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RESEARCH

At-sea foraging behaviour in Hutton's shearwater (*Puffinus huttoni*) as revealed by stable isotope analysis

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Abstract: Stable isotope analysis of feathers can provide an indirect method to investigate the diet and foraging locations of birds during the time the feathers were growing. We used the isotopic composition of experimentally-induced feathers to investigate the foraging locations of the Hutton's shearwater (*Puffinus huttoni*), an endangered seabird that is a breeding endemic to the Kaikōura region of New Zealand. The isotopic composition of feathers was first compared with potential prey items collected from the near-shore marine environment near the breeding colony. By applying trophic fractionation factors (2–4 ‰ increase in $\delta^{15}N$ for every 1 ‰ increase in $\delta^{13}C$) and comparing the isotopic composition of the induced tail feathers and sampled prey items, we found that feather isotopic compositions were not consistent with a diet based on feeding locally. Both the $\delta^{13}C$ and $\delta^{15}N$ from zooplankton and fish collected within 8 km of Kaikōura were significantly different than the isotopic composition of induced feathers and were outside of the range expected for consumed local prey items. Instead, we found the isotopic composition of Hutton's shearwater feathers was more consistent with feeding on potential prey items in the seas north-east and around Banks Peninsula, an area c. 100 km south of the breeding colony and where they had been tracked previously. Stable isotope analysis can provide insight into the foraging behaviour of birds at sea and demonstrates the importance of isotopic research in pinpointing foraging locations in seabirds with large geographic ranges.

Keywords: New Zealand, seabird, diet, feather composition, tracking

Introduction

Studies of foraging behaviour and diet can be difficult in highly pelagic seabirds that spend long periods of time at sea. Direct collection techniques to determine diet can be invasive, and these samples may be limited in temporal and spatial scope, or difficult to identify if partially digested (West & Imber 1985; Barrett et al. 2007). Although recent developments in tracking technology have greatly aided in determining movements and locations of seabirds in the marine environment (Matsumoto et al. 2017; Alonso et al. 2018; Bennet et al. 2019), linking locations with variation in diet is still problematic as the occurrence of a bird in an area does not necessarily mean they are feeding nor can their diet be determined from location data alone.

Stable isotope analysis (SIA) is a powerful ecological tool that can be used to indirectly investigate the diet of seabirds across a range of spatial and temporal scales (Inger & Bearhop 2008) and thus pinpoint key feeding locations. For example, in species that moult in the non-breeding range, SIA of feathers from birds returning to the breeding grounds can be used to determine their diet during the period where the feathers were grown, while forced regrown feathers that were induced on the breeding grounds can provide an indication of diet during the breeding period (Quillfeldt et al. 2005). By applying different trophic enrichment factors (Linnebjerg et al. 2016) associated with the metabolism of prey items of known isotopic composition, it is possible to investigate sexual and temporal variation in diet, infer the trophic position of a species, and to make a more direct link between the locations of birds with the areas in which they are feeding (Rau et al. 1992; Quillfeldt et al. 2005; Gladbach et al. 2007; Caut et al. 2009; Phillips et al. 2009).

Pelagic seabirds (Order Procellariiformes) occur in most of the world's oceans, and many temperate-breeding species make trans-equatorial migrations between the breeding and non-breeding period (Warham 1990). Unlike these species, the Hutton's shearwater (*Puffinus huttoni*) remains in the Southern Hemisphere and migrates from its breeding grounds in Kaikōura, South Island, New Zealand to the Indian Ocean off the coast of Western Australia during the non-breeding period (Halse 1981). Although details of its movements are poorly known, adult Hutton's shearwaters undergo their post-breeding moult away from the New Zealand breeding grounds

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and presumably while residing in the Indian Ocean (Robinson 1973; Halse 1981; Marchant & Higgins 1990). Up until 1965, the breeding location of Hutton's shearwater was unknown although they were observed at sea, rafting within coastal areas near Kaikōura (Harrow 1965, 1976). Eventually eight breeding colonies were identified within the Seaward and Inland Kaikōura Ranges, all above 1200 m a.s.l. (Harrow 1965, 1976; Sherley 1992). By the 1980s only two breeding areas remained (Kaikōura River and Shearwater Stream), and the population had declined due to predation, predominantly by feral pigs (*Sus scrofa*; Cuthbert 2002; Sommer et al. 2009). As a result, the Hutton's shearwater is currently classified as endangered (IUCN 2018) and threatened and nationally vulnerable under the New Zealand Threat Classification (Birdlife International 2017). To ensure their conservation, a new population has been established by translocation to a lowland site on the Kaikōura Peninsula (Rowe 2014). To date, research on the Hutton's shearwater has focused on monitoring population size and assessing predation risk within the alpine colonies (Cuthbert 2001), but little is known about their foraging behaviour and diet, either on their breeding or non-breeding grounds. It is believed that Hutton's shearwater feed on a variety of small fish, crustaceans, and squid (Tarburton 1981; West & Imber 1985).

