



Stable isotope record from a resident New Zealand seabird community suggests changes in distribution but not trophic position since 1878

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ABSTRACT: Globally, human population growth, its associated pollution and the vast scale of industrialised fisheries are having negative impacts on oceanic food webs, affecting top predators such as seabirds. We used stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analyses of feathers to investigate the contemporary structure and long-term changes in a near-shore community of 5 seabird species in northern Aotearoa New Zealand. Feathers were collected from museum specimens or live individuals (collected between 1878 and 2019) in Tīkapa Moana, the Hauraki Gulf, a marine habitat increasingly threatened by overfishing and urbanisation. To tease out the effects of baseline ecosystem versus seabird distributional changes, we analysed muscle isotope values of forage fishes collected over 43 yr (1976–2019) and provide isotopic data from contemporary prey species sampled within the region. Contemporary $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values were consistent with existing data on diet and foraging distribution of the 5 seabird species. Values of $\delta^{15}\text{N}$ declined in only 1 of 5 species studied, suggesting little change in the trophic position of the other species over time. However, $\delta^{13}\text{C}$ values declined in 3 species, and a lack of change in the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of forage fish suggests that this change is reflective of a behavioural shift in the distribution of the birds. However, changes in isotopic baselines over the sampling period cannot be ruled out and require further investigation. Our results demonstrate the value of stable isotope analyses of contemporary and archived samples as a cost effective, non-invasive method for monitoring coastal seabirds in a changing world.

KEY WORDS: Carbon and nitrogen isotope · Feathers · Euphausiids · Salps · Forage fish · Museum collections · Hauraki Gulf

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1. INTRODUCTION

Globally, human stressors on marine food webs, such as overfishing, marine pollution and climate change, are having negative population impacts on seabirds that depend on lower trophic level prey for breeding and survival (Paleczny et al. 2015, Gagné et

al. 2018a, Roman et al. 2019). An understanding of drivers of population fluctuations relies on knowledge of species' breeding biology, community food web structure and changes in diet and foraging habitat of individual taxa. Collecting dietary data typically requires intensive field studies at breeding sites, using techniques such as photographic counts

of species carrying prey (Gaglio et al. 2017), forced regurgitations of adults returning to provision chicks (Barrett et al. 2007) and analysis of stomach contents of dead birds (Imber 1996). Likewise, studies investigating habitat use away from breeding sites are intensive undertakings, requiring field observations and tracking techniques that are expensive and time consuming. Moreover, seabirds are typically long-lived study organisms and integrate ecological processes over broad spatial and temporal scales (Weimerskirch 2007, Oro 2014). As a result, their populations can exhibit complex interannual variability in foraging dynamics requiring long-term studies, that can sometimes span the lives of individual researchers to establish meaningful trends in measured parameters (see Lewison et al. 2012 for review). Long-term field datasets tracking ecological change in seabird food webs are thus rare, but increasingly important in a changing world.

Retrospective analysis of bird specimens from museum collections, paired with contemporary field samples, is increasingly being used to investigate avian food webs (Blight et al. 2015, Grecian et al. 2016, English et al. 2018). A wide range of techniques are now available to extract chemical and molecular data from the tissues of methodically collected, dated and provenanced specimens, providing decades or even centuries of information relating to species' biology and ecology (Webster 2017). Carbon and nitrogen stable isotope ratios of seabird tissues can be used to delineate food web structure and trace long-term dietary and habitat changes (Hobson et al. 1994, Hilton et al. 2006). Nitrogen isotopes (expressed as $\delta^{15}\text{N}$, the ratio of ^{15}N to ^{14}N) are predictably enriched in marine food webs, increasing step-wise with each trophic level by an average of 3–4‰, thus providing a tool to reliably estimate the trophic position of an animal and its change in diet over time (Minagawa & Wada 1984, Post 2002). In contrast, carbon isotopes (expressed as $\delta^{13}\text{C}$, the ratio of ^{13}C to ^{12}C) increase minimally with trophic level in marine systems, making them a useful indicator of carbon source and hence potential feeding habitats of organisms. At broad spatial scales, carbon isotope ratios decrease with decreasing water temperature and thus change predictably with latitude, in particular south of 40° S (Goericke & Fry 1994). At regional scales, highly productive inshore habitats have greater carbon turnover and thus have more enriched carbon isotope values compared to offshore habitats (Hobson et al. 1994, Hobson 1999, Quillfeldt et al. 2005, Cherel & Hobson 2007).

