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RESEARCH

The karoro *Larus dominicanus* in northern Aotearoa | New Zealand: diet and evidence of changing trophic position from regurgitated pellets and stable isotope analysis of contemporary and historic feathers and bones

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Abstract: Coastal seabirds are valuable indicators of ecological change in nearshore marine systems impacted by human activities. This study examined how human population growth and urban expansion have influenced the long-term dietary patterns of karoro (southern black-backed gull *Larus dominicanus*) in Auckland, Aotearoa | New Zealand. Specifically, we assessed whether increasing urbanisation has led to a dietary shift from marine-based prey to greater reliance on terrestrial and anthropogenic food sources. Contemporary diet composition was analysed using regurgitated pellets from two island breeding sites (Rangitoto and Tiritiri Matangi) in the Hauraki Gulf—sites differing in proximity to urban influence—and an urban roosting site at Western Springs Park. To assess long-term dietary trends, we conducted nitrogen stable isotope analysis of feathers from museum specimens spanning 109 years and collagen from contemporary karoro bones and subfossil bones from Tokerau Beach predating human arrival in Aotearoa. Pellet analysis indicated a diverse diet comprising marine vertebrates, invertebrates, and terrestrial or anthropogenic food sources, with city proximity influencing dietary composition. Stable isotope analysis revealed significant changes in karoro trophic ecology over the past century with birds shifting from a predominantly marine-based diet to one more reliant on terrestrial food, likely due to declining marine prey and increased urban food availability. Stable isotope data from ancient bones indicated that pre-human karoro were obligate coastal marine predators and scavengers, occupying a higher trophic level than their modern counterparts. These findings provide insight into how urbanisation and ecological change have shaped karoro diets over time.

Keywords: carbon dating, Hauraki Gulf, southern black-backed gull, $\delta^{13}C$, $\delta^{15}N$

Introduction

Coastal marine habitats are amongst the most heavily degraded ecosystems due to multiple, cumulative, negative ecological impacts of human activities (Roberts & Hawkins 1999; Crain et al. 2009). In north-eastern Aotearoa | New Zealand the decline of coastal marine habitats has tracked human population growth, mirroring global patterns of environmental degradation. Aotearoa was one of the last land masses to be colonised by humans (Taylor et al. 1997), with Polynesian colonisation in the 14th century initiating a wave of environmental impacts (Walter et al. 2017), that intensified following en masse European colonisation from the 1850s (Taylor et al. 1997). Fifty percent of Aotearoa's population is concentrated in the northern half of the North Island. In Auckland city in particular, population growth is having profound impacts on marine food webs through overfishing, pollution, and runoff of toxins and silt from land to sea (Hauraki Gulf Forum 2020). Despite these impacts, understanding of long-term effects on nearshore food webs in the region remains limited (Pinkerton et al. 2015).

As top predators, seabirds are useful indicators of structure and change within marine ecosystems, where data on populations and ecology can be linked with ecosystem processes over time (Piatt et al. 2007). The use of seabirds as ecological indicators is not without challenge. Seabirds are typically long-lived with k-selected reproductive strategies that favour interannual adult survival over reproductive output (Brooke 2004). They are also highly mobile and forage across dynamic marine habitats on an interannual basis (Rayner et al. 2011; Clay et al. 2018). This tendency to integrate ecological signals over broad temporal and spatial scales means that understanding ecological changes in marine ecosystems through a seabrid lens requires long-term insight to gain understanding of ecological process.

Analyses of stable isotope values from the tissues of coastal seabirds is a useful tool to gain insight into ecological

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change in nearshore marine systems impacted by anthropogenic stressors (Norris et al. 2007; Wiley et al. 2013; Gagne et al. 2018; Rayner et al. 2021). The stable isotope composition of phytoplankton at the base of the food chain (the isotopic baseline) is transferred to higher trophic levels with relatively predictable relationships (Minagawa & Wada 1984; Vander Zanden & Rasmussen 1999). Nitrogen and carbon stable isotope ratios are particularly useful as proxies to investigate the dietary trophic level of coastal seabirds, the contributions of terrestrial versus marine food souces to their diets, and how those diets might change over time (Hobson et al. 1994; Hilton et al. 2006; Rayner et al. 2021). Nitrogen stable isotope values (the ratio of ^{15}N to ^{14}N expressed as $\delta^{15}N$ in ‰ units) are an indicator of dietary trophic level, increasing predictably in food webs by an average of 3–4 ‰ per trophic level. This process occurs as a result of stable isotopic fractionation due to the preferential use and excretion of ^{14}N during protein synthesis (Minagawa & Wada 1984; Hobson et al. 1994; Post 2002). Carbon is less affected by trophic fractionation than nitrogen, increasing by only 0.4–0.8 ‰ per trophic level (Vander Zanden & Rasmussen 1999; Post 2002). This means that bulk carbon stable isotope values (the ratio of ^{13}C to ^{12}C, expressed as $\delta^{13}C$ in ‰ units) can be used to trace the source of carbon to an organism or system, if carbon sources are isotopically distinct within that system (Fry & Sherr 1984; Rounick & Winterbourne 1986; France & Peters 1997). Carbon isotope analysis of tissues from coastal species can thus differentiate between those foraging on resources from mainly terrestrial (nearshore) or marine (offshore) environments (Hobson et al. 1995; Hobson 1999; Blight et al. 2015). Distinct base carbon sources result from different photosynthetic processes in these respective habitats. Terrestrial land plants (including almost all trees and most shrubs) take up atmospheric carbon using the C_3 photosynthetic pathway, which is less efficient at incorporating ^{13}C than the C_4 pathway, producing lower $\delta^{13}C$ values (Fry 2006). In contrast, primary production in coastal marine habitats is dominated by macroalgae and seagrasses, which utilise bicarbonate from seawater as a carbon source using a C_4 photosynthetic pathway, producing higher $\delta^{13}C$ values than C_3 terrestrial plants (Hobson et al. 1994; Hobson 1999; Quillfeldt et al. 2005; Cherel & Hobson 2007). The stable isotope approach is particularly advantageous when contemporary tissue samples are partnered with the same tissues from museum specimens, enabling investigations into ecological time series spanning centuries or more. For example Wiley et al. (2013) used stable isotope analysis of contemporary and subfossil bones of Hawaiian petrel (*Pterodroma sandwichensis*) to show a 3000 year record of dietary stasis followed by a fisheries-induced trophic decline within the last century.

In Aotearoa, the karoro (southern black-backed gull *Larus dominicanus*, hereafter karoro) is an ideal species for investigating the long-term impacts of human-induced environmental change in coastal marine ecosystems. As year-round resident coastal natives and generalist consumers, karoro populations respond strongly to changes in food availability (Fordham 1967; Coulson & Coulson 1993). In the Hauraki Gulf, karoro populations experienced rapid 20th century growth of island-breeding colonies, a trend linked to the availability of anthropogenic food sources such as city refuse dumped at sea (Galbraith et al. 2015). The cessation of this dumping was followed by a decline in breeding bird numbers from the 1980s. However, the historic and contemporary diets of karoro remain unstudied (Galbraith et al. 2015).

This study examines long-term dietary changes in karoro in response to environmental and anthropogenic influences. By analysing contemporary diets from regurgitated pellets and $\delta^{15}N$ and $\delta^{13}C$ values from feathers of contemporary specimens, we investigate patterns of dietary variation. We further examine stable isotope values from feathers of historic museum specimens to track changes in feeding ecology and trophic position over a 109-year period. Additionally, we analyse $\delta^{15}N$ and $\delta^{13}C$ values from contemporary karoro bones and subfossil bones from natural deposits predating the early 13th century human settlement of Aotearoa. This allows us to assess long-term ecological shifts in karoro diets before and after major anthropogenic impacts on the marine environment.