In a recent study using GPS (global positioning systems) tracking devices, we confirmed that movements of Hutton's shearwaters included forays into the seas adjacent to the breeding colony as well as longer trips south towards the seas off the east and north-east coast of Banks Peninsula (Bennet et al. 2019). However, it was not clear from our tracking study exactly where birds were feeding as some areas may have been used for rafting or other non-foraging activities. The objective of this paper was to identify the foraging locations of Hutton's shearwaters during the breeding season using isotopic signatures from shearwater feathers and their potential prey. To achieve this goal, we compared the $\delta^{13}C$ and $\delta^{15}N$ values of induced tail feathers to the carbon and nitrogen isotope composition of potential prey items collected from coastal environments both near the colony and further out to sea. The ability to identify likely foraging areas based on the isotopic composition of feather specimens represents an important non-invasive approach for identifying regions for targeted fisheries bycatch risk reduction of seabirds (Oliveira et al. 2015; Meier et al. 2017), including Hutton's shearwaters (West & Imber 1985).

Methods

Feather collection and prey sampling

During the 2014–2015 breeding season, adult Hutton's shearwater (*Puffinus huttoni*) tail feathers were collected from the alpine Kowhai River colony (> 1200 m a.s.l.; $n = 34$ feathers) and the coastal Kaikōura Peninsula (Te Rae O Atiu; c. 80 m a.s.l.; $n = 28$ feathers) colony for stable isotope analysis (Fig. 1). From mid-November to early December 2014, birds were captured and a single tail feather (rectrices R5) was removed