Globally, longitudinal stable isotope studies of seabird food webs are demonstrating changes in oceanic ecosystems and seabird ecology. For example, in pelagic ecosystems, the dual impact of over-exploitation by commercial fisheries and climate-based declines in marine productivity are reducing seabird trophic levels as species are forced to feed down the food web (Hilton et al. 2006, Wiley et al. 2013, Grecian et al. 2016, Gagné et al. 2018a) and/or change foraging distributions in search of prey (Wiley et al. 2013, Cherel et al. 2014, Grecian et al. 2016). Closer to the coast in neritic habitats, studies have shown a decline in marine prey sources and trophic position (Blight et al. 2015) with a shift to more human-derived food sources in species with flexible foraging strategies, such as Laridae (Auman et al. 2011). However, with a broad range of anthropogenic impacts, including recreational and commercial over-fishing, habitat damage from benthic trawling and terrestrially derived siltation of foraging habitat, further studies of impacted inshore seabird communities are required.

Tikapa Moana (also known as the Hauraki Gulf), which is situated off the east coast of Auckland, Aotearoa New Zealand, is a globally significant seabird biodiversity hotspot. A total of 27 seabird species breed in the region, making use of diverse inshore to pelagic habitats, productive waters and predator-free islands for breeding (Gaskin & Rayner 2013). This abundant seabird community belies long-term declines in the biodiversity of the gulf as a result of overfishing and marine habitat destruction, which have caused the collapse of many fish stocks (Pinker-ton et al. 2015, Hauraki Gulf Forum 2020). Understanding of the trophic structure and response of this community to environmental change over time is lacking. To date, research has focussed on single-species investigations of the at-sea ecology of predominantly migratory taxa (Rayner et al. 2008, 2011, 2016, 2017, Freeman et al. 2010, Dunphy et al. 2020), and few ecological data are available for year-round resident species, despite observed population declines linked to human activities (Frost 2017, Rawlence et al. 2019).

We used a stable isotope approach to investigate the contemporary trophic partitioning within a resident seabird community of 5 species sampled from the Hauraki Gulf. Furthermore, we used contemporary and historical samples from museum collections to investigate patterns of ecological change in these seabird taxa over time. We also attempted to gain insight into potential baseline shifts in isotopic values with an analysis of historic museum and contemporary specimens of forage fish collected from the same region.

2. MATERIALS AND METHODS

2.1. Study region and sample collection

Individual breast feathers were collected from museum skins or live individuals between 1878 and 2019 for stable isotope analysis. The location of individuals sampled was restricted to the inner portion of the Hauraki Gulf marine park, defined as waters southwards of a boundary between Kawau Island and Cape Colville on the Coromandel Peninsula, including the Firth of Thames, and Waitematā Harbour (Fig. 1). In total, 145 feathers were sampled from adult individuals of 5 seabird species (Table 1): pied shag *Phalacrocorax varius* ($n = 25$), spotted shag *P. punctatus* ($n = 37$), little penguin *Eudyptula minor* ($n = 39$), white-fronted tern *Sterna striata* ($n = 21$) and red-billed gull *Larus novaehollandiae* ($n = 23$). Loose feathers were collected at nesting sites or from indi-

viduals captured by hand at colonies. Museum samples were obtained from study skins and mounted birds, collected across different years and held in the collections of Auckland Museum, Te Papa Tongerewa (Museum of New Zealand) and Canterbury Museum. Feathers were stored dry in zip-lock plastic bags prior to laboratory analysis.

As the stable isotope values of feathers represent the period of feather growth following moult, we selected species for which available data suggest year-round residency and moult within the Hauraki Gulf ecosystem (Marchant & Higgins 1990a). Timing of moult could potentially affect isotopic comparisons between species of birds that grow feathers at different times of year, due to differing levels of primary productivity (impacting carbon isotope values) and prey availability (impacting nitrogen isotope values). Little penguin, white-fronted tern and red-billed gull commence a single moult in mid- to late

summer following breeding (Marchant & Higgins 1990a); however, moult has been poorly described for the 2 shag species in this study. Turbott (1956) suggested that spotted shag in the Hauraki Gulf moult in November following chick rearing, but to our knowledge there are no data on moult in pied shag from the region. Given that both shag species have multiple breeding peaks during the year in February–April and August–October, it may be that replacement of feathers occurs across the year outside these periods (Millener 1972, Powlesland et al. 2008). A small number of white-fronted tern banding returns suggest limited migration of immature birds to the coast of Australia, with a potential moult of these individuals occurring in a different food web, thus biasing results. However, large numbers of these birds are present within the Hauraki Gulf year-round, suggesting year-round residency for most of this population (Marchant & Higgins 1990a).