Methods

Pellet sampling

Karoro regurgitate the indigestible remains of food as discrete pellets. Between February and April (2012–2017) intact pellets were collected through opportunistic sampling at breeding colonies on Rangitoto and Tiritiri Matangi Islands (Fig. 1). Rangitoto is approximately 3 km from Auckland's nearest high density urban suburbs, whereas Tiritiri Matangi is more remote, located approximately 15 km from Auckland's northern fringe. Pellets were also collected from within Auckland city centre at Western Springs Park, where karoro roost in large numbers (Gill & West 2016). At all sites, the pellets could be attributed solely to karoro as the breeding colonies and the urban roosting flock were single-species aggregations. Breeding colonies had been abandoned at the time of field collection with the pellets having been deposited during the breeding season from November to January and preserved due to the dehydrating conditions of the rocky sites. Pellets collected at the urban site were recently deposited as they were prone to destruction from reserve maintenance (lawn mowing) and the movement of people within the park. Pellets collected in the field, which were naturally air-dried in situ, were stored in dry zip-lock plastic bags prior to laboratory analysis. Subsequently, pellet contents were analysed visually to identify the frequency with which major food groups were present. This level of analysis is considered appropriate for an indication of non-digestible components of gull diet (Kubetzki & Garthe 2003). Pellet components were categorised as: fish, aquatic arthropod, mollusc, terrestrial arthropod, chicken bone, terrestrial bird (non-chicken small passerine sp.), mammal, plant, and other (i.e. unidentified).

Feather and bone sampling

Karoro feathers (primary coverts) were obtained from skins or mounts held in the collections of Auckland Museum. These specimens were originally collected in the Auckland region with collection dates ranging from 1914 to 1982. In addition, contemporary samples of primary covert feathers were obtained from the Rangitoto nesting colony in 2017 from deceased adult individuals. In total, feathers from 33 individuals were analysed (23 from museum specimens 1914–1982, and ten from wild birds in 2017) (Fig. 1). Contemporary samples of karoro femurs ($n = 8$) were obtained from deceased carcasses of adult gulls collected from the Rangitoto nesting colony in 2017 (Fig. 1). Historical karoro femora were obtained from the Auckland Museum collection, comprising five sub-fossil bones collected North of Auckland

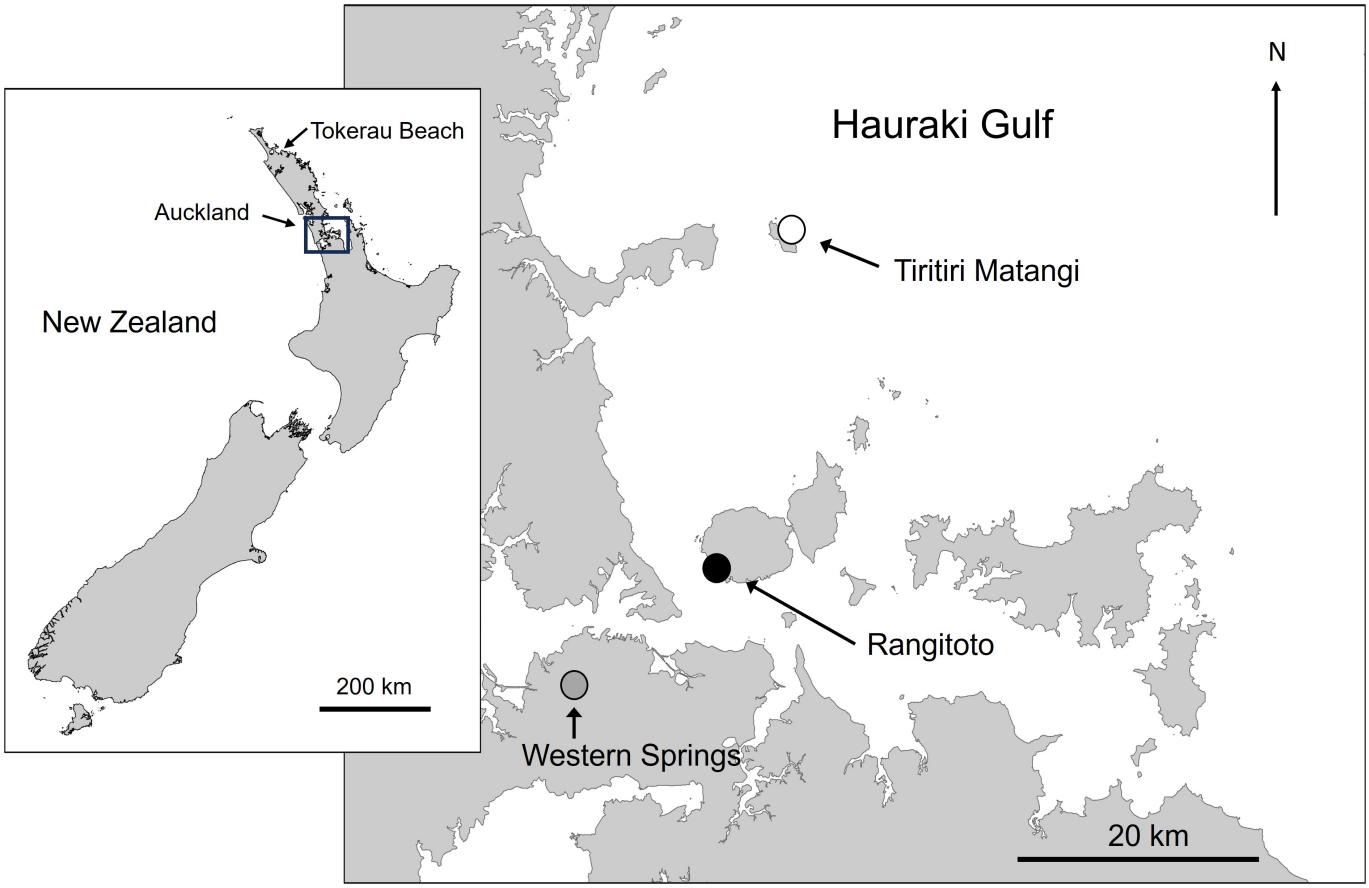

Figure 1. Hauraki Gulf showing the location of two karoro *Larus dominicanus* breeding colonies on Tiritiri Matangi (collection location of $n = 45$ karoro pellets between 2012–2017) and Rangitoto Island (collection location of $n = 314$ karoro pellets between 2012–2017, $n = 10$ primary covert feathers in 2017, and $n = 8$ bones in 2017), a roosting site at Western Springs Park (collection location of $n = 46$ pellets between 2012 and 2017) in Auckland City, and Tokerau Beach where $n = 5$ historic karoro bones from the Auckland Museum were collected from sand dune deposits. Collection locations within the Auckland region of $n = 23$ karoro skins (collected between 1914 and 1982) from the Auckland Museum collection that were sampled for primary covert feathers are not shown on this map. See methods.

at Tokerau Beach (Fig. 1) This location is a recognised paleo fauna site holding Holocene bone deposits of extant and extinct Aotearoa | New Zealand avifauna dating back to 6500 years BP (Millener 1981). To confirm the age of bones, radiocarbon dating was conducted as outlined below. See Appendix S1 in Supplementary Material for catalogue numbers of Auckland Museum specimens.

Feather processing and bone collagen extraction methods

Feathers were washed in 70% ethanol, then rinsed three times in distilled de-ionised water (DDW) to remove contaminants before oven drying at 60°C. Using clean scissors, vanes were removed from each side of the feather shaft and were then cut into very small fragments to homogenise the sample before sub-sampling for stable isotope analysis. Collagen was extracted from whole bone fragments, as it is a protein that reflects dietary composition, unlike the mineral bone component that incorporates carbon from a broader range of sources. Surface organic debris was cleaned off the bone using a new metal scalpel (previously cleaned with 70% ethanol) and fine grade sandpaper following recommendations of Ambrose (1990) and Sealy et al. (2014). Samples were rinsed with DDW, sonicated in DDW to remove any remaining loose fragments, and dried off with 70% ethanol (Ambrose 1990). Small chunks or shards of the bone sample were removed using a scalpel. Preparing small pieces of bone for analysis is better than generating a powder sample, as the structure remains better preserved, sample loss during the extraction procedure is minimised, and a higher yield of collagen is obtained (Collins & Galley 1998; Jørkov et al. 2007). For trial tests that we ran on 50 mg dry weight of powdered bone material, we obtained a collagen yield of 15%, compared to 50 mg of shards which yielded 21% collagen. For the lipid extraction stage, getting solvents on and off powdered samples is also more difficult (P. Koch, University of California, pers. comm.). The bone sub-samples were stored in an airtight container with desiccant until ready to process. Using a six decimal place balance, approximately 200 mg of bone were weighed for each bone specimen to provide sufficient material for stable isotope analysis and ^{14}C dating.

