into two groups according to stable isotope values (Table 2): cephalopod samples of group 1 (cephalopods 1), including ram's horn squid (typical internal shell found inside mantles of some samples and in all the regurgitations from which these samples were collected), exhibited low δ^{15}N and relatively high δ^{13}C values; while cephalopod samples of group 2 (cephalopods 2) exhibited high δ^{15}N and lower δ^{13}C values. We aggregated the grey-faced petrel prey types into groups of similar taxa and similar isotopic values (Fig. 1): group I (hereafter named fish or FI) included the five fish samples, group II (hereafter named cephalopods 1 or CE1) included the 10 cephalopods 1 samples, group III (hereafter named cephalopods 2 or CE2) included the five cephalopods 2 samples), and group

Table 1 Prevalence of main prey types in the diet of grey-faced petrels *Pterodroma gouldi* during the 2013 and 2014 breeding seasons at Ihumoana, New Zealand, as obtained by the analysis of spontaneous regurgitations mainly from chicks

	n	Cephalopods	Fish	Crustaceans
Frequency of occurrence (%)				
2013	43	88.4	53.5	72.1
2014	19	84.2	47.4	78.9
Relative percentage of occurrence (%)				
2013	43	57.4 ± 27.8	15.3 ± 20.4	22.6 ± 24.7
2014	19	53.2 ± 31.3	12.5 ± 16.3	29.0 ± 24.7
Numerical frequency (%)				
2013	227	67.0	15.9	17.2
2014	80	68.8	11.3	20.0

Diet parameters were calculated based either on numbers of regurgitations (frequency of occurrence and relative percentage of occurrence) or based on numbers of individual prey items that regurgitations contained (numerical frequency)

Table 2 Stable isotopic values and C:N mass ratios (means ± SD) of flesh (delipidated) of grey-faced petrel *Pterodroma gouldi* main prey types obtained from spontaneous regurgitations in 2013 and 2014 at Ihumoana, New Zealand

Year	Prey type	*n*	δ^{13}C (‰)	δ^{15}N (‰)	C:N
2013	Cephalopods[a]	11	− 18.6 ± 0.8	11.3 ± 2.0	3.24 ± 0.17
	Cephalopods 1[a]	7	− 18.0 ± 0.3	9.9 ± 0.6	3.25 ± 0.21
	Cephalopods 2	4	− 19.6 ± 0.2	13.7 ± 0.7	3.23 ± 0.03
	Fish	3	− 18.7 ± 0.6	14.2 ± 0.6	3.21 ± 0.06
	Crustaceans[a]	3	− 19.8 ± 0.6	11.1 ± 1.3	3.52 ± 0.27
2014	Cephalopods[a]	4	− 18.0 ± 0.5	11.3 ± 2.7	3.44 ± 0.44
	Cephalopods 1[a]	3	− 17.8 ± 0.1	10.0 ± 0.4	3.49 ± 0.53
	Cephalopods 2	1	− 18.9	15.3	3.28
	Fish	2	− 18.9 ± 0.1	14.6 ± 1.5	3.20 ± 0.09

Cephalopods were separated into two groups according to stable isotope values: cephalopod samples of group 1 (cephalopods 1) exhibiting low δ^{15}N and relatively high δ^{13}C values and cephalopod samples of group 2 (cephalopods 2) exhibiting high δ^{15}N and lower δ^{13}C values

[a]Group containing a sample with C:N > 3.5 for which δ^{13}C was normalised

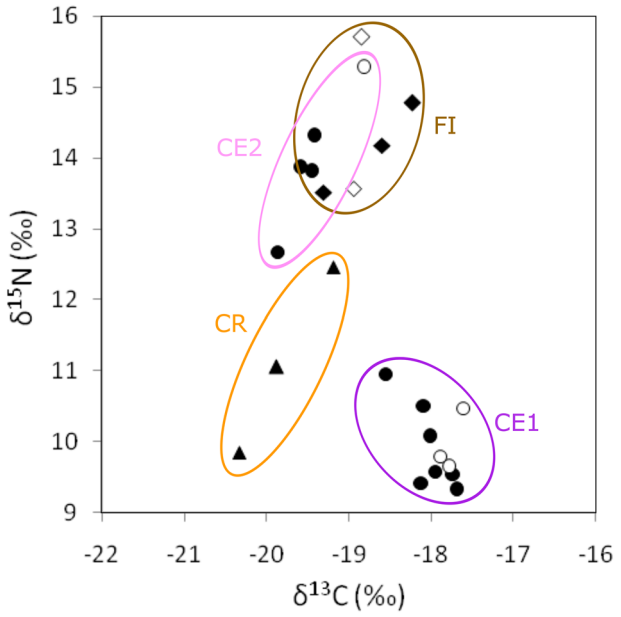

Fig. 1 Biplot of isotopic values of delipidated flesh of grey-faced petrel *Pterodroma gouldi* prey types obtained from spontaneous regurgitations in 2013 and 2014 at Ihumoana, New Zealand. Circles: cephalopods; diamonds: fish; triangles: crustaceans; filled shapes: 2013; open shapes: 2014. Food items of similar taxa and with similar isotopic values were clustered into groups of food sources: *FI* fish (brown), *CE1* cephalopods 1 (purple), *CE2* cephalopods 2 (pink), *CR* crustaceans (orange)