Contemporary marine taxa known to be prey of seabirds were collected in the Hauraki Gulf between 2018 and 2019 using 2 methods. Samples of zooplankton, crustaceans (*Nyctiphanes australis*, hereafter krill) and salps *Thalia democratica* (hereafter salps)

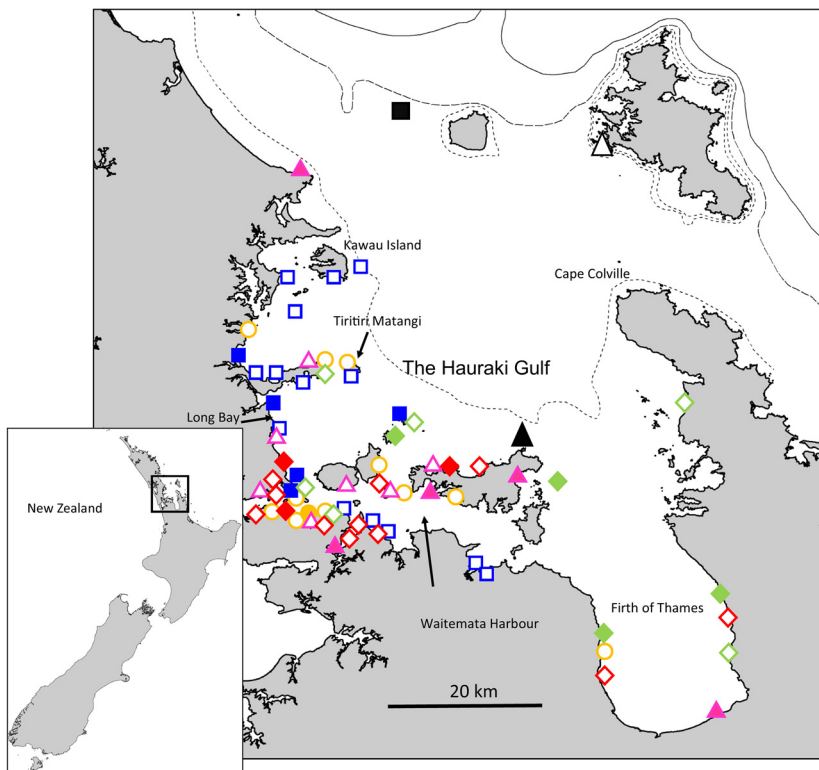


Fig. 1. Tikapa Moana, the Hauraki Gulf, study region in Aotearoa New Zealand, showing feather sample locations of seabird species including pied shag (pink triangles), spotted shag (green diamonds), white-fronted tern (orange circles), little penguin (blue squares) and red-billed gull (red diamonds). Contemporary samples, post 2010, are shown by filled symbols with some duplication of samples at certain locations. Also shown are locations of gannet colonies where fish and squid samples were collected (filled black triangle at Horuhoru Rock, unfilled black triangle at Mahuki Island) and approximate location of zooplankton salp sampling tows (filled black square). Depth contours are shown as fine dashed line (40 m), dashed line (60 m) and solid line (80 m)

Table 1. Contemporary (2010–2019) carbon and nitrogen stable isotope values (mean \pm SE) of feathers of resident Hauraki Gulf seabirds and their potential prey. PSHG: pied shag; SSHG: spotted shag; WFTE: white-fronted tern; LPEN: little penguin; RBGU: red-billed gull; n = number of samples

Species	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	n
PSHG	-14.91 ± 1.08	17.98 ± 0.89	6
SSHG	-15.99 ± 0.51	17.48 ± 0.67	20
WFTE ^a	-14.82 ± 0.89	17.28 ± 1.28	23
LPEN	-17.24 ± 0.24	15.54 ± 1.04	17
RBGU	-17.96 ± 1.05	13.27 ± 2.16	8
Fish	-18.22 ± 0.48	13.49 ± 0.94	22
Squid	-19.32 ± 0.43	11.23 ± 0.76	10
Crustacean	-19.77 ± 0.33	9.13 ± 0.27	10
Salp	-21.68 ± 0.36	8.17 ± 0.26	10