The bone collagen extraction method outlined below is a modification of Sealy et al. (2014) and Jørkov et al. (2007). Samples were placed in individually labelled, 15 mL glass vials with Teflon®-lined lids for decalcification to remove carbonate preserved within the hydroxyapatite mineral of the bone. Approximately 10 mL of 0.5 N hydrochloric acid (HCl) was added to the sample, which was agitated for about 10 minutes in a sonicator, then refrigerated for 10 days until there was no further release of carbon dioxide (CO_2). The acid

was changed every other day. The exact concentration of the acid is not critical. Pestle (2010) has shown that variations in acid concentration from 0.05 to 0.2M have no effect on $\delta^{13}C$ and $\delta^{15}N$ values, and the Max Planck protocol uses 1M HCl with no change to stable isotope values (Sealy et al. 2014). However, it is important to avoid heating the sample as this denatures the collagen. Decalcification was complete once the sample had become translucent and could be easily bent. HCl was then removed from the vials using a pipette and each sample was rinsed five times with DDW until a neutral pH was achieved.

Since lipids yield $\delta^{13}C$ values that are lower than other tissues, it is important to remove all lipids from collagen samples prior to stable isotope analysis. Samples were lipid-extracted in a fume hood, following the original method of Bligh and Dyer (1959), with the full process taking four days. Approximately 10 mL of an extraction mixture of chloroform, methanol, and DDW in the ratio of 1.0:2.0:0.8, respectively was added to each sample, which was then sonicated for 30 minutes. About 2 mL of DDW was then added to each solution to produce an upper layer of methanol and water and a milky-looking bottom layer of chloroform, containing the lipids. Lipids were poured off the sample and disposed of safely, and then this process was repeated until the chloroform lipid phase was clear. Following an adaptation of Jørkov et al. (2007) and Sealy et al. (2014) the sample was then rinsed with a polar solvent, acetone (this step is necessary for ^{14}C analysis), then rinsed three times with DDW and placed in DDW water for 24 hours. The water was then tested for a neutral pH. If the pH was not neutral, the previous process was repeated until a neutral water pH was obtained. The sample was then removed and further rinsed three times in DDW before being freeze-dried overnight. For each bone collagen sample, 0.7–0.8 mg of dried material was weighed out into a tin capsule and sealed for stable isotope analysis.

Mass spectrometry radiocarbon and stable isotope analysis methods

Extracted bone collagen samples were ^{14}C-dated at the Rafter Radiocarbon Laboratory at the Institute of Geological and Nuclear Sciences Ltd. (GNS Science) Wellington. Samples were loaded into individual quartz tubes with silver wire and copper oxide. These tubes were evacuated to remove atmospheric contamination and flame-sealed. The sealed samples were then combusted at 900°C and the CO_2 produced from the samples was purified. The sample CO_2 was then converted to graphite by reduction with hydrogen over an iron catalyst and measured using a 0.5 MV XCAMS accelerator mass spectrometer. Radiocarbon calibration was performed following Reimer et al. (2016) using the Marine20 calibration curve (Heaton et al. 2020).

Carbon and nitrogen stable isotope analyses on both feathers and extracted bone collagen samples were carried out on a DELTA V Plus (Thermo Fisher Scientific, Bremen, Germany) continuous flow, isotope ratio mass spectrometer (IRMS) at the National Institute of Water & Atmospheric Research Ltd. (NIWA) Environmental and Ecological Stable Isotope Analytical Facility in Wellington. Samples were introduced via a MAS200 autosampler to a Flash 2000 elemental analyser (Thermo Fisher Scientific) and were combusted at 1020°C in a flow of oxygen and helium carrier gas. Oxides of nitrogen were converted to nitrogen (N_2) gas in a reduction furnace at 650°C. Nitrogen and CO_2 gases were separated on a Porapak Q gas chromatograph column before being introduced to the IRMS detector via an open split Conflo IV interface (Thermo Fisher Scientific) with every sample analysis. The software ISODAT (Thermo Fisher Scientific) was used to calculate $\delta^{15}N$ values against atmospheric air, and $\delta^{13}C$ values against the CO_2 reference gas relative to the National Bureau of Standards 19-calcite (NBS19-calcite) standard (calibrated against Vienna Pee Dee Belemnite), correcting for ^{17}O. Sample $\delta^{15}N$ values were two-point normalised using stable isotope data from the daily analysis of National Institute of Standards and Technology NIST 8573 USGS40 L-glutamic acid and NIST 8548 IAEA-N2 ammonium sulphate (Paul et al. 2007). Sample $\delta^{13}C$ values were two-point normalised using stable isotope data from the daily analysis of NIST 8573 USG40 L-glutamic acid and NIST 8542 IAEA-CH-6 sucrose. Percent C and % N values were calculated relative to a solid laboratory reference standard of DL-leucine (DL-2-amino-4-methylpentanoic acid, $C_6H_{13}NO_2$, lot 127H1084, Sigma, Australia) at the beginning of each run. Repeat analysis of United States Geological Sciences USGS65 glycine ($n = 7$) produced data accurate to better than 0.30 ‰ for $\delta^{15}N$ and $\delta^{13}C$. Repeat analysis of the laboratory reference standard DL-leucine ($n = 26$) produced a precision of 0.13 ‰ for $\delta^{15}N$ and 0.08 ‰ for $\delta^{13}C$. Reproducibility of replicate collagen extractions of bone shard samples were 0.54 ‰ for $\delta^{15}N$ and 0.13 ‰ for $\delta^{13}C$.

Statistical analysis

The proportion of karoro pellets containing marine or terrestrial food sources were compared between the city roosting site at Western Springs and at breeding sites on Rangitoto and Tiritiri Matangi using contingency analysis with two predictor variables (site: Western Springs, Rangitoto, or Tiritiri Matangi; and food source: terrestrial and marine). The burning of fossil fuels since the industrial revolution has caused a decrease in $\delta^{13}C$ values in atmospheric and ocean ecosystems from phytoplankton to top predators, known as the "Suess Effect" (Keeling et al. 1979). Before statistical tests were carried out, to correctly interpret changes in $\delta^{13}C$ values of the gulls over time, we corrected each of our measured feather $\delta^{13}C$ values by subtracting a year and site-specific Suess-effect factor for $\delta^{13}C$, following the process described by Hilton et al. (2006; Appendix S1) and Quillfeldt et al. (2010). Linear regression analysis was then used to test for long-term changes in the $\delta^{15}N$ and $\delta^{13}C$ values of feathers.

Comparisons between the $\delta^{15}N$ and $\delta^{13}C$ values of contemporary bone collagen and feathers (femora and feathers collected in 2017), historic feathers (collected between 1914 and 1982), and sub-fossil bone collagen (carbon-dated sub-fossil femurs) were made by first scaling all feather stable isotope values to bone values using tissue-specific fractionation factors. These factors, developed by Hobson & Clark (1992) in experiments on a congeneric species (*Larus delawarensis*), involve adding 0.1 ‰ to $\delta^{15}N$ values and 2.2 ‰ to $\delta^{13}C$ values for each feather data point. Bone collagen in birds reflects dietary signals integrated over periods of months to a few years, depending on metabolic rates and bone turnover, whilst the composition of feathers represents the diet during the short period of feather growth. This temporal difference necessitates the use of tissue-specific fractionation factors to align feather stable isotope values with bone values, enabling valid comparisons of trophic and dietary patterns across tissues and time periods (Hobson & Clark 1992).