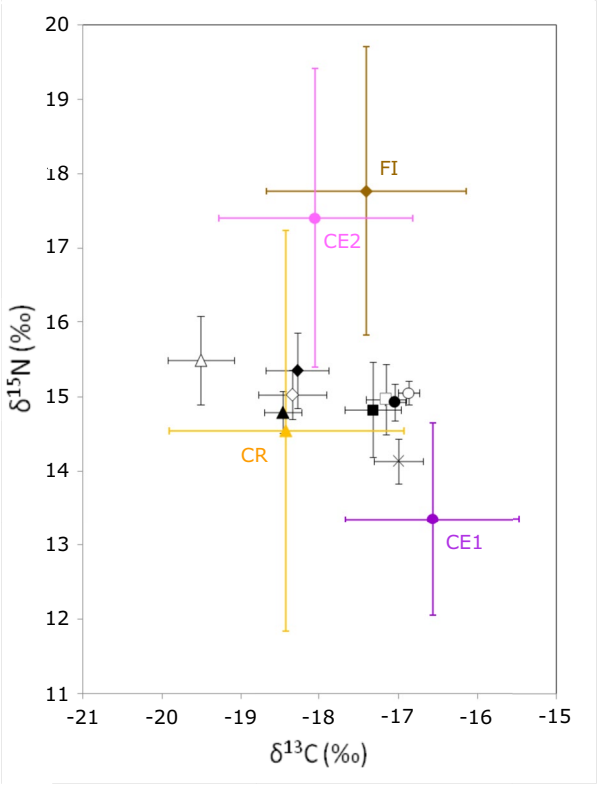

Fig. 2 Isotopic values (mean ± SD) of adult and chick grey-faced petrels *Pterodroma gouldi* during various annual cycle stages in 2013 and 2014 and their main prey types (delipidated) at Ihumoana, New Zealand. Petrel blood isotope values were corrected and prey muscle isotope ratios were adjusted by adding assumed diet-tissue (feathers) discrimination factors (see "Materials and methods"). Squares: non-breeding (adults, primary 4 covert); circles: incubation (adults, blood); black cross: mid-chick rearing (adults, blood); triangles: early chick rearing (chicks, down); diamonds: late chick rearing (chicks, breast feathers); filled symbols: 2013; open symbols: 2014; *FI* fish, brown diamond; *CE1* cephalopods 1, purple circle; *CE2* cephalopods 2, pink circle; *CR* crustaceans, orange triangle

IV (hereafter named crustaceans or CR) included the three crustacean samples.

MANOVA revealed that stable isotope values varied significantly among the four main prey groups (Wilk's lambda, $F_{6,30} = 27.8$, $P < 0.001$) but did not differ significantly between 2013 and 2014 (Wilk's lambda, $F_{2,15} = 1.6$, $P = 0.226$) nor vary in relation to the interaction between prey groups and years (Wilk's lambda, $F_{4,30} = 1.2$, $P = 0.322$). Thus, values from the two years were combined in isotopic mixing models. δ^{15}N values varied significantly among the four groups (ANOVA, $F_{3,16} = 42.4$, $P < 0.001$, Fig. 2), all post-hoc Bonferroni comparisons being significant (all $P < 0.002$) but between CE2 and FI ($P = 1.000$) and between CE1 and CR ($P = 0.248$). Similarly, δ^{13}C values varied significantly among the four groups (ANOVA, $F_{3,16} = 22.3$, $P < 0.001$) and all post-hoc Bonferroni comparisons were significant (all $P < 0.007$), except for between CE2 and FI ($P = 0.059$) and between CE2 and CR ($P = 0.980$).

Petrel stable isotope ratios

The δ^{13}C and δ^{15}N values of grey-faced petrels ranged from -19.5 ± 0.4 ‰ in chick down in 2014 to -17.3 ± 0.2 ‰ in adult feathers in 2014, and from 13.5 ± 0.3 ‰ in adult blood during chick rearing in 2013, to 15.5 ± 0.6 ‰ in chick down in 2014, respectively (Table 3). Blood values reported hereafter were corrected using linear regressions (Cherel et al. 2014b) to standardise blood and feather values.

MANOVA revealed that stable isotope values in adults differed significantly between years (Wilk's lambda, $F_{2,55} = 10.5$, $P < 0.001$) and between males and females (Wilk's lambda, $F_{2,55} = 7.5$, $P = 0.001$), and varied significantly among non-breeding period and the various breeding stages (Wilk's lambda, $F_{4,110} = 27.8$, $P < 0.001$). It also revealed a significant effect of individual identity (Wilk's lambda, $F_{166,110} = 1.4$, $P = 0.023$), of the interaction between year and sex (Wilk's lambda, $F_{2,55} = 3.3$, $P = 0.044$) and of the interaction between annual cycle stage and sex (Wilk's lambda, $F_{4,110} = 3.6$, $P = 0.008$). Interactions between year and annual cycle stage, and between year, annual cycle stage and sex did not

Table 3 Stable isotopic values and C:N mass ratios (means ± SD) of tissues collected on grey-faced petrel *Pterodroma gouldi* adults and chicks at Ihumoana, New Zealand