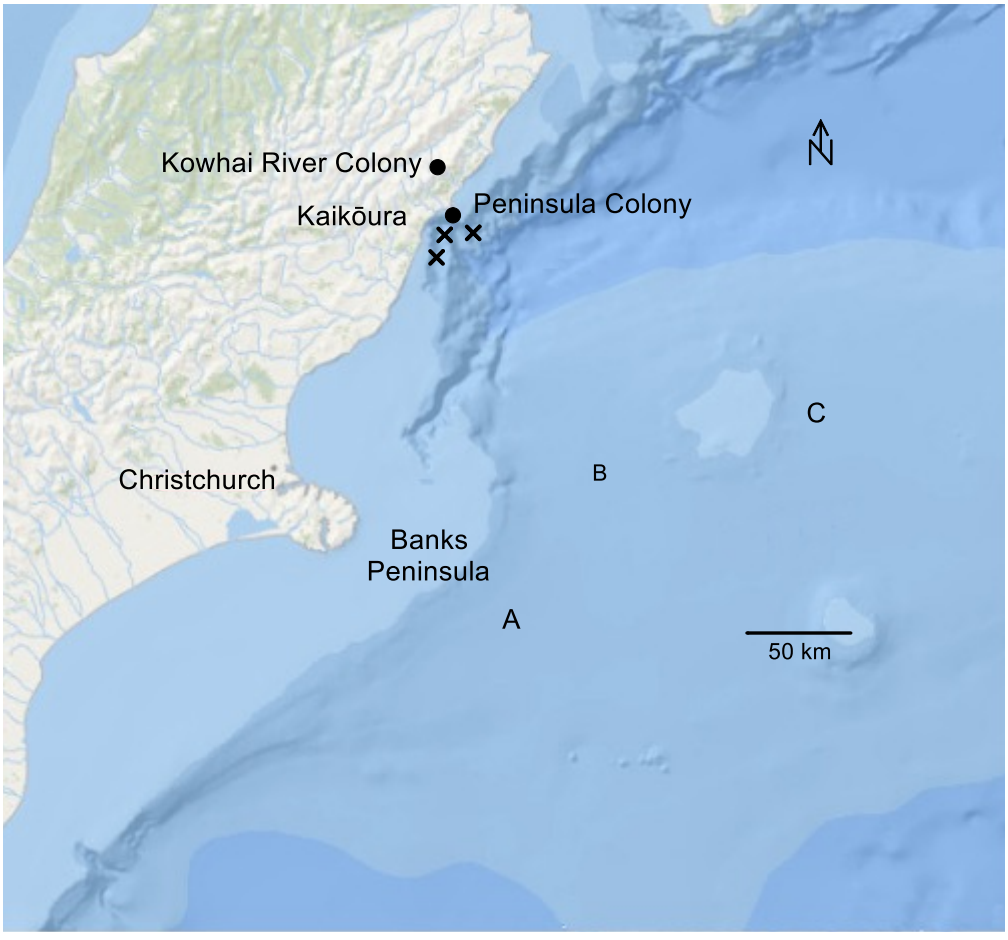

Figure 1. Map illustrating the location of the breeding colonies of Hutton's shearwaters (circles) in Kaikōura and zooplankton and larval fish collection sites near Kaikōura (crosses) and Banks Peninsula (A) and open ocean areas (B and C), New Zealand.

from each adult. These first-plucked feathers were grown on their non-breeding grounds, presumably in the Indian Ocean (Halse 1981; Marchant & Higgins 1990). In January 2015, we then collected the induced regrown feathers. Leg band number was used to identify birds and the same tail feathers (R5) were collected. As induced feathers were grown while birds were on the breeding grounds, their isotopic signature should reflect the local diet. All feathers were stored in individual paper envelopes before being prepared for analyses. Each feather was cleaned of surface contaminants using 2:1 chloroform:methanol, rinsed in nano-pure deionised water, and air-dried in glass vials with silicon natural/PTFE septa EPA caps.

To determine the $\delta^{13}C$ and $\delta^{15}N$ values of potential shearwater prey items (zooplankton and fish), samples were collected at two sites: (1) between two to eight km off the Kaikōura coast, an area near the breeding colony where shearwaters are often seen in large rafts and potentially feeding, and (2) off the coast of Banks Peninsula (Fig. 1), an area of offshore seas c. 100 km south of the breeding colony to which Hutton's shearwaters have been tracked by GPS (Bennet et al. 2019). Collecting in Kaikōura was done with an oblique tow using a box-pyramid design plankton net (250 µm). Tows were run between November 2014 and January 2015. The tow was run from a depth of 50 m and the net was gradually winched to the surface over a 10 min period. Tow samples were sorted into one of nine groups (amphipod, cephalopod, crustacean larvae, copepod, euphausiid, Munidae, mysis, stomatopod, and fish), and dried at 55°C. Samples from the open ocean (north-east of Banks Peninsula) and east of Banks Peninsula were collected using a multiple opening/closing net and environmental sensing system (MOCNESS) by the National Institute of Water and Atmospheric Research (NIWA). Mixed zooplankton species were collected from depths of 5–50 m from 6 to 12 December 2015. Hutton's shearwaters dive to depths of 35 m (Bennet et al. 2020), thus our samples encompassed the range of prey they would likely encounter while foraging.

Isotopic analysis

To run the isotopic analyses, fish, zooplankton, and feather vane samples were finely chopped and 500 micrograms (± 100 µg) placed into tin capsules (OEA Laboratories 8 mm × 5 mm). Samples were analysed for $\delta^{13}C$, $\delta^{15}N$, %C and %N using continuous-flow isotopic-ratio mass spectrometry. Data were normalised to Vienna PeeDee Belemnite (PDB) for $\delta^{13}C$ and Air for $\delta^{15}N$ based on replicate analyses of certified reference materials IAEA-N-1, IAEA-N-2, IAEA-CH-3, NBS22, and NBS19 in each analytical sequence. Results are expressed in conventional δ-notation, expressed in parts per thousand (‰) according to the following equation:

$$\delta X = [(R_{sample}/R_{standard}) - 1] \times 1000 \quad (1)$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio $^{13}C/^{12}C$ or $^{15}N/^{14}N$ (Cherel et al. 2005a; Hobson 2005). The $R_{standard}$ values were based on the PDB for ^{13}C and atmospheric N_2 (AIR) for $\delta^{15}N$. We have applied caution when assessing the feather isotopic composition compared to the potential food items $\delta^{13}C/\delta^{15}N$ values by applying various trophic fractionation factors (e.g. 2–4 ‰ increase in $\delta^{15}N$ for every 1 ‰ increase in $\delta^{13}C$) (Cherel et al. 2005b; Caut et al. 2009).