Following tests for normality (Shapiro-Wilk) and homogeneity of variance (Levene's tests), nonparametric (Kruskal-Wallis) tests were used to test for differences between

$\delta^{15}N$ and $\delta^{13}C$ values of the four groups. Pairwise comparisons were conducted using Dwass-Steel-Critchlow-Fligner (DSCF) tests, an alternative to the Bonferroni correction, to protect error rate against multiple comparisons. All analyses were conducted using JMP®, Version 15.0.0 (SAS Institute), with a level of significance set at $\alpha = 0.05$.

Results

Pellet sample composition

The composition of pellets was diverse, with pellets from all sites containing a range of food types including fish bone, marine arthropods, mollusc shell, passerine leg and wing bones, chicken leg bones, and small mammal bones (*Rattus* spp. and *Mus musculus*) (Table 1). However, the composition of pellets differed significantly between the three sites (X^2 (DF = 2, n = 614) = 30.10, P < 0.0001; Figs. 2 & 3). Pellets from the Western Springs roosting site contained the broadest range of dietary groups. This was the only site where pellets contained terrestrial arthropods, plants, and inorganic material (glass and rocks). Pellets sampled from Rangitoto were similar in composition to those from Western Springs in terms of terrestrial versus marine food sources. Rangitoto was the only site where pellets contained the remnants of large mammal bones, predominantly the broken fragments of lamb bone. The composition of pellets from Tiritiri Matangi was notably different from those sampled from Western Springs and Rangitoto, containing a higher proportion of marine-derived foods, particularly fish bone and mollusc shell.

Stable isotope values of feather and bone samples

The feather $\delta^{15}N$ and $\delta^{13}C$ values of karoro declined significantly by 3.09 ‰ and 2.35 ‰, respectively, between 1914

Table 1. Count (*n*) and percentage of dietary groups found within karoro pellets at two breeding colonies on Rangitoto and Tiritiri Matangi and at an urban roosting site at Western Springs Park.

Dietary Group	Rangitoto		Tiritiri Matangi		Western Springs	
	n	%	*n*	%	*n*	%
Fish	89	28	26	58	10	22
Marine arthropod	43	14	6	13	15	33
Mollusc	58	18	27	60	6	13
Echinoderm	1	0	0	0	0	0
Terrestrial arthropod	0	0	0	0	14	30
Passerine bone	42	13	18	40	22	48
Chicken bone	103	33	3	7	8	17
Small mammal bone	33	11	1	2	1	2
Large mammal bone	72	23	0	0	0	0
Plants	0	0	0	0	12	26
Stone and glass	1	0	0	0	3	7
Number of pellets	314		45		46	

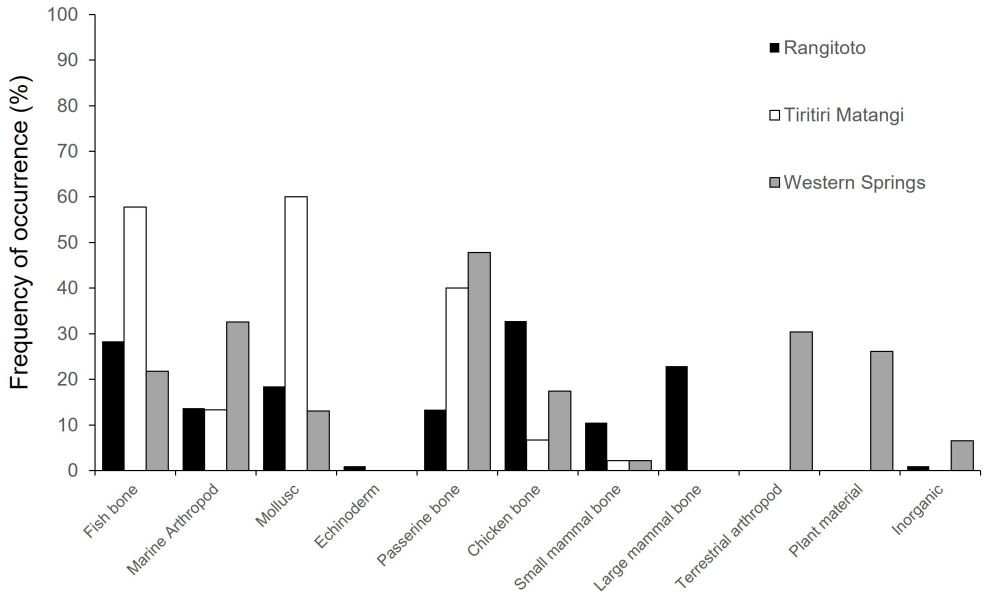

Figure 2. Main dietary groups identified from contents of regurgitated pellets from karoro *Larus dominicanus* at two breeding sites (Rangitoto: n = 314; Tiritiri Matangi: n = 45) and one roosting site (Western Springs: n = 46) in the Auckland region.

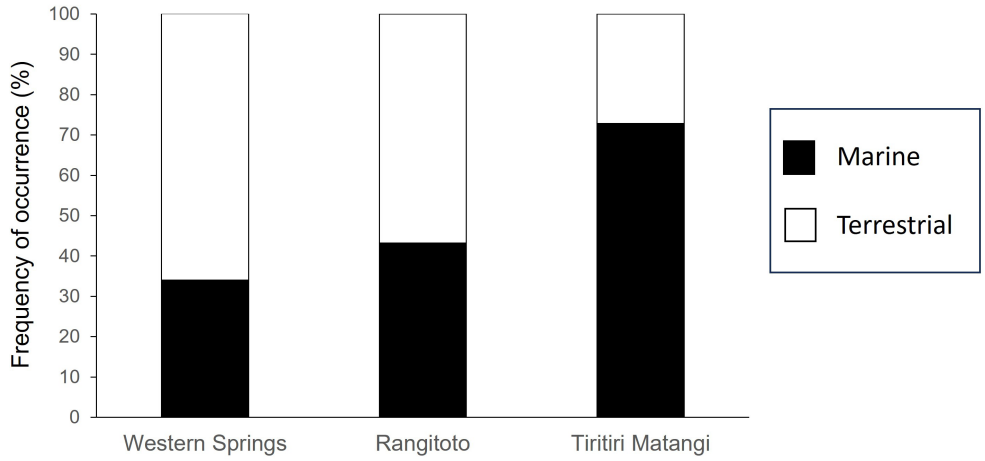

Figure 3. Marine and terrestrial food source composition of karoro *Larus dominicanus* pellets collected at three sites in the Auckland region.