Year	Tissue = annual cycle stage represented	*n*	δ^{13}C (‰)	δ^{15}N (‰)	C:N
2013	Adults				
	Primary 4 covert = non-breeding[a]	60	− 17.3 ± 0.3	14.8 ± 0.6	3.28 ± 0.12
	Females[a]	26	− 17.2 ± 0.3	14.7 ± 0.6	
	Males[a]	34	− 17.4 ± 0.3	14.9 ± 0.7	
	Blood = incubation (uncorrected)[a]	26	− 18.5 ± 0.1	14.3 ± 0.2	3.38 ± 0.08
	Females[a]	12	− 18.5 ± 0.1	14.3 ± 0.2	
	Males[a]	14	− 18.5 ± 0.2	14.3 ± 0.3	
	Blood = incubation (corrected)[a]	26	− 17.0 ± 0.1	14.9 ± 0.2	
	Females[a]	12	− 17.1 ± 0.1	14.9 ± 0.3	
	Males[a]	14	− 17.0 ± 0.1	14.9 ± 0.3	
	Blood = mid-chick rearing (uncorrected)[a]	16	− 18.5 ± 0.3	13.5 ± 0.3	3.38 ± 0.15
	Females[a]	6	− 18.6 ± 0.4	13.3 ± 0.3	
	Males[a]	10	− 18.4 ± 0.2	13.6 ± 0.2	
	Blood = mid-chick rearing (corrected)[a]	16	− 17.0 ± 0.3	14.1 ± 0.3	
	Females[a]	6	− 17.1 ± 0.4	14.0 ± 0.4	
	Males[a]	10	− 16.9 ± 0.2	14.2 ± 0.2	
	Chicks				
	Down = Early chick rearing[a]	23	− 18.5 ± 0.2	14.8 ± 0.3	3.24 ± 0.11
	Breast feathers = Late chick rearing	23	− 18.3 ± 0.4	15.3 ± 0.5	3.21 ± 0.10
2014	Adults				
	Primary 4 covert = non-breeding	27	− 17.2 ± 0.3	15.0 ± 0.5	3.23 ± 0.07
	Females	12	− 17.0 ± 0.2	14.8 ± 0.4	
	Males	15	− 17.3 ± 0.2	15.1 ± 0.5	
	Blood = incubation (uncorrected)	20	− 18.3 ± 0.1	14.4 ± 0.2	3.31 ± 0.04
	Females	8	− 18.4 ± 0.1	14.4 ± 0.1	
	Males	12	− 18.3 ± 0.1	14.4 ± 0.2	
	Blood = incubation (corrected)	20	− 16.9 ± 0.1	15.0 ± 0.2	
	Females	8	− 16.9 ± 0.1	15.1 ± 0.1	
	Males	12	− 16.9 ± 0.1	15.0 ± 0.2	
	Chicks				
	Down = early chick rearing[a]	22	− 19.5 ± 0.4	15.5 ± 0.6	3.74 ± 0.36
	Breast feathers = late chick rearing	22	− 18.3 ± 0.4	15.0 ± 0.3	3.21 ± 0.10

Stable isotope values are raw (uncorrected) and corrected by applying linear regressions between feather and blood isotopic ratios (Cherel et al. 2014b) for blood

[a]Datasets containing samples with C:N > 3.5 for which δ^{13}C was normalised

significantly affect stable isotope values (Wilk's lambda, $F_{2,55} < 0.4$, $P > 0.688$). ANOVAs revealed significant differences in both δ^{13}C and δ^{15}N values between years and between males and females (Table 4). Both δ^{13}C and δ^{15}N values also varied among non-breeding period and the various breeding stages (Table 4, Fig. 2). Finally, ANOVAs showed significant interactions between annual cycle stage and sex, and between year and sex on δ^{13}C values (Table 4). The MANOVA on 2013 chick rearing data revealed that stable isotope values differed significantly between adults and chicks (Wilk's lambda, $F_{2,145} = 217.3$, $P < 0.001$). Univariate ANOVAs on these data showed significant differences in both δ^{13}C and δ^{15}N values (Table 4, Fig. 2). Repeated measures ANOVAs on chick data showed significant effects of year, breeding stage (early vs late chick rearing) and their interaction on δ^{13}C values and of the interaction of year and breeding stage on δ^{15}N values.

Petrel isotopic niche

Grey-faced petrel isotopic niches were well separated between annual cycle stages within years, but relatively fixed across years for any given annual cycle stage (Fig. 3). Overlap across years for a given annual cycle stage was 0.0% for early chick rearing, 10.5% for incubation, 34.1%

Table 4 Results of factorial ANOVAs analysing variations in stable isotope values in grey-faced petrels *Pterodroma gouldi* among annual cycle stages, years, ages (adults vs chicks) and sexes at Ihumoana, New Zealand

	$\delta^{13}C$			$\delta^{15}N$		
	F	*P*	Main effects	*F*	*P*	Main effects
Adults						
Year	$F_{1,56}=17.4$	<0.001	2013 < 2014	$F_{1,56}=11.3$	0.001	2013 < 2014
Cycle stage	$F_{2,56}=30.1$	<0.001	NBR < (INC = MCR)	$F_{2,56}=19.3$	<0.001	MCR < (NBR = INC)
Sex	$F_{1,56}=4.1$	0.049	M < F	$F_{1,56}=5.7$	0.021	F < M
Individual ID	$F_{83,56}=1.5$	0.059		$F_{83,56}=1.3$	0.172	
Year × cycle stage	$F_{1,56}=0.3$	0.567		$F_{1,56}=0.5$	0.463	
Year × sex	$F_{1,56}=5.9$	0.019	F: 2013 < 2014	$F_{1,56}=3.1$	0.085	
Cycle stage × sex	$F_{2,56}=4.0$	0.025	M: NBR < (INC = MCR), F = NBR < INC, NBR: M < F	$F_{2,56}=1.2$	0.304	
Year × cycle stage × sex	$F_{1,128}=0.2$	0.647		$F_{1,56}=0.3$	0.604	
Chicks						
Year	$F_{1,43}=43.0$	<0.001	2014 < 2013	$F_{1,43}=2.7$	0.111	
Cycle stage (repeated measures)	$F_{1,43}=85.3$	<0.001	ECR < LCR	$F_{1,43}=0.5$	0.484	
Year × cycle stage	$F_{1,43}=45.5$	<0.001	2014: ECR < LCR, ECR: 2014 < 2013	$F_{1,43}=53.0$	<0.001	2013: ECR < LCR, 2014: LCR < ECR, ECR: 2013 < 2014
Adults and chicks (2013 chick rearing)						
Age	$F_{1,146}=407.4$	<0.001	Chicks < adults	$F_{1,146}=11.2$	0.001	Adults < chicks