Results

The composition of potential food items varied over the season and between collecting areas near Kaikōura and the open ocean by Banks Peninsula (Fig. 2; Table 1). Values of $\delta^{13}C$ and $\delta^{15}N$ from samples collected between November to January overlapped extensively, but we observed a negative shift in the average $\delta^{13}C$ values of zooplankton from $-21.3^{0}/_{00}$ in November to −22.3‰ in January, and of fish from −21.1‰ to −22.1‰, in the same time period (Table 1). The $\delta^{15}N$ values for fish were initially 11.3‰ in November and December, before declining to 10.4‰ in January, whereas $\delta^{15}N$ values for zooplankton increased and remained high over the same period (9.3 to 9.7‰, respectively). Zooplankton samples collected off Banks Peninsula and from the open ocean north-east of Banks Peninsula during December (−21.1‰) were comparable to the Kaikōura $\delta^{13}C$ value, but showed a much lower $\delta^{15}N$ value (7.3‰ to 9.7‰, respectively).

The average values of $\delta^{13}C$ and $\delta^{15}N$ for induced Hutton's shearwater (*Puffinus huttoni*) tail feathers are shown in Fig. 2 and Table 1. Values of $\delta^{13}C$ and $\delta^{15}N$ from feather samples were -17.2 ± 0.2 and 13.0 ± 0.3, respectively. The induced tail feather samples were enriched in both ^{13}C and ^{15}N compared to potential prey values with the magnitude of enrichment depending on the trophic fractionation factor used (2–4‰ increase in $\delta^{15}N$ for every 1 ‰ increase in $\delta^{13}C$). Variability was also observed between months for $\delta^{13}C$ and $\delta^{15}N$ prey and feather values (Fig. 2; Table 1). The average $\delta^{13}C$ values for larval fish (-21.1 ± 0.4 to -22.1 ± 0.3) and zooplankton (-21.2 ± 0.3 to -22.3 ± 0.3) from near-shore Kaikōura waters were less positive compared to the induced tail feathers (-17.2 ± 0.2) collected during the breeding season (Table 1). Irrespective of the trophic fractionation factor used, the induced tail feathers were outside of the range expected if the birds were foraging in the near-shore Kaikōura waters. However, the induced feather composition was consistent with a 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ if the birds were foraging offshore of Banks Peninsula or in the open ocean north-east of Banks Peninsula.

As it is possible that the different time periods of sampling potential prey items (November to January in Kaikoura, and only in December in waters off Banks Peninsula) affected our interpretation, we also compared trophic fractionation in December alone to control for any seasonal effects (Figs 2b, d). However, the pattern we found is the same as that when using prey samples from the entire period from November to January.

Discussion

Using isotopic analysis of induced Hutton's shearwater (*Puffinus huttoni*) feathers and prey collected from potential foraging locations, we show that foraging at sea occurs primarily south of their breeding colony, in the seas surrounding Banks Peninsula, an area to which they had been tracked previously using GPS locators (Bennet et al. 2019). The apparent lack of foraging within the Kaikōura near-shore area was not expected as birds are regularly seen rafting and flying in this area in large numbers. Despite the range in available prey in the local area and the overlap in prey species between months, the isotopic composition of the induced Hutton's shearwater feathers was not consistent with foraging on the local food web. Instead, our results indicate the Hutton's shearwater forage away from the