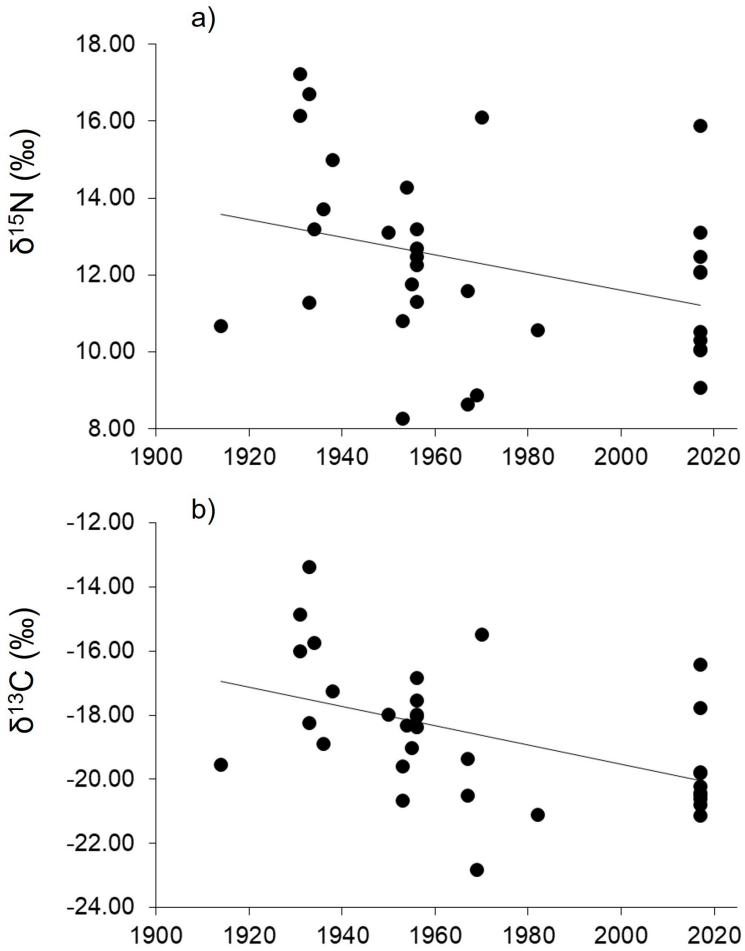

Figure 4. Interannual variation in stable isotope values of feathers from karoro *Larus dominicanus* (n = 33) breeding in Hauraki Gulf over a 103-year period (1914–2017) for a) $\delta^{15}N$ ($y = -0.0228x + 57.303$; $R^2 = 0.13$) and b) $\delta^{13}C$ ($y = -0.03x + 40.475$; $R^2 = 0.24$). Linear regression fit shown as straight line.

and 2017 ($\delta^{15}N$: F = 3.9, DF = 32, P = 0.05; $\delta^{13}C$: F = 9.6, DF = 32, P < 0.01; Fig. 4). The five radiocarbon dates for historic karoro bone collagen from Tokerau Beach provided calibrated ages of between 1596 (AD 354) and 4571 (2621 BC) years before present (average age of 3826 B.P.; 1876 BC) (Table 2). Nitrogen and carbon stable isotope values differed significantly between sub-fossil bone collagen, contemporary bone collagen and feather samples collected in 2017, and historic feathers collected between 1914 and 1982 ($\delta^{15}N$ Kruskal Wallis X^2 (DF = 3, n = 47) = 11.23, P < 0.01; $\delta^{13}C$ Kruskal Wallis X^2 (DF = 2, n = 47) = 20.61, P < 0.0001) (Fig. 5).

The $\delta^{15}N$ values of contemporary bone collagen ($\delta^{15}N$ 12.16 ± 2.92 ‰), contemporary feather ($\delta^{15}N$ 11.65 ± 1.99 ‰), and historic feather ($\delta^{15}N$ 12.72 ± 2.01 ‰) samples did not differ from each other (DSCF P values all > 0. 40) but were lower than those of historic bone collagen ($\delta^{15}N$ 16.17 ± 1.10‰;

Table 2. Results of nitrogen and carbon stable isotope and radiocarbon analyses of karoro bone from Tokerau Beach and Rangitoto Island.

Site	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	Radiocarbon age B.P. collection date
Tokerau Beach	14.71	−10.41	1596
Tokerau Beach	17.53	−10.48	2779
Tokerau Beach	15.61	−12.18	3153
Tokerau Beach	16.95	−11.88	3753
Tokerau Beach	16.10	−11.21	4571
Rangitoto	13.61	−17.90	2017
Rangitoto	9.80	−20.56	2017
Rangitoto	13.70	−16.44	2017
Rangitoto	10.23	−19.50	2017
Rangitoto	9.76	−19.37	2017
Rangitoto	13.94	−17.02	2017
Rangitoto	13.62	−17.74	2017
Rangitoto	10.90	−18.58	2017

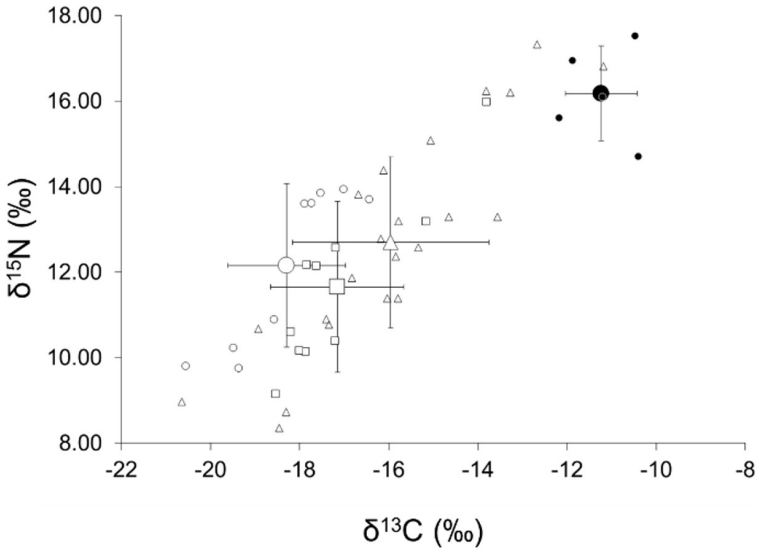

Figure 5. Nitrogen and carbon stable isotope values of contemporary karoro *Larus dominicanus* bone collagen (unfilled circles, mean is the larger circle with error bars; 1 standard deviation) and feathers (unfilled squares, mean is the larger square with error bars; 1 standard deviation) collected from Rangitoto Island in 2017, historic feathers (unfilled triangles, mean is the larger triangle with error bars; 1 standard deviation) collected between 1914 and 1982, and sub-fossil bone collagen (1596–4571 years B.P.) from Tokerau Beach (filled circles, mean is the larger filled circle with error bars; 1 standard deviation). Feather nitrogen and carbon stable isotope values were scaled by tissue-specific fractionation factors developed by Hobson & Clark (1992) in experiments on a congeneric species, the ring-billed gull *Larus delawerensis*.

DSCF tests: contemporary bone collagen $Z = 2.93$, $P < 0.01$; contemporary feather $Z = -2.76$, $P < 0.01$; historic feather $Z = -2.58$, $P < 0.05$; Fig. 5). Similarly, $\delta^{13}C$ values of contemporary bone collagen ($\delta^{13}C$ −18.29 ± 1.32 ‰), contemporary feather ($\delta^{13}C$ −17.15 ± 1.49 ‰), and historic feather ($\delta^{13}C$ −15.96 ± 2.20 ‰) samples did not differ from each other (DSCF Z P all > 0. 20) but were lower than those of historic collagen ($\delta^{13}C$ −11.23 ± 0.80 ‰; DSCF tests: contemporary bone collagen $Z = 2.93$, $P < 0.01$; contemporary feather $Z = -3.00$, $P < 0.01$; historic feather $Z = -3.24$, $P < 0.01$; Fig. 5).

Discussion

Contemporary diet

Karoro regurgitate the indigestible remains of food as discrete pellets. Although there is debate as to the efficacy of pellets as an indicator of the complete diet of gulls (Kubetzki & Garthe 2003; Barrett et al. 2007), there is recognition that pellets can provide an indication of the relative importance of prey types (Spaans 1971; Carss et al. 1997; Votier et al. 2003). This method was also particularly favoured because of the potential to collect large numbers of pellets through a non-invasive process (Barrett et al. 2007). It was also seen as a useful method to complement and potentially validate integrated dietary information gleaned from stable isotope analyses.