^aData for WFTE span 1880–2019 (see Section 2.3)

were obtained using horizontal surface tows (<2 m depth) of a zooplankton net (780 mm diameter at the mouth, 2 m long and 250 μm cod end) as part of a wider study of seabird prey in the Hauraki Gulf (Fig. 1). Tows were undertaken in fish workups, areas where larger fish work smaller fish up to the sea surface, where seabirds were seen feeding. On completion of a zooplankton tow, the contents of the cod end were washed into a large sieve. Samples were placed in a labelled sample container containing 70% ethanol for subsequent identification and enumeration.

Samples of whole fresh pelagic fish and squid were obtained from regurgitations of adult Australasian gannets *Morus serrator* (hereafter gannets) across 2 consecutive breeding seasons (December to January 2017–2018 and 2018–2019), as part of a wider study characterising the diet of gannets in the Hauraki Gulf (N. J. Adams unpubl. data). These species are ubiquitous in the Hauraki Gulf and include Australian pilchard *Sardinops neopilchardus* (n = 12; hereafter pilchard), Australian anchovy *Engraulis australis* (n = 10; hereafter anchovy) and arrow squid *Nototodarus gouldi* (n = 10; hereafter squid). Gannets were sampled from 2 colonies: Horuhoru Rock, positioned within the inner gulf, and Mahuki Island, some 55 km to the northeast off the coast of Great Barrier Island (Fig. 1). Adult gannets were caught at their breeding colony immediately on arrival to feed chicks using a modified shepherd's hook. Regurgitated samples were collected into buckets held in front of the bird's bill. When necessary, gentle massaging of the throat from the base to its junction with the mouth was applied to move food out of the oesophagus. On collection, prey samples were placed in plastic bags and

frozen for preservation. In the laboratory, samples were defrosted, and a small sample of muscle was taken from each specimen.

Muscle tissue was also obtained from additional prey specimens of pilchard (n = 12) and anchovy (n = 14), collected in the inner Hauraki Gulf in 1976 using unknown methods. These specimens were held in the collections of Auckland Museum having been initially preserved in formalin and then stored in ethanol.

In a separate study for New Zealand Ministry of Fisheries biodiversity project ZBD2005-09, muscle samples from pilchards (n = 5) and sweep *Scorpius lineolatus* (n = 66) were collected for stable isotope analysis from within the Hauraki Gulf (Long Bay, Tiritiri Matangi and Kawau Island, Fig. 1) in 2005 (Beaumont et al. 2009).

2.2. Stable isotope analysis

Feathers were washed in 70% ethanol, then rinsed 3 times in distilled de-ionised water before oven drying at 60°C. Using clean scissors, vanes were removed from each side of the feather shaft, then cut into very small fragments to homogenise the sample for analysis. Approximately 0.70 mg of mixed dried material from a single feather was weighed out into a tin capsule and sealed for stable isotope analysis.

Fish and squid muscle tissues were sub-sampled using a sterile scalpel and stored frozen. Muscle tissue samples were then thawed, and approximately 10 mg wet weight was removed and freeze-dried overnight. A subset of 10 individual euphausiids were freeze-dried overnight and analysed as whole single individuals. Salps were subsampled as 2 or 3 individuals into a single vial and freeze-dried overnight; individual samples were then ground into a homogenate using a pestle and mortar prior to analysis.

All stable isotope analyses were carried out on a DELTA V Plus (Thermo Fisher Scientific) continuous-flow isotope ratio mass spectrometer (IRMS) at the National Institute of Water and Atmospheric Research (NIWA) stable isotope facility in Wellington. Samples were introduced via a MAS200 autosampler to a Flash 2000 (Thermo Fisher Scientific) elemental analyser and were combusted at 1020°C in a flow of oxygen and helium carrier gas. Oxides of nitrogen were converted to N_2 gas in a reduction furnace at 650°C. N_2 and CO_2 gases were separated on a Porapak Q gas chromatograph column before being introduced to the mass spectrometer detector via an