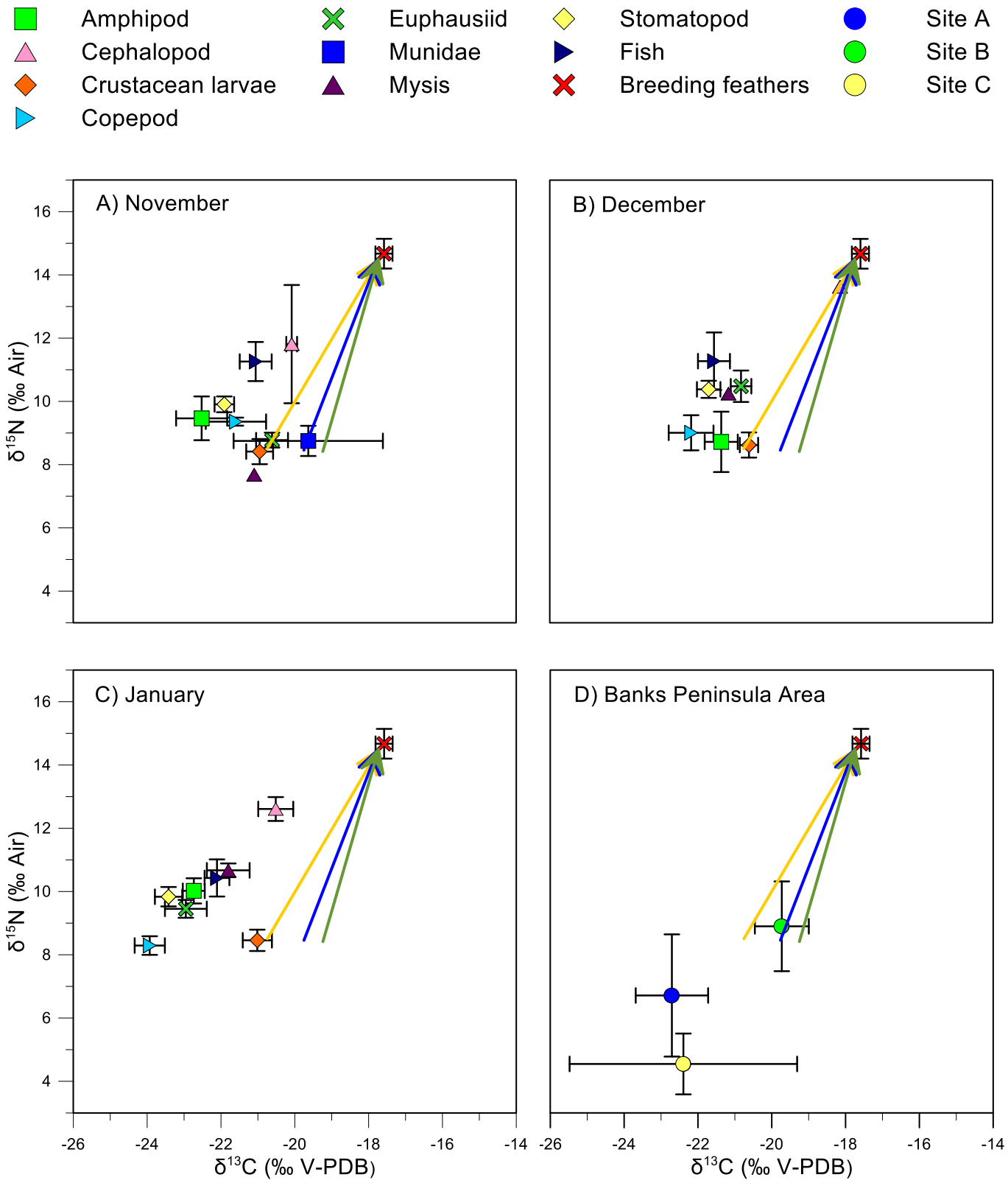

Figure 2. Stable isotope compositions for zooplankton and fish and the isotopic composition of Hutton's shearwater tail feathers (mean ± CI and values for single prey items). Feather data plotted include samples from both the Kaikōura alpine and peninsula sites. Plankton tow samples collected monthly (2014–15) from the near-shore Kaikōura coastline (A) November, (B) December (crustacean larvae obscured by arrows), and (C) January compared to induced tail feather $\delta^{13}C/\delta^{15}N$ values from the breeding season; (D) Zooplankton (December 2015) collected from offshore waters (site A 44.1473 S, 174.039 E; site B 43.519 S, 174.573 E; site C 43.236 S, 175.865 E), east and north-east of the Banks Peninsula compared to regrown breeding season tail feather $\delta^{13}C/\delta^{15}N$ values. The arrows indicate the 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ (yellow 2‰, blue 3‰ and green 4‰ increase in $\delta^{15}N$).

Table 1. Summary of $\delta^{13}C$ and $\delta^{15}N$ values (mean ± CI) for fish, zooplankton and Hutton's shearwater adult tail feathers sampled during 2014–15. BP: zooplankton collected from offshore waters, east coast of the Banks Peninsula area; all other samples are from the Kaikōura near-shore waters; breeding season feathers were induced and regrown during this study.