Pellets from the inner-city roosting site at Western Springs had the broadest range of food types, incorporating marine as well as terrestrial food resources such as plant material and terrestrial arthropods. Birds from island-based breeding colonies had higher proportions of marine foods, particularly fish bone and mollusc shell, reflecting their maritime feeding environments. Interestingly, pellets from all sites contained the bones of small passerines, chicken, and mammals such as rodents and sheep. These food sources are likely scavenged from urban environments, as roadkill (small passerines and rodents) or from food refuse (chicken and lamb). Except for passerines, none of these foods are naturally present at the Rangitoto and Tiritiri Matangi colonies, which are free

of rodents and farmed chicken or sheep. We also noted the regular occurrence of large chicken femora and tibiotarsi on the surface surrounding karoro nests at the Rangitoto breeding colony. These bones most likely come from regurgitated pellets that have been degraded by the weather over time. Our data are consistent with previous studies indicating that karoro and other large gull species are opportunistic foragers, incorporating human food waste in their diet at roosting and breeding sites close to urban environments (Coulson et al. 1987; Coulson & Coulson 1993; Ludynia et al. 2005; Reusch et al. 2025). The increasing presence of marine food sources at the two island breeding sites likely reflects easier access to marine prey for the birds (including recreational fishing waste) and the greater distance of their breeding sites from the human food waste sources in Auckland city and environs than at the Western Springs roosting site. Other studies of this globally distributed generalist species from Canada and South America have shown that where urban food sources are limited, diet is typically dominated by fish, often common discards from fisheries, and benthic prey such as intertidal marine bivalves (Silva-Costa & Bugoni 2013; Marinao et al. 2019).

The $\delta^{15}N$ and $\delta^{13}C$ values of karoro feathers collected on Rangitoto in 2017 indicate a lower trophic position and differing foraging habitat compared with the feathers of five other gulf resident seabirds analysed by Rayner et al. (2021) during the same period (kāruhiruhi | pied shag *Phalacrocorax varius*, kawau tikitiki | spotted shag *Phalacrocorax punctatus*, kororā | little penguin *Eudyptula minor*, tara | white-fronted tern *Sterna striata*, and tarāpunga | red-billed gull *Chroicocephalus novaehollandiae*) (Fig. 6; Rayner et al. 2021). Feather $\delta^{15}N$ values were 1.3 ‰ below those of fish prey species analysed by Rayner et al. (2021) suggesting that although fish prey is featured in pellets, they may not dominate the diet during moult when feathers are regrown. Conversely feather $\delta^{15}N$ values were 3.0 ‰ above those of marine arthropods (Enaupli), suggesting a likely role for marine invertebrates in the diet. The dietary role of marine invertebrates was indicated also by pellet analysis and averaged trophic level enrichments factors (3–5 ‰; Mizutani et al. 1992; Post 2002). Interestingly, karoro $\delta^{15}N$ feather values were 1.1 ‰ below those of tarāpunga, a species known to target marine invertebrates at sea in the intertidal zone and to consume terrestrially-based anthropogenic food sources with lower $\delta^{15}N$ and $\delta^{13}C$ values (Blight et al. 2015; Rayner et al. 2021). Combined pellet and stable isotope data, as well as comparisons with other Hauraki Gulf seabirds of known foraging ecology analysed in the same year, suggest present-day karoro in the gulf have a broad diet including fish and marine invertebrates and anthropogenic and/or terrestrially-derived food sources (predominantly terrestrial vertebrates and invertebrates). Further research using stable isotope mixing models incorporating a broad range of prey sources would be required to draw more informed conclusions.

Dietary change over time

Our analysis of karoro feathers from 1914–2017 indicated a significant decline in $\delta^{15}N$ and $\delta^{13}C$ values of 2.4 ‰ and 3.1 ‰ respectively over 103 years. The decline in $\delta^{15}N$ values represents close to one trophic level (Mizutani et al. 1992; Post 2002; Cherel et al. 2005) and is similar to trends observed for other large gulls including great black-backed gull *Larus marinus* (2.3 ‰) and glaucous-winged gull *Larus glaucescens* (3.8 ‰), where human impacts have reduced fish abundance and increased birds' reliance on marine invertebrates and terrestrial garbage-based diets (Farmer & Leonard 2011; Blight et al. 2015). In the Hauraki Gulf, Rayner et al. (2021) found no evidence for a decline in the feather $\delta^{15}N$ values of tarāpunga over the 20th century and it appears that, despite an increased availability of urban-based food sources, this smaller taxon has maintained a unique feeding niche to karoro, with diets dominated by marine and intertidal invertebrates.

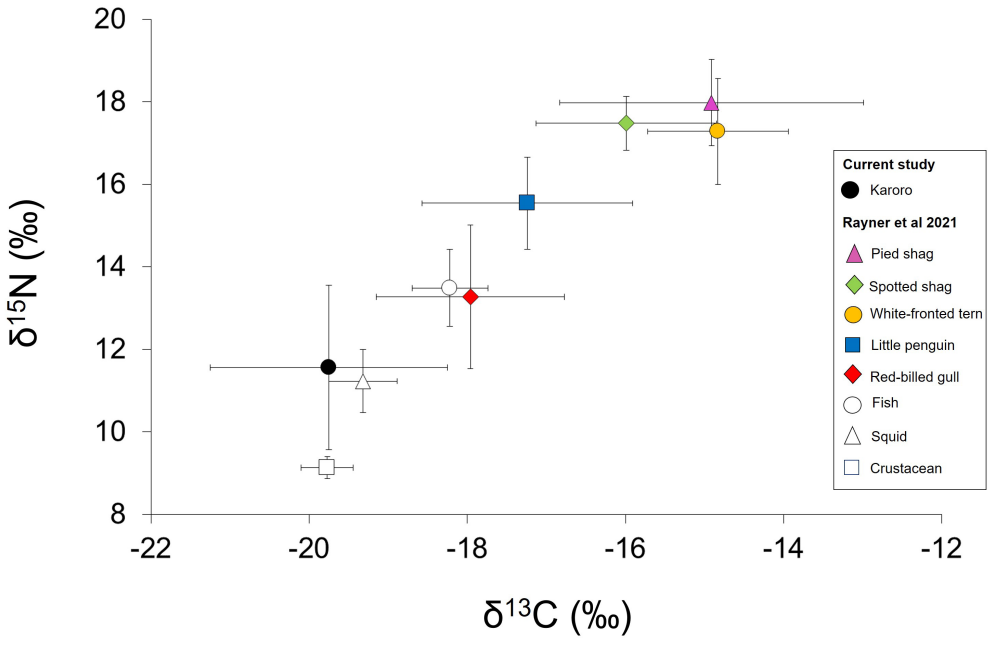

Figure 6. Nitrogen and carbon stable isotope values of feathers collected from karoro *Larus dominicanus* at the Rangitoto breeding colony in 2017 (filled black circle; current study) in comparison with those of pied shag *Phalacrocorax varius*, spotted shag *Phalacrocorax punctatus*, white-fronted tern *Sterna striata*, little penguin *Eudyptula minor*, and red-billed gull *Larus novaehollandiae* collected in the inner Hauraki Gulf during the same period (2010–2019) as well as muscle tissue from Hauraki Gulf fish, squid, and euphausiid crustaceans collected between 2017–2019 (all other symbols; data from Rayner et al. 2021). Error bars represent standard deviations.

The decline in $\delta^{13}C$ values of 3.10 ‰ in karoro was similar to the decline of 2.3 ‰ observed for glaucous-winged gull (Blight et al. 2015), but not to trends for great black-backed gull, which showed no significant change over the 20th century (Farmer & Leonard 2011). In the Hauraki Gulf, Rayner et al. (2021) found no significant decrease in $\delta^{13}C$ values of tarāpunga, but significant declines in values for three other species: kāruhiruhi, kawau tikitiki, and kororā. They concluded that these declines were linked to anthropogenic disturbance driving a shift in foraging habitat to more offshore environments with lower $\delta^{13}C$ values. An alternative hypothesis, that lower $\delta^{13}C$ values could be linked to shifts in phytoplankton community structure and reduction in primary productivity, was considered unlikely as elevated nutrient inputs have increased primary productivity in the inner Hauraki Gulf (Chang et al. 2003; Seers & Shears 2015; Zeldis & Swaney 2018), which would likely produce higher $\delta^{13}C$ values. Moreover, a separate analysis showed no significant change in $\delta^{13}C$ values of forage fish (another food web component), over time (Rayner et al. 2021). The lack of change in gulf environmental baselines over the 20th century (Rayner et al. 2021) and the fact that contemporary karoro extensively exploit urban habitats for food (current study), suggest the decline in karoro $\delta^{15}N$ and $\delta^{13}C$ values since the early 1900s is a result of a decrease in the marine contribution to the diet and increasing reliance on terrestrially-based food sources as observed in other gull taxa (Blight et al. 2015). Diet change of karoro through the 20th century also correlates with the documented decline in the availability of marine prey in the Hauraki Gulf, in particular forage fish which have been reduced to 40% of their prehistoric biomass (Pinkerton et al. 2015).