Main effects relate to significant ANOVAs and post-hoc Bonferroni tests

NBR non-breeding, *INC* incubation, *ECR* early chick rearing, *LCR* late chick rearing, *MCR* mid-chick rearing

for late chick rearing and 44.3% for non-breeding. Within a given year, the overlap was the highest between incubation and non-breeding (10.8% in 2013 and 5.2% in 2014), and between early and late chick rearing in 2013 (5.7%). There was no overlap between all other annual cycle stages within a year.

Isotopic niche was the narrowest during incubation (Table 5, Fig. 4). Isotopic niche width did not vary significantly among all other annual cycle stages.

Diet changes inferred by isotopic mixing models

SIAR mixing models based on grey-faced petrel and prey isotope values during the breeding period indicated that cephalopods 1 were the largest component in the diet of the sampled breeding adult grey-faced petrels (mean proportional contributions: 46.3–58.8%), while crustaceans were the largest component in the diet of chicks (49.4–67.0%; Fig. 5). This pattern was consistent across breeding stages and years. Cephalopods 2 and fish consistently constituted secondary prey groups across breeding stages and years, contributing from 5.3 to 28.4% of grey-faced petrel diet.

Discussion

Understanding how marine top predators cope with spatiotemporal heterogeneity in food availability and the variable energetic constraints of their annual life cycle is essential to evaluate their ability to withstand current and future global changes. It also informs the usefulness of marine top predators as indicators of changes in food web structure or in prey abundance and diversity across their foraging areas. The analysis of stable isotope values in the blood and feathers of grey-faced petrels highlighted seasonal (i.e. non-breeding, incubation and early, late and mid-chick rearing) and annual variations in carbon and nitrogen stable isotopes, isotopic niches and diet of the species. Our analyses also showed a trophic segregation between adults and chicks and between males and females. Finally, grey-faced petrel isotopic niches were more similar between the breeding and non-breeding periods in adults than between breeding adults and their chicks. These results demonstrate grey-faced petrel foraging strategy plasticity in response to the changing nutritional demands of their annual cycle stages and potentially to changes in oceanographic conditions.

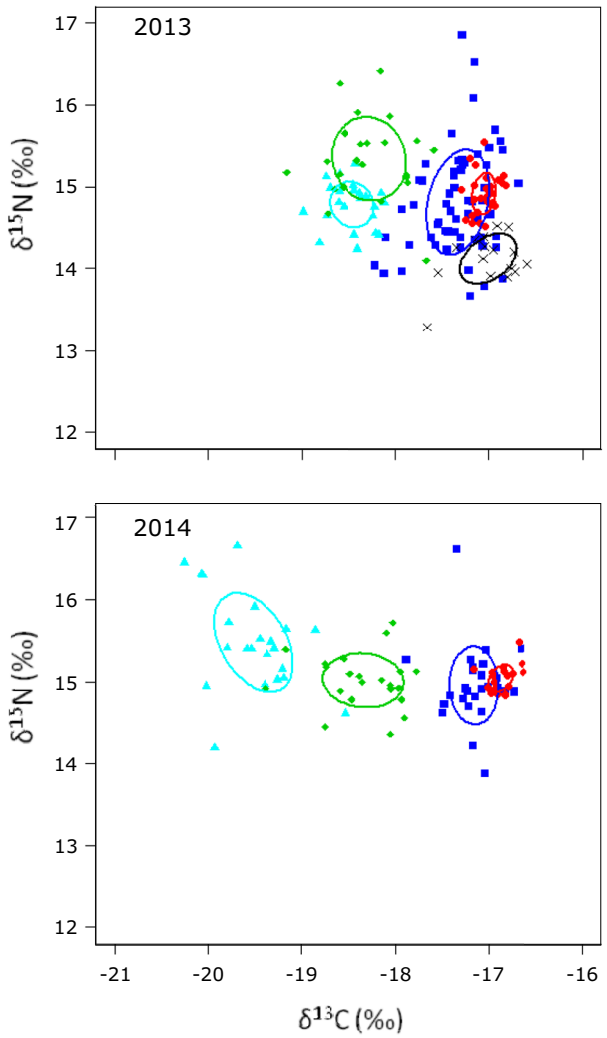

Fig. 3 Isotopic niche occupancy of adult and chick grey-faced petrels *Pterodroma gouldi* during various annual cycle stages in 2013 and 2014 at Ihumoana, New Zealand. The biplot depicts δ^{13}C and δ^{15}N isotope values. We applied the linear regression equations of Cherel et al. (2014b) to correct blood to feather δ^{15}N and δ^{13}C values. Ellipses represent the isotopic niche width (SEAc) of 40% of typical individuals within the group based on bivariate normal distribution. Blue squares: non-breeding (adults, primary 4 covert); red circles: incubation (adults, blood); black crosses: mid-chick rearing (adults, blood); cyan triangles: early chick rearing (chicks, down); green diamonds: late chick rearing (chicks, breast feathers)

Seasonal variation in isotopic niche

Grey-faced petrel isotopic niches overlapped little within years as the overlap among non-breeding, incubation, early, mid- and late chick rearing stages averaged $1.4 \pm 3.1\%$, $n = 16$. Isotopic niche width was narrower during incubation in both the two years studied.