open split Conflo IV interface (Thermo Fisher Scientific). CO₂ and N₂ reference gas standards were introduced to the IRMS with every sample analysis. Following standard protocols, carbon (¹³C, ¹²C) and nitrogen (¹⁵N, ¹⁴N) isotope ratios are represented as δ (delta) notations in units of parts per thousand (‰). ISODAT (Thermo Fisher Scientific) software was used to calculate δ¹⁵N values against atmospheric air, and δ¹³C values against the CO₂ reference gas relative to the National Bureau of Standards 19-calcite (NBS19-calcite) standard (calibrated against Vienna Pee Dee belemnite), correcting for ¹⁷O. Sample δ¹⁵N values were 2-point normalised (following Paul et al. 2007) using isotopic 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. Sample δ¹³C values were 2-point normalised using isotopic data from the daily analysis of NIST 8573 USGS40 L-glutamic acid and NIST 8542 IAEA-CH-6 Sucrose. We calculated ‰C and ‰N values relative to a solid laboratory reference standard of DL-leucine (DL-2-Amino-4-methylpentanoic acid, C₆H₁₃NO₂, Lot 127H1084, Sigma, Australia) at the beginning of each run. Repeat analysis of individual NIST standards (n = 4) produced data accurate to 0.02 ‰ for δ¹⁵N and 0.07 ‰ for δ¹³C. Repeat analysis of an internal laboratory squid standard (n = 8), with a similar sample matrix to the study samples produced a precision of better than 0.15 ‰ for N and 0.18 ‰ C.

2.3. Statistical analysis

Since the industrial revolution, the release of isotopically light carbon in fossil fuels, which are depleted in ¹³C, has resulted in a decrease in the carbon isotopic value of the atmosphere, known as the Suess effect (Keeling et al. 1979). Oceanic uptake of this ¹³C-depleted CO₂ has resulted in a decreasing δ¹³C value of oceanic dissolved inorganic carbon and a subsequent decrease in δ¹³C values of the oceanic food chain from phytoplankton to top predators (Lorain et al. 2020). It is essential to attempt to control for the Suess effect when samples are collected over time, in order to differentiate between behavioural change in study taxa (e.g. changing foraging habitats, diets) versus baseline changes across the food web as a whole (Quillfeldt et al. 2010). First, data from historical museum feather samples and forage fish tissues were normalised to the end of our dataset (analysis year) by subtracting a year-specific factor for δ¹³C = -1 + 1.1(analysis year – sample collection

year) × 0.027 following the methods of Quillfeldt et al. (2010) and Hilton et al. (2006). Second, a proxy indicator for possible changes in baseline environmental values was investigated using a separate analysis of δ¹³C and δ¹⁵N isotopic values of muscle tissue from historic forage fish (pilchard, anchovy and sweep) held in the collections of Auckland Museum (collected in 1976) and historic (2005) and contemporary field samples (2018–2019). Formalin for the preservation of fish muscle in museum specimens can affect isotopic values and weaken interpretation of results. In a comprehensive study of 17 fish species from a wide range of trophic characteristics, González Bergonzoni et al. (2015) showed that formalin preservation decreases δ¹³C values by 0.94 ‰ (range 0.60–1.40 ‰) and δ¹⁵N values by 0.33 ‰ (range 0.30–0.50 ‰). To control for this bias, corrections were applied to the formalin-preserved fish muscle data using the following models developed by González Bergonzoni et al. (2015): Predicted fresh δ¹³C value = 1.07 × (preserved δ¹³C value) + 2.90; Predicted fresh δ¹⁵N value = 0.98 × (preserved δ¹⁵N value) – 0.16.

Comparisons of the feather δ¹⁵N and δ¹³C values of the 5 seabird taxa were made using nonparametric methods following tests for normality (Shapiro-Wilk) and homogeneity of variance (Levene's tests) that showed normal distributions, but unequal variances within data for each species. Subsequently, Kruskal-Wallis nonparametric tests were used to test for differences in δ¹⁵N and δ¹³C values followed by Dunn's post hoc nonparametric pairwise tests. To investigate contemporary trophic structure of the seabird taxa, these analyses were conducted only on data from contemporary feather samples collected after 2010 and not on historic museum sampled feathers. However, in the case of white-fronted tern, there were insufficient contemporary samples and, as this species showed no significant change in δ¹⁵N and δ¹³C values during the study period (1880–2020) (see Section 3), all white-fronted tern data were used in the analysis.