Analysis of karoro bones pre-dating the arrival of humans in Aotearoa provides an intriguing insight into the trophic ecology of the species prior to anthropogenic ecosystem disturbance. Both $\delta^{15}N$ and $\delta^{13}C$ historical bone collagen values were significantly higher than those of contemporary bone and feather samples, suggesting karoro had a trophic level similar to piscivorous species such as little penguin (kororā) and shags in the Hauraki Gulf (Rayner et al. 2021). Most likely, these ancient karoro were predators and scavengers within the coastal marine food web, consuming higher trophic level food sources such as fish and the remains of marine mammals, including cetaceans and pakake | New Zealand sea lions (*Phocarctos hookeri*). The latter had extensive rookeries in the region prior to human arrival, including at Doubtless Bay (Gill 1998; Collins et al. 2014). An alternative explanation , that climate change may have influenced $\delta^{15}N$ and $\delta^{13}C$ values, is unlikely given that an increase in oceanic water temperatures elevates primary productivity and results in higher stable isotope values, particularly for carbon (Fry & Sherr 1984). This further underscores the pronounced effect of a higher trophic level for historical karoro.

Contemporary karoro in the Hauraki Gulf exhibit flexibility in a diet that includes marine vertebrates and invertebrates and anthropogenic and/or terrestrially-derived food sources. There is some evidence that the proximity of breeding colonies to city foraging habitats can influence the degree to which terrestrial foods dominate the diet, with the more distant Tiritiri Matangi breeding colony showing a higher proportion of marine foods in pellet analyses. Hauraki Gulf karoro $\delta^{15}N$ and $\delta^{13}C$ data from feathers spanning the past century indicate a shift from more marine to more terrestrial-based diets, likely driven by both the decline in marine prey sources and the increased availability of food sources from a growing city. Stable isotope values from ancient karoro bones indicate that prior to human arrival in Aotearoa the trophic ecology of karoro was that of a coastal marine predator and scavenger.

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Additional information and declarations

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Author contributions: MG, MR and DF conceived and designed this study and MR, MG and SB carried out the data collection and analysis. MR wrote the manuscript with editorial contributions from SB and DF. MG initiated a first rough draft of the manuscript, but did not contribute to later versions due to his death in 2023.

References

Ambrose SH 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis. Journal of Archaeological Science 17: 431–451.

Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW, Furness RW, Garthe S, Hüppop O, Leopold MF, Montevecchi WA, Veit RR 2007. Diet studies of seabirds: a review and recommendations. ICES Journal of Marine Science 64: 1675–1691.

Bligh EG, Dyer WJ 1959. A rapid method of total lipid extraction and purification. Canadian Journal of Biochemistry and Physiology 37: 911–917.

Blight LK, Hobson KA, Kyser TK, Arcese P 2015. Changing gull diet in a changing world: A 150-year stable isotope (δ13C, δ15N) record from feathers collected in the Pacific Northwest of North America. Global Change Biology 21: 1497–1507.

Brooke MDL 2004. Albatrosses and petrels across the world, Oxford, Oxford University Press. 499 p.

Carss D, Bevan R, Feltham M, Grade N, Granadeiro J, Grémillet D, Gromadzka J, Harari Y, Holden T, Keller Y, Lariccia G, Mantovani R, McCarthy T, Mellin M, Wilson B 1997. Techniques for assessing cormorant diet and food

intake: towards a consensus view. Proceedings of the 4th conference on cormorants. Supplemento Alle Richerche di Biologia della Selvaggina XXVI. Pp. 197–230.
Chang FH, Zeldis J, Gall M, Hall J 2003. Seasonal and spatial variation of phytoplankton assemblages, biomass and cell size from spring to summer across the north-eastern New Zealand continental shelf. Journal of Plankton Research 25: 737–758.
Cherel Y, Hobson KAH 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Marine Ecology Progress Series 329: 281–287.
Cherel Y, Hobson K, Weimerskirch H 2005. Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. Oecologia 145: 533–540.
Clay TA, Pearmain EJ, McGill RAR, Manica A, Phillips RA 2018. Age-related variation in non-breeding foraging behaviour and carry-over effects on fitness in an extremely long-lived bird. Functional Ecology 32: 1832–1846.
Collins CJ, Rawlence NJ, Worthy TH, Scofield RP, Tennyson AJD, Smith I, Knapp M, Waters JM 2014. Pre-human New Zealand sea lion (*Phocarctos hookeri*) rookeries on mainland New Zealand. Journal of the Royal Society of New Zealand 44: 828761.
Collins M, Galley P 1998. Towards an optimal method of archaeological collagen extraction: The influence of pH and grinding. Ancient Biomolecules 2: 209–222.
Coulson JC, Butterfield J, Duncan N, Thomas C 1987. Use of refuse tips by adult British herring gulls *Larus argentatus* during the week. Journal of Applied Ecology 24: 789–800.
Coulson R, Coulson G 1993. Diets of the Pacific gull *Larus pacificus* and the kelp gull *Larus dominicanus* in Tasmania. Emu - Austral Ornithology 93: 50–53.
Crain CM, Halpern BS, Beck MW, Kappel, CV 2009. Understanding and managing human threats to the coastal marine environment. Annals of the New York Academy of Sciences 1162: 39–62.
Farmer RG, Leonard ML 2011. Long-term feeding ecology of great black-backed gulls (*Larus marinus*) in the Northwest Atlantic: 110 years of feather isotope data. Canadian Journal of Zoology 89: 123–133.
Fordham RA 1967. History and status of the dominican gull in Wellington. Notornis 14: 144–153.
France RL, Peters RH 1997. Ecosystem differences in the trophic enrichment of C-13 in aquatic food webs. Canadian Journal of Fisheries and Aquatic Sciences 54:1255–1258.
Fry B 2006. Stable isotope ecology. New York, Springer. 308 p.
Fry B, Sher EB 1984. δ13C measurements as indicators of carbon flow in marine and freshwater ecosystems. Contributions in Marine Science 27: 13–47.
Hauraki Gulf Forum 2020. State of our Gulf 2020. Auckland, Hauraki Gulf Forum. 208 p.
Gagne TO, Hyrenbach KD, Hagemann ME, Van Houtan KS 2018. Trophic signatures of seabirds suggest shifts in oceanic ecosystems. Science Advances 4: eaao3946.
Galbraith M, Krzyosiak J, Aguilar G, Jones G, Oliver R 2015. Changes in the breeding status of the southern black-backed gull (*Larus dominicanus*) colonies on Rangitoto Island (Hauraki Gulf, New Zealand). Notornis 62: 192–201.
Gill B 1998. Prehistoric breeding sites of New Zealand sea lions (*Phocarctos hookeri, Carnivora: Otariidae*) at North Cape. Records of the Auckland Museum: 55–64.
Gill B, West RC 2016. Counts of waterbirds at Western Springs Lake, Auckland, New Zealand. Notornis 63: 142–151.
Heaton TJ, Köhler P, Butzin M, Bard E, Reimer RW, Austin WE, Ramsey CB, Grootes PM, Hughen KA, Kromer B 2020. Marine20—the marine radiocarbon age calibration curve (0–55,000 cal BP). Radiocarbon 62: 779–820.
Hilton MG, Thompson DR, Sagar PM, Cuthbert RJ, Cherel Y, Bury SJ 2006. A stable isotopic investigation into the causes of decline in a sub-Antarctic predator, the rockhopper penguin *Eudyptes chrysocome*. Global Change Biology 12: 611–625.
Hobson KA 1999. Tracing origins and migration of wildlife using stable isotopes: a review. Oecologia 120: 314–326.
Hobson KA, Clark RG 1992. Assessing avian diets using stable isotopes 1: turnover of 13C in tissues. Condor 94: 181–188.
Hobson KA, Piatt JF, Pitocchelli J 1994. Using stable isotopes to determine seabird trophic relationships. Journal of Animal Ecology 63: 786–798.
Hobson KA, Ambrose WG, Renaud PE 1995. Sources of primary production, benthic-pelagic coupling, and trophic relationships within the Northeast Water Polynya: insights from δ13C and δ15N analysis. Marine Ecology Progress Series, 128: 1–10.
Jørkov MLS, Heinemeier J, Lynnerup N 2007. Evaluating bone collagen extraction methods for stable isotope analysis in dietary studies. Journal of Archaeological Science 34: 1824–1829.
Keeling CD, Mook WG, Tans PP 1979. Recent trends in the 13C/12C ratio of atmospheric carbon dioxide. Nature 277: 121–123.
Kubetzki U, Garthe S 2003. Distribution, diet and habitat selection by four sympatrically breeding gull species in the south-eastern North Sea. Marine Biology 143: 199–207.
Ludynia K, Stefan G, Guillermo L 2005. Seasonal and regional variation in the diet of the kelp gull in Northern Chile. Waterbirds: The International Journal of Waterbird Biology 28: 359–365.
Marinao C, Suárez N, Yorio P. 2019. Trophic interactions between the kelp gull (*Larus dominicanus*) and royal and cayenne terns (*Thalasseus maximus maximus* and *Thalasseus sandvicensis eurygnathus*, respectively) in a human-modified environment. Canadian Journal of Zoology 97: 904–913.
Millener PR 1981. Geology of Auckland. Unpublished PhD thesis, University of Auckland, Auckland, New Zealand.
Minagawa M, Wada E 1984. Stepwise enrichment of 15N along food chains: Further evidence and the relation between δ15N and animal age. Geochimica et Cosmochimica Acta 48: 1135–1140.
Mizutani H, Fukuda M, Kabaya Y 1992. 13C and 15N enrichment factors of feathers of 11 species of adult birds. Ecology 73: 1391–1395.
Norris DR, Arcese P, Priekshot D, Bertram DF, Kyser TK 2007. Diet reconstruction and historic population dynamics in a threatened seabird. Journal of Applied Ecology 44: 875–884.
Paul D, Skrzypek G, Fórizs I 2007. Normalization of measured stable isotopic compositions to isotope reference scales - a review. Rapid Communications in Mass Spectrometry 21: 3006–3014.
Pestle WJ 2010. Chemical, elemental, and isotopic effects of acid concentration and treatment duration on ancient bone collagen: an exploratory study. Journal of Archaeological Science 37: 3124–3128.
Piatt IJF, Sydeman WJ, Wiese F 2007. Introduction: seabirds as indicators of marine ecosystems. Marine Ecology