Carbon isotope ratio enrichment is higher in inshore than in offshore food chains (Cherel and Hobson 2007; Bond and Jones 2009) and in benthic than in surface species (Hobson et al. 1994; France 1995). Lower δ^{13}C values in adult grey-faced petrels during the non-breeding period compared to those during the breeding season (differences: 0.3 ‰) could, thus, indicate a change in foraging habitat, in particular the use of more pelagic foraging areas during the non-breeding period. This is consistent with the fact that, outside the breeding season, grey-faced petrels are not central place foragers and can move freely through vast oceanic areas, far from coasts. In contrast, lower δ^{13}C values in chicks during early chick rearing rather than during late chick rearing in 2014 (difference: 1.2 ‰) are more surprising. This suggests that chicks were fed with more pelagic prey during the earlier breeding stage. Yet, Procellariiform chicks are generally fed more frequently during early chick rearing than during late chick rearing since they are gradually fed less towards fledging (Warham 1990). Higher feeding frequency during early chick rearing is not likely to allow adults to travel for longer trips, farther from the nesting site than during late chick rearing. Enrichment in the carbon isotope ratio can also be due to consuming more non-epi-pelagic prey, in particular meso-pelagic and demersal species (Hobson et al. 1994; Navarro et al. 2009; Thabet et al. 2019). However, δ^{15}N values and isotope mixing models do not support this hypothesis for grey-faced petrels since δ^{15}N values in adults were not higher during the breeding season than during the non-breeding period or those in chicks were not higher during late chick rearing than during early chick rearing in 2014, and neither adult nor chick diet composition differed between the two periods or breeding stages, respectively. Higher δ^{13}C values in incubating adult grey-faced petrels and in chicks during late chick rearing in 2014 could also be an artefact due to adult fasting during incubation and chick starvation in late chick rearing, as fasting and nutritional restriction can result in a δ^{13}C increase (Hertz et al. 2015). However, studies of several seabird species have shown no or contrary effects of fasting and starvation on δ^{13}C values (Cherel et al. 2005a; Williams et al. 2007; Sears et al. 2009) and nutritional stress would probably not explain higher adult δ^{13}C values during mid-chick rearing nor the absence of significant difference in chick δ^{13}C values between early and late chick rearing in 2013. Finally, differences in adult δ^{13}C values between the non-breeding and the breeding periods could also be due to differences in baseline δ^{13}C values in the areas used for feeding by adult grey-faced petrels during these two periods (see later).

The nitrogen isotope ratio increases with increasing trophic level (Kelly 2000; Bearhop et al. 2004) and with the depth of marine organism habitat in some particular areas (Choy et al. 2015). Adult grey-faced petrel δ^{15}N values varied among annual cycle stages and were lower during mid-chick rearing (differences: 0.7–0.8 ‰) than during incubation and non-breeding. Thus, grey-faced petrels may have consumed prey richer in protein and energy or prey from

Table 5 Isotopic niche areas of tissues collected on grey-faced petrel *Pterodroma gouldi* adults and chicks at Ihumoana, New Zealand

Year	Tissue = annual cycle stage represented	*n*	SEAc ($‰^2$)	SEAb ($‰^2$)		TA ($‰^2$)
				mode	95% CI	
2013	Adults					
	Primary 4 covert = non-breeding	60	0.65	0.63	0.48–0.81	2.71
	Blood = incubation	26	0.10	0.09	0.06–0.14	0.31
	Blood = mid-chick rearing	16	0.28	0.24	0.15–0.42	0.62
	Chicks					
	Down = early chick rearing	23	0.21	0.20	0.13–0.30	0.63
	Breast feathers = late chick rearing	23	0.66	0.59	0.40–0.94	2.23
2014	Adults					
	Primary 4 covert = non-breeding	27	0.39	0.37	0.25–0.54	1.75
	Blood = incubation	20	0.07	0.06	0.04–0.10	0.19
	Chicks					
	Down = Early chick rearing	22	0.75	0.68	0.46–1.08	2.61
	Breast feathers = late chick rearing	22	0.46	0.41	0.28–0.66	1.48

SEAc standard ellipse area corrected for sample size, *SEAb* Bayesian standard ellipse area, *CI* confidence interval of SEAb, *TA* total area of the convex hull

more complex food webs (Shaffer et al. 2003; Navarro et al. 2007; Thabet et al. 2019) during incubation and perhaps also during the non-breeding period. However, our mixing models failed to detect a significant variation in adult diet among breeding stages, although the contribution of cephalopods 2 and fish could have been lower and the contribution of cephalopods 1 could have been higher during mid-chick rearing. In contrast, repetitive periods of fasting during incubation could increase δ^{15}N values (Cherel et al. 2005a; Hertz et al. 2015; Doi et al. 2017). Indeed, during incubation, both members of pairs alternately incubate the eggs for shifts averaging 17 days over a total of ca. 55 days (Imber 1976). These long fasting shifts deplete incubating bird lipid reserves and the birds begin catabolising muscular proteins for energy, thus consuming their own lipid and protein reserves during their stay in their burrow (Cherel et al. 2005a; Hertz et al. 2015; Doi et al. 2017). This increases the δ^{15}N values of their blood (by ca. 0.5 ‰; Hertz et al. 2015; Doi et al. 2017) and raises their apparent trophic level. However, such physiological and metabolic factors cannot explain δ^{15}N values in adults during the non-breeding period. For this period, it is more likely that baseline δ^{15}N values are different in foraging areas used by grey-faced petrels.