The tissue δ¹⁵N and δ¹³C values of potential contemporary fish, squid and zooplankton species were checked for normality and homogeneity of variance using Shapiro-Wilk and Levene's tests, and differences in δ¹³C values between prey were analysed using 1-way ANOVA with Tukey's post hoc tests. Kruskal-Wallis nonparametric testing was used on prey δ¹⁵N data due to unequal variances between groups followed by Dunn's post hoc nonparametric pairwise tests.

Following tests for normality and homogeneity of variance via Shapiro-Wilk and Levene's tests, Welch's unequal variances *t*-tests were used to detect differ-

ences between the means of historic and contemporary fish muscle stable isotope values. Data for fish species within each group (1976, 2005 and 2018–2019) were combined as they were not significantly different from each other in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ($\alpha > 0.05$, Welch's test).

Linear regression analysis was used to test for long-term changes in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of feathers from our study species. All analyses were conducted using JMP®, Version 15.0.0, SAS Institute, with a level of significance set at $\alpha = 0.05$.

3. RESULTS

3.1. Contemporary seabird stable isotope values

The contemporary feathers of seabird species analysed were significantly different in both $\delta^{15}\text{N}$ (Kruskal-Wallis $H = 43.21$, $df = 4$, $p < 0.0001$) and $\delta^{13}\text{C}$ values (Kruskal-Wallis $H = 57.43$, $df = 4$, $p < 0.0001$) (Table 1, Fig. 2). Post hoc tests showed that samples from pied shag, spotted shag and white-fronted tern were not significantly different from each other in either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ data (Dunn's tests $\alpha = 0.05$), but each had higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than little penguin (Dunn's tests, $\delta^{15}\text{N}$: $p = 0.02$, $p < 0.0001$, $p = 0.001$ respectively; $\delta^{13}\text{C}$: $p < 0.0001$, $p < 0.001$, $p < 0.001$). Samples from red-billed gulls were separated from little penguin due to lower $\delta^{15}\text{N}$ values (Dunn's test < 0.001) but were not significantly different in $\delta^{13}\text{C}$ values (Dunn's test = 0.26).

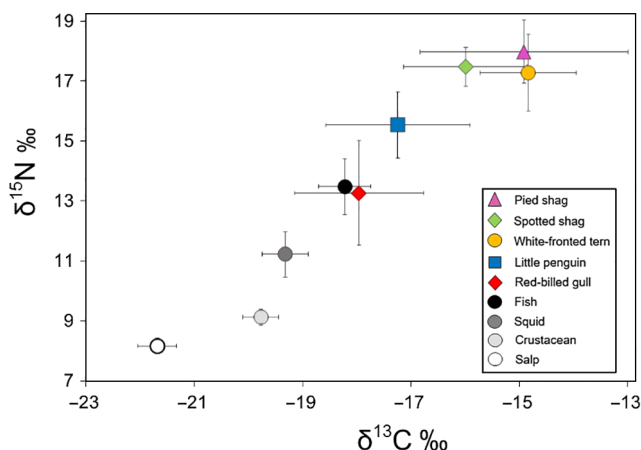


Fig. 2. Contemporary (2010–2019) average carbon and nitrogen stable isotope values of feathers from pied shag, spotted shag, white-fronted tern, little penguin, red-billed gull and from tissues of fish, squid, crustacean and salp prey sources (see Section 2) (mean \pm SD). Data for WFTE span 1880–2019 (see Section 2.3)

3.2. Contemporary prey stable isotope values

The contemporary fish, squid, crustacean and zooplankton tissue samples collected in the Hauraki Gulf were significantly different in both $\delta^{15}\text{N}$ (Kruskal-Wallis $H = 44.00$, $df = 3$, $p < 0.0001$) and $\delta^{13}\text{C}$ values (ANOVA $F_{5,74} = 54.32$, $p < 0.0001$) (Table 1, Fig. 2). Fish had significantly higher $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values than squid (Dunn's test $\delta^{15}\text{N}$, $p < 0.05$; Tukey HSD test $\delta^{13}\text{C}$, $p < 0.0001$). Squid had significantly higher $\delta^{15}\text{N}$ values than crustaceans (Dunn's tests, $p < 0.001$), although there was no significant difference between the $\delta^{13}\text{C}$ values of these 2 groups (Tukey HSD test, $p = 0.25$). Salps had significantly lower $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values (Dunn's and Tukey HSD tests) than all prey species except for crustaceans, which shared similar $\delta^{15}\text{N}$ values (Dunn's test, $p = 0.20$). There was no significant difference between fish muscle $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from 1976 ($n = 26$), 2005 ($n = 26$) and 2018–2019 ($n = 23$) ($\delta^{15}\text{N}$ Kruskal-Wallis $H = 1.44$, $df = 2$, $p = 0.47$ and $\delta^{13}\text{C}$ Kruskal-Wallis $H = 5.07$, $df = 2$, $p = 0.09$).