Sample	Season	$\delta^{13}C$ (‰)		$\delta^{15}N$ (‰)	
		Mean ± CI	Range (‰)	Mean ± CI	Range (‰)
Fish	November (*n* = 18)	−21.1 ± 0.4	−18.7 to −24.2	11.3 ± 0.6	12.5 to 7.4
	December (*n* = 12)	−21.6 ± 0.4	−17.3 to −23.5	11.3 ± 0.8	14.7 to 6.0
	January (*n* = 31)	−22.1 ± 0.3	−19.1 to −24.9	10.4 ± 0.6	13.4 to 7.1
Zooplankton	November (*n* = 66)	−21.3 ± 0.3	−19.6 to −22.2	9.3 ± 0.2	13.3 to 9.1
	December (*n* = 57)	−21.2 ± 0.3	−20.7 to −22.7	9.7 ± 0.4	12.3 to 7.2
	January (*n* = 82)	−22.3 ± 0.3	−20.5 to −23.6	9.7 ± 0.3	14.0 to 8.4
	December: BP (*n* = 20)	−21.1 ± 0.9	−17.4 to −24.0	7.3 ± 1.0	10.8 to 3.7
Feathers	Breeding (*n* = 31)	−17.2 ± 0.2	−16.1 to −18.2	13.0 ± 0.3	14.4 to 10.5

Kaikōura region as the isotopic composition of their induced feathers was more comparable to isotopic ratios from prey collected c. 100 km south towards Banks Peninsula.

By selecting trophic discrimination factors between potential prey items and the consumer's tissues (i.e. feathers), we were able to investigate whether Hutton's shearwaters had consumed a diet from the prey collected from two locations in which foraging was suspected (Hobson 1993; Cherel et al. 2005b; Labbé et al. 2013). However, setting rates of isotopic enrichment between trophic levels may vary, and setting a single fractionation value may influence the interpretation of the food web (Table 2; Hobson & Welch 1992;, Bearhop et al. 2002; Linnebjerg et al. 2016). For example, the trophic fractionation factor for breast feathers from four penguin species varied between 2.1–4.8‰ in $\delta^{15}N$ for wild and captive fed individuals (Mizutani et al. 1992; Cherel et al. 2005b; Cherel et al. 2005a; Polito et al. 2011). As trophic fractionation factors are not available for most Procellariiformes, we used other species of seabirds (i.e. Sphenisciformes, Charadriiformes, and Suliformes) as the closest analogues. Like Hutton's shearwaters, all these species are avian predators in the marine environment and, although there is variation in feeding behaviours across species, we assumed metabolic assimilation would be similar enough to imply similar enrichment factors. Without undertaking a captive feed study and comparing it to wild animals, the exact differences in trophic discrimination factors cannot be measured directly, but this was beyond the scope of our study. Hence, we used a range of $\delta^{15}N$ values (2–4‰) to account for the variation found within each trophic level, allowing for any potential error (Cherel et al. 2005b).

Variation in isotopic composition of potential prey species was observed between months and between the Kaikōura near-shore and Banks Peninsula. The 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ corresponded with the greatest diversity of prey species in November (Fig. 2a). The 2‰ increase in $\delta^{15}N$ for November and December was due to cephalopod and crustacean larvae prey caught at this time, while only crustacean larvae were identified as potential prey to explain the 2‰ increase in $\delta^{15}N$ for the plankton tows in January (Fig. 2c). Potentially, a change in shearwater diet to feeding extensively on Munidae and cephalopods in waters near Kaikoura could explain a 3–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ (Figs 2a, b). Nevertheless, we suggest this is less likely conclusion than the shearwaters feeding primarily in waters off Banks Peninsula as the replacement feathers took eight to ten weeks to grow, and the period in which these prey items were available off the coast of Kaikoura would not cover the entire growth period of the feathers. When compared to the values of $\delta^{13}C$ and $\delta^{15}N$ in Hutton's shearwater tail feathers, the best trophic fractionation model (2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$) observed between the induced tail feathers and the Kaikōura near-shore samples was a 2‰ increase in $\delta^{15}N$. In contrast, a more likely trophic relationship was observed for the induced feather composition following the 2–4‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ between the zooplankton collected offshore (80–200 km) from Banks Peninsula, during the breeding period (Fig. 2d). These results suggest that the Hutton's shearwater predominantly forage further south and not in the local area near the colonies.