Progress Series 352: 199–204.
Pinkerton M, Macdiarmid A, Beaumont J, Bradford-Grieve J, Francis M, Jones E, Lalas C, Lundquist C, McKenzie A, Nodder SD, Paul L, Stenton-Dozey J, Thompson D, Zeldis J 2015. Changes to the food-web of the Hauraki Gulf during the period of human occupation: a mass-balance model approach. New Zealand Aquatic Environment and Biodiversity Report No. 160. Ministry of Primary Industries, Wellington. 349 p.
Post DM 2002. Using stable isotopes to estimate trophic position: Models, methods, and assumptions. Ecology. 83(3): 703–718.
Quillfeldt P, McGill RA, Furness RW 2005. Diet and foraging areas of Southern Ocean seabirds and their prey inferred from stable isotopes: review and case study of Wilson's storm-petrel. Marine Ecology Progress Series 295: 295–304.
Quillfeldt P, Masello J, McGill R, Adams M, Furness R 2010. Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? Frontiers in Zoology 7: 15.
Rayner MJ, Hauber ME, Steeves TE, Lawrence HA, Thompson DR, Sagar PM, Bury SJ, Landers TJ, Phillips RA, Ranjard L, Shaffer, SA 2011. Contemporary and historic separation of transhemispheric migration between two genetically distinct seabird populations. Nature Communications 2: 332.
Rayner MJ, Dunphy BJ, Lukies K, Adams N, Berg M, Kozmian-Ledward L, Pinkerton MH, Bury SJ 2021. Stable isotope record from a resident New Zealand seabird community suggests changes in distribution but not trophic position since 1878. Marine Ecology Progress Series 678: 171–182
Reusch K, Connan M, Ryan PG, Butler M, Pichegru L 2025. Spatio-temporal differences in the diet and trophic ecology of Kelp Gulls (*Larus dominicanus*) in South Africa. Ibis 167: 124–144.
Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Ramsey CB, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Haflidason H, Hajdas I, Hatté C, Heaton TJ, Hoffmann DL, Hogg AG, Hughen KA, Kaiser KF, Kromer B, Manning SW, Niu M, Reimer RW, Richards DA, Scott EM, Southon JR, Staff RA, Turney CSM, van der Plicht J 2016. IntCal13 and marine13 radiocarbon age calibration curves 0–50,000 years cal bp. Radiocarbon 55: 1869–1887.
Roberts C, Hawkins JP 1999. Extinction risk in the sea. Trends in Ecology & Evolution 14: 241–246.
Rounick JS, Winterbourne MJ 1986. Stable carbon isotopes and carbon flow in ecosystems. BioScience 36: 171– 177.
Silva-Costa A, Bugoni L 2013. Feeding ecology of kelp gulls (*Larus dominicanus*) in marine and limnetic environments. Aquatic Ecology 47: 211–224.
Sealy J, Johnson M, Richards M, Nehlich O 2014. Comparison of two methods of extracting bone collagen for stable carbon and nitrogen isotope analysis: comparing whole bone demineralization with gelatinization and ultrafiltration. Journal of Archaeological Science 47: 64–69.
Seers B, Shears N 2015. Spatio-temporal patterns in coastal turbidity – Long-term trends and drivers of variation across an estuarine-open coast gradient. Estuarine Coastal and Shelf Science 154: 137–151.
Spaans AL 1971. On the feeding ecology of the herring gull *Larus argentatus* in the northern part of the Netherlands. Ardea 59: 75–186.
Taylor R, Stephenson B, Cochrane P, Smith IWG, Gibbs N 1997. The state of New Zealand's environment 1997. Wellington, Ministry for the Environment. 456 p.
Votier SC, Bearhop S, MacCormick A, Ratcliffe N, Furness RW 2003. Assessing the diet of great skuas, *Catharacta skua*, using five different techniques. Polar Biology 26: 20–26.
Walter R, Buckley H, Jacomb C, Matisoo-Smith E 2017. Mass migration and the Polynesian settlement of New Zealand. Journal of World Prehistory 304: 351–376.
Wiley AE, Ostrom PH, Welch AJ, Fleischer RC, Gandhi H, Southon JR, Stafford TW, Penniman JF, Hu D, Duvall FP, James HF 2013. Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. Proceedings of the National Academy of Sciences 110: 8972–8977.
Zanden, MJV, Rasmussen JB 1999. Primary consumer δ15N and δ13C and the trophic position of aquatic consumers. Ecology 80: 1395–1404.
Zeldis JR, Swaney DP 2018. Balance of catchment and offshore nutrient loading and biogeochemical response in four New Zealand coastal systems: implications for resource management. Estuaries and Coasts 41: 2240–2259.

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Supplementary Material

Additional supporting information may be found in the online version of this article.

Appendix S1. Historic specimen details, Auckland Museum collection.

The New Zealand Journal of Ecology provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.