Isotopic niche segregation between sexes and between adults and chicks

Male and female grey-faced petrels had slightly different isotopic niches throughout the annual cycle (overall difference in δ^{13}C: 0.1 ‰, in δ^{15}N: 0.2 ‰). Lower δ^{13}C values found in males were mainly due to the lowest values of males during the non-breeding period. Males exhibited higher overall δ^{15}N values throughout the annual cycle but the difference between sexes was not significant for any individual annual cycle stage. Significant isotopic differences between sexes are more common in seabirds during the pre-laying or breeding than the non-breeding period (Phillips et al. 2011). This presumably reflects greater between sex partitioning of resources when foraging ranges are more constrained and competition is greater. In medium-sized Procellariiformes, sexual differences in foraging strategy could also be the result of differences in reproductive roles (burrow defence and maintenance by males) and/or energetic constraints (egg development in females, first post-laying long fasting bout in

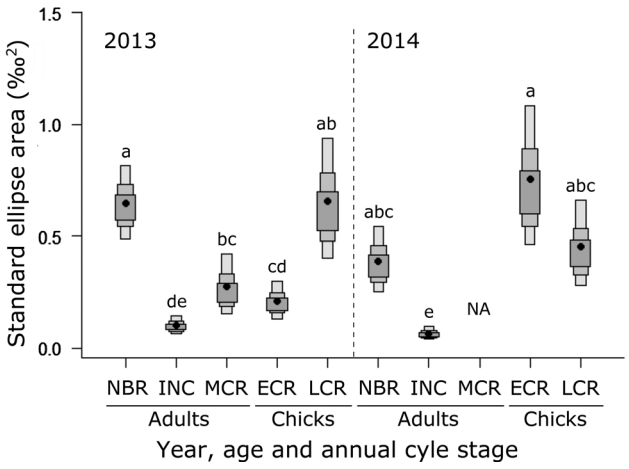

Fig. 4 Density plot depicting the mean Bayesian standard ellipse areas (black dot) and their confidence intervals for adult and chick grey-faced petrels *Pterodroma gouldi* during various annual cycle stages in 2013 and 2014 at Ihumoana, New Zealand. Shaded boxes represent the 50%, 75% and 95% intervals from dark grey to light grey. *NBR* non-breeding, *INC* incubation, *MCR* mid-chick rearing, *ECR* early chick rearing, *LCR* late chick rearing. Different letters indicate significant differences in SEAb between groups