Hutton's shearwater forage on small fish, crustaceans, and squid (Harrow 1976; Tarburton 1981; West & Imber 1985), although the actual diet has not been studied in detail, nor how it may vary with season or geographic area. During the breeding season, foraging locations and diet of seabirds may vary depending on chick requirements and adult self-maintenance (Cherel et al. 2005a). Our analysis of zooplankton and larval fish samples collected during the breeding season from the Kaikōura near-shore demonstrated that a variety of potential prey items can be identified if nitrogen isotope trophic fractionation ranged between 2 and 4‰ for each 1‰ increase in $\delta^{13}C$, and these varied across the range in $\delta^{15}N$ values (Fig. 2). For example, samples collected in November included cephalopods and a variety of crustaceans for all trophic fractionation factors, but no fish were detected within any of the trophic fractionation factors. However, this pattern did not continue in December or January (Figs 2a–c). If shearwaters were utilising a 2‰ increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$, the availability of prey species in Kaikōura remains a plausible explanation for tail feather isotopic composition, but this explanation is less likely as the $\delta^{15}N$ values increases, and it becomes difficult to associate a trophic fractionation model with the tail feather isotopic composition over the 3‰ and 4‰ $\delta^{15}N$ increase as no prey items were observed within the 10–13‰ isotopic ranges (Fig. 2) when an increase in $\delta^{15}N$ for every 1‰ increase in $\delta^{13}C$ is considered. This suggests that the shearwaters must be predominantly foraging away from the near-shore coastal system, or alternatively they were foraging in the Kaikōura area but not feeding on the prey items sampled during the collection period. As our tows sampled the full range of prey likely to occur in the diet of Hutton's shearwaters (from zooplankton to fish; see methods section), this interpretation seems less likely.

As variability in $\delta^{13}C$ in the range of 4–6‰ has been observed in captive species (Mizutani et al. 1992; Cherel

Table 2. Published carbon ($\Delta^{13}C$) and nitrogen ($\Delta^{15}N$) discrimination factors between feathers and diet for a range of seabird species.

Seabird	Diet	Diet analysis	Feather	Environment	*n*	$\Delta^{13}C$	$\Delta^{15}N$	Source
Little blue penguin (*Eudyptula minor*)	Sprat	Whole	Body	Captive	12	2.36	3.66	Bushman (2016)*
Humboldt's penguin (*Spheniscus humboldti*)	Anchovy	Whole	Body	Captive	16/14	2.9 ± 0.2	4.8 ± 0.5	Mizutani et al. (1992)*
Rockhopper penguin (*Eudyptes chrysocome*)	Capelin	Muscle	Back	Captive	9	0.6	3.5	Cherel et al. (2005b)
Rockhopper penguin (*Eudyptes chrysocome*)	Capelin	Whole	Back	Captive	9	0.1	4.4	Cherel et al. (2005b)
King penguin (*Aptenodytes patagonicus*)	Herring	Muscle	Back	Captive	10	0.3	2.7	Cherel et al. (2005b)
King penguin (*Aptenodytes patagonicus*)	Herring	Whole	Back	Captive	10	0.1	3.5	Cherel et al. (2005b)
King penguin (*Aptenodytes patagonicus*)†	Myctophids	Whole	Body	Wild	10/12	–	3.3–3.6	Cherel et al. (2005a)
Gentoo penguin (*Pygoscelis papua*)	Herring	Whole	Body	Captive	20	1.3 ± 0.5	3.5 ± 0.4	Polito et al. (2011)
Common murre (*Uria aalge*)†	Sandeel	Whole	Body	Wild	8	1.0	3.3	Thompson & Furness (1995)
Common murre (*Uria aalge*)	Capelin	Muscle	Body	Captive	11	2.5 ± 0.2	3.6 ± 0.2	Becker et al. (2007)
Common murre (*Uria aalge*)	Capelin	Muscle	Primary	Captive	11	1.9 ± 0.3	3.7 ± 0.2	Becker et al. (2007)
Common cormorant (*Phalacrocorax carbo*)	Mackerel	Whole	Primary	Captive	17/16	3.8 ± 0.5	3.7 ± 0.6	Mizutani et al. (1992)*
Broad-billed prion (*Pachyptila vittata*)	Zooplankton	Whole	Body	Wild	6	2.5	4.3	Thompson & Furness (1995)
Arctic tern (*Sterna paradisaea*)	Sandeel	Whole	Back	Wild	8	2.1	3.4	Thompson & Furness (1995)
Subantarctic skua (*Catharacta lonnbergi*)	*P. vittata*	Feather	Body	Wild	8	0.4	3.0	Thompson & Furness (1995)
Great skua (*Stercorarius skua*)	Sprat	Whole	Remiges	Captive	9	5.3	4.4	Bearhop et al. (2002)*
Ring-billed gull (*Larus delawarensis*)	Perch	Whole	Feather	Captive	14	0.2 ± 1.3	3 ± 0.2	Hobson and Clarke (1992a)
Black-tailed gull (*Larus crassirostris*)	Saurel	Whole	Primary	Captive	22	3.6 ± 0.5	5.3 ± 0.8	Mizutani et al. (1992)*
Yellow-legged gull (*Larus michahellis*)†	Marine fish	Whole	Scapular	Wild	107	0.9	1.7	Ramos et al. (2009)
Mean (±SD) All feather-diet studies (marine lipids not extracted from prey)						3.6 ± 1.1	4.4 ± 0.7	