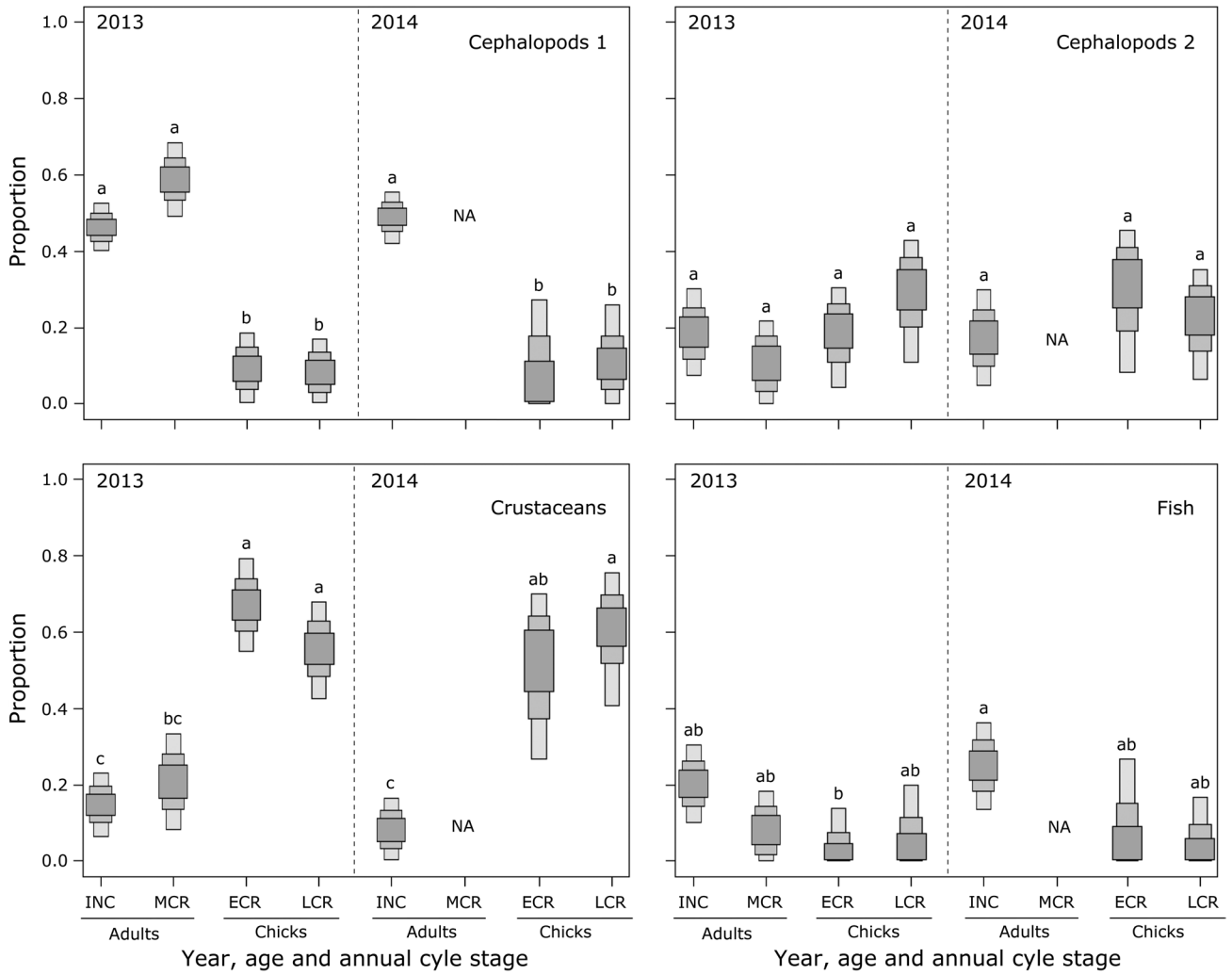

Fig. 5 Proportion of estimated prey groups in the diet of adult and chick grey-faced petrels *Pterodroma gouldi* during various breeding stages in 2013 and 2014 at Ihumoana, New Zealand. Estimates are from SIAR mixing models, and shaded box plots represent the 50%, 75% and 95% credibility intervals from dark grey to light grey. *INC* incubation, *MCR* mid-chick rearing, *ECR* early chick rearing, *LCR* late chick rearing. For each prey group, different letters indicate significant differences in contribution proportion in the diet between breeding stages

males) during the breeding period (Pinet et al. 2012; Hedd et al. 2014; Yamamoto et al. 2015; Danckwerts et al. 2016). Yet, isotopic differences between sexes were more marked during the non-breeding period in grey-faced petrels. This suggests that males and females could use different marine habitats and/or areas and potentially feed on prey of different trophic levels during non-breeding. There is also a relationship between seabird sexual size dimorphism and their sexual segregation in diet or distribution, with size-dimorphic taxa more commonly exhibiting sex differences in δ^{15}N than δ^{13}C (Phillips et al. 2011). This is more consistent with size-mediated competitive exclusion or dietary specialisation than just habitat specialisation. Higher δ^{15}N values in males have been observed in Procellariiformes with various levels of sexual size dimorphism (Quillfeldt et al. 2008b; Paiva et al. 2018). Grey-faced petrels are slightly sexually dimorphic with males being larger than females in all measurements and sexual size dimorphism being the greatest for bill depth (Bourgeois et al. 2017). Males could thus catch larger prey of higher trophic level.

Adult and chick grey-faced petrel isotopic niches were clearly segregated during chick rearing (no isotopic niche overlap), with chicks showing lower δ^{13}C (difference: 1.4 ‰) and higher δ^{15}N (difference: 1.0 ‰) values than adults. These differences in stable isotope values may reflect the use of a dual-foraging strategy, which was also suggested by an adult burrow attendance study of the species (authors' unpubl data). The δ^{13}C values found in grey-faced petrel chicks and adults suggest that adults feed in more inshore areas for themselves and chicks are fed more on oceanic prey

caught offshore by adults. This contradicts the pattern generally accepted for seabirds that use a dual-foraging strategy, which finds that adults alternate short chick-provisioning trips of 1–4 days with longer self-maintenance trips during which they generally target more productive but more distant areas (Catard et al. 2000; Magalhães et al. 2008; Jakubas et al. 2012; Shoji et al. 2015). However, the inference from stable isotope analyses that chicks consume more oceanic prey than their parents has been commonly observed in Procellariiformes (e.g. Alonso et al. 2012; Danckwerts et al. 2016; Leal et al. 2017; Thabet et al. 2019). On the other hand, metabolic and physiological factors can affect isotopic discrimination and lead to differences in isotope values between chicks and adults (Sears et al. 2009). In particular, Procellariiformes are able to convert fresh prey into concentrated stomach oil (Warham 1977). Adults feed their chicks this oil which is highly energetic but poor in protein and depleted in δ^{13}C (Warham 1977, 1996; Thompson et al. 2000). This may thus explain the low δ^{13}C values measured in grey-faced petrel chicks, but not the δ^{15}N difference. However, adults may also provide whole prey to their chicks in order to supply the protein required for their growth (Warham 1977, 1996). These whole prey often had higher trophic levels than prey used for self-provisioning as suggested by seabird chicks having higher δ^{15}N values (by 1–2‰) than adults (e.g. Hodum and Hobson 2000; Cherel et al. 2008; Forero et al. 2005; Richoux et al. 2010; González-Medina et al. 2017). Stable isotope mixing models revealed that a group of cephalopods was the main diet component of breeding adult grey-faced petrels. This group of cephalopods was characterised by low δ^{15}N values. Because the typical internal shell of the ram's horn squid was found inside mantles of this cephalopod group and in all the regurgitations from which flesh samples of this cephalopod group were collected, we assume that ram's horn squids constituted this group of cephalopod prey. This assumption is supported by the low trophic position of this squid in comparison with other cephalopods (Ohkouchi et al. 2013). In contrast, crustaceans were the main diet component of grey-faced petrel chicks and they exhibited higher δ^{15}N values than ram's horn squids. This difference in diet between adults and chicks could thus explain the difference in δ^{15}N values in their tissues, and potentially the difference in δ^{13}C values as well, particularly if chicks were fed with oil produced from crustaceans as suggested by the orange coloured carotenoid rich oil found in grey-faced petrel regurgitations (Warham 1977, 1996).

Stable isotope values in wing feathers

Because petrels generally spend their non-breeding period in foraging areas several thousand kilometres away from their foraging areas during the breeding period (e.g. Rayner et al. 2012; Priddel et al. 2014; Ramos et al. 2017), we expected different stable isotope values between the two periods in grey-faced petrels. Yet, our study revealed values more similar between these two periods than between breeding adults and chicks. Most grey-faced petrels from Ihumoana disperse to the western Tasman Sea and to the south-western Coral Sea, off the eastern coast of Australia, during the non-breeding period (GLS data; G.A. Taylor unpubl data). During the breeding period, they forage in the eastern and central Tasman Sea, several hundred kilometres west of New Zealand (from more than 50 km and up to about 1500 km from the coast, GPS data; K. Bourgeois unpubl data). The two areas are not as distant as in some other petrel species (e.g. Rayner et al. 2012; Priddel et al. 2014; Ramos et al. 2017) and the similarities of δ^{15}N and δ^{13}C values in grey-faced petrel tissues reflecting the two periods could be coherent with marine isoscapes in the region (Graham and Bury 2019). Indeed, the area off the eastern coast of Australia (between 0 and 500 km from the coast), particularly around the limit between the Tasman and the Coral seas (i.e. the parallel of 30°S), exhibits slightly more depleted δ^{13}C values than the central and eastern Tasman Sea, while grey-faced petrel tissues reflecting the non-breeding period exhibited depleted δ^{13}C values compared to tissues reflecting the breeding period. This area also exhibits slightly depleted δ^{15}N values suggesting that grey-faced petrels could feed on higher trophic level prey during the non-breeding period, since δ^{15}N values in their tissues reflecting the two periods were similar. However, stable isotope values were obtained from blood for the breeding period and from the fourth primary covert feather for the non-breeding period. We thus cannot exclude that the use of linear regressions to correct blood δ^{15}N and δ^{13}C values in order to compare grey-faced petrel blood and feather isotopic ratios could have biased our results.

Annual variation in isotopic niche

Grey-faced petrel isotopic niches overlapped substantially between years for the various annual cycle stages as the inter-annual overlap of isotopic niches during each annual cycle stage averaged 22.2 ± 20.5%, $n = 4$. However, isotopic niches did not overlap between 2013 and 2014 during early chick rearing. Isotopic niche width did not exhibit a clear difference between the two years studied as it was narrower in 2014 during incubation and wider the same year during early chick rearing. Adult grey-faced petrels exhibited lower δ^{13}C and δ^{15}N values in 2013. In chicks, δ^{13}C values were lower in 2014 and δ^{15}N values in 2013 but these differences were significant only for the early chick rearing period. During years of unfavourable oceanographic conditions, seabirds generally engage in longer trips, resulting in larger home ranges and foraging areas, and they exhibit a wider isotopic niche (Kowalczyk et al. 2014; Ramos et al. 2015, 2018; Cerveira et al. 2020). In contrast, during years of apparent good oceanographic conditions, they have a smaller

isotopic niche suggesting a higher specialization, potentially related to the greater abundance of their main food items (Leal et al. 2017; Ramos et al. 2018). The values of δ^{13}C and δ^{15}N measured in adult grey-faced petrels and the corresponding isotopic niche widths suggest that oceanographic conditions in 2013 could have been less favourable than in 2014. During the 2013 breeding period, the Southern Oscillation Index leant towards La Niña while during the 2014 breeding period it leant towards El Niño. A La Niña phase means warmer air temperatures around New Zealand, more north-easterly winds and more rain in north-eastern parts of the North Island. During La Niña like conditions, positive sea surface temperature anomalies are located in the west Pacific. In the 2013 La Niña conditions, sea surface temperatures were higher and this likely affected grey-faced petrel prey distribution and/or abundance. Overall, grey-faced petrel breeding success (excluding on-land causes of breeding failure such as egg and chick predation) and chick growth on Ihumoana did not differ between 2013 and 2014 (authors' unpubl data). This suggests that their foraging strategy plasticity allows them to buffer the effects of inter-annual environmental differences on these two reproductive parameters, at least to a certain point for the moderate differences over the two years of our study, as has been observed in other seabird species (Dehnhard et al. 2016). However, long-term studies relating isotopic niche, if possible combined with tracking data, with demographic parameters would help evaluate the role of oceanographic conditions in the demography of this species and ultimately the impact of global changes on its populations. Indeed, although the grey-faced petrel is overall not threatened, it is only abundant at a few sites and in very small declining populations at most other sites (small island and mainland colonies; Greene et al. 2015). Causes for decline are interactive; introduced mammal predation on land and changes in oceanographic conditions at sea. Independently of predation, marked spatiotemporal variation in chick development and breeding success has been found, with high chick mortality due to starvation some years at some colonies (authors' unpubl data). This spatial variation is hypothesised to arise from different marine foraging strategies, either through foraging area location or trophic levels fed upon, while temporal variation is more probably related to variation in oceanographic conditions and in prey distribution and abundance. Grey-faced petrels are thus considered a priority monitoring species in New Zealand because their population status is highly correlated to marine ecosystem health (Monks et al. 2013; Russell et al. 2017). The spatiotemporal monitoring of grey-faced petrel trophic ecology could be informative about the changes in food web structure or in prey abundance and diversity across the Tasman Sea and the southwest Pacific Ocean and serve as a valuable bio-indicator of prey populations that could themselves be affected by the combined effects of overfishing and climate change.

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Author contributions KB and JCR conceived and designed the research. KB, JRW, SD and GAT carried out the fieldwork. KB and JRW analysed regurgitates. KB and JCR performed statistical analyses. KB wrote the manuscript and made the figures, with inputs from JCR and GAT. All authors contributed to and commented on manuscript drafts, and gave final approval for publication.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Ethics approval This work was conducted with ethics approval from the University of Auckland Animal Ethics Committee (AEC R898), and banding permit (#2010/021) and research permission (34780-RES and 38573-FAU) from the New Zealand Department of Conservation. Thus, all applicable international, national, and institutional guidelines for the sampling and the care of animals alive have been followed and all necessary approvals have been obtained.

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