†feathers sampled from chicks; *Studies that did not lipid extract prey items prior to analysis.

et al. 2005b; Bushman 2016), a higher trophic discrimination factor (4‰ $\delta^{13}C$: 2‰ $\delta^{15}N$) would lead to the conclusion that small fish in the Kaikōura region could explain the isotopic composition of induced feathers in Hutton's shearwater. Indeed, observations have been made of Hutton's shearwater consuming small shoaling fish close to the Kaikōura coastline (Harrow 1976; West & Imber 1985), although how important this may be in the overall diet is not clear. There are a variety of possible explanations for the discrepancy between our isotopic results and observations of fish being taken by shearwaters near the colony. First, a lot of variability in stable isotope analysis remains unexplained (Boecklen et al. 2011) and caution is needed when selecting enrichment factors, especially for a wild species where no controlled experiment has been undertaken (Cherel et al. 2005b; Swan et al. 2020). Conducting experimental feeding trials on wild seabirds is difficult as these animals would need to be monitored for months or years (Hobson & Clark 1992a; Cherel et al. 2005b). Second, the rate of trophic fractionation and dietary change detected in tissues may vary due to metabolic rate, stress, fasting, and physical activity (Hobson & Clark 1992a; Cherel et al. 2005b; Cherel et al. 2005c), as wild animals actively forage to acquire resources whereas captive animals are provided with food (Hobson & Clark 1992b, Cherel et al. 2005a; Bond & Jones 2009). Third, the estimated trophic fractionation and trophic shift in N can greatly vary with prey type (e.g. invertebrates +1.4‰, alga and plants +2.2‰, vertebrates +3.3‰; McCutchan et al. 2003). Depending on the proportion of each prey type consumed, the trophic fractionation values may under- or over-estimate the consumer's trophic position, and this uncertainty

increases for each additional rise in trophic step (McCutchan et al. 2003; Caut et al. 2009; Swan et al. 2020). Ultimately, more systematic observations of Hutton's shearwaters foraging at sea are needed to confirm the importance of fish in their diet as well as our interpretation of the trophic position of this seabird based on the SIA data.

Understanding the spatial distribution of a species can enable a more accurate assessment of diet and key areas used for foraging. During the breeding season, Hutton's shearwaters have been tracked flying south from their breeding colony at distances of 125–365 km, in an area off the coast of Banks Peninsula and near the Chatham Rise (Bennet et al. 2019). The $\delta^{13}C$ and $\delta^{15}N$ composition of zooplankton species collected between 85–220 km off the coast of Banks Peninsula (Fig. 2d), were more consistent with induced tail feathers suggesting these represent prey items of the Hutton's shearwater diet. Thus, our isotopic data from the induced tail feathers are consistent with tracking data that indicates most foraging dives occurred at coastal sites (Canterbury Bight and Pegasus Bay) and oceanic banks (Mernoo Bank and Urry Bank) near Banks Peninsula (Bennet et al. 2019). Although we cannot discount the possibility that the Hutton's shearwater may sometimes forage on near-shore Kaikōura on small fish, depending on the trophic discrimination factor ratio, it is more likely they are primarily feeding on zooplankton when at the more distant Banks Peninsula.

Here, we offer an insight into the potential foraging locations of the Hutton's shearwater during the breeding period. We found the isotopic composition of induced Hutton's shearwater tail feathers did not conform with the potential prey species composition in the local area, and therefore we suggest that either the birds are foraging on something we did not sample, or they are foraging in areas outside of the Kaikōura near-shore environment. A possible foraging area offshore from Banks Peninsula was consistent with the isotopic composition of induced shearwater feathers and GPS tracking data supports this conclusion. In contrast, trophic fractionation models applied to the Kaikōura near-shore plankton and fish samples did not explain the observed isotopic composition, suggesting that any foraging in this location may be less than expected based on the visual presence of birds in the area. The spatial patterns in foraging behaviour we recorded in Hutton's shearwater highlight the need to manage the marine environment in areas that can sometimes be quite distant from their breeding colonies.

Conflict of Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Author Contributions

The study was designed jointly by all authors. DB and LR undertook the field-work and collection of data. DB carried out the data analysis and writing. TH, SG and JB supervised the study and contributed to the writing.

Data Availability Statement

The datasets generated for this study are available on request to the corresponding author.

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