3.3. Chronological stable isotope changes in seabirds

Linear regression analyses of carbon and nitrogen stable isotope values for seabird feathers showed species-specific results. For pied shag and little penguin, nitrogen isotope values were not significantly different over time, whereas carbon values declined significantly by 2.96‰ for pied shag between 1878 and 2019 and by 3.05‰ for little penguin between 1905 and 2018 (Table 2, Fig. 3). For spotted shag, both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values declined significantly over time by 0.78 and 2.59‰, respectively, between 1887 and 2017. White-fronted tern and red-billed gull showed no significant change in either $\delta^{15}\text{N}$ or $\delta^{13}\text{C}$ values (Table 2, Fig. 3).

4. DISCUSSION

Carbon and nitrogen stable isotope values of feathers from seabirds breeding in the Hauraki Gulf, and tissue samples from potential prey sources, were used to characterise trophic positions and foraging habitats and track relative changes in these values over 141 yr. Stable isotope values for contemporary feather samples indicate a range of trophic positions in the seabird species studied, from the highest in pied shag and spotted shag, to the lowest in red-billed gull.

Table 2. Trends in feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of resident Hauraki Gulf seabirds based on linear regression analysis. Data represented are from 1878 to 2019. Abbreviations as in Table 1

	n	p	Slope
$\delta^{15}\text{N}$			
PSHG	23	0.17	-0.006
SSHG	37	<0.01	-0.006
WFTE	20	0.80	-0.002
LPEN	39	0.40	0.004
RBGU	23	0.95	0.0004
$\delta^{13}\text{C}$			
PSHG	25	<0.001	-0.02
SSHG	36	<0.0001	-0.02
WFTE	21	0.22	-0.007
LPEN	39	<0.0001	-0.03
RBGU	23	0.09	-0.001

The 2 shag species studied occupied the highest trophic levels as indicated by nitrogen isotope values. Previous studies of these species suggest they feed predominantly on fish (Lalas 1983, Blaber & Wassenberg 1989), and our $\delta^{15}\text{N}$ values support this conclusion, being on average a respective 4.44‰ higher than the fish species analysed (consistent with averaged trophic level enrichment factors of 3–5‰ (Mizutani et al. 1992, Post 2002). Average nitrogen stable isotope values were similar to the imperial cormorant *Phalacrocorax impericeps*, for which fish are a dominant component of the diet during moult ($\delta^{15}\text{N}$ 16.05‰, Weiss et al. 2009), but higher than Galapo-

gos cormorant *P. harrisi* ($\delta^{15}\text{N}$: 13.73‰), which have a mixed diet of benthic fish and cephalopods (Jiménez-Uzcátegui et al. 2019). The higher $\delta^{13}\text{C}$ feather isotope values of both pied and spotted shags suggest that the 2 species feed in more inshore waters and/or on more benthic prey than the other study species. Whilst the $\delta^{13}\text{C}$ values of the 2 shag species were not significantly different, those of pied shags were greater on average than spotted shags. This result is consistent with behavioural observations that, unlike spotted shags, pied shags are opportunistic foragers in freshwater, estuarine and intertidal habitats (Marchant & Higgins 1990a), all locations with greater carbon cycling, higher productivity and higher carbon isotope values. Conversely, spotted shags forage further offshore than freshwater and/or estuarine habitats in the neritic zone (Lalas 1983), which is associated with lower productivity and lower carbon isotope values (Hobson et al. 1994, Hobson 1999).

Nitrogen isotope values for white-fronted terns were not significantly different from those of the shags studied and suggest a diet dominated by fish during feather growth. These data are consistent with a range of studies, confirming the importance of larval and small fishes in the diet of this species taken predominantly by surface seizing and shallow dives (Marchant & Higgins 1990b). Higher $\delta^{13}\text{C}$ values, most similar to those of pied shag, are consistent with observed estuarine and inshore foraging habitats for this species (Marchant & Higgins 1990b, Brägger 1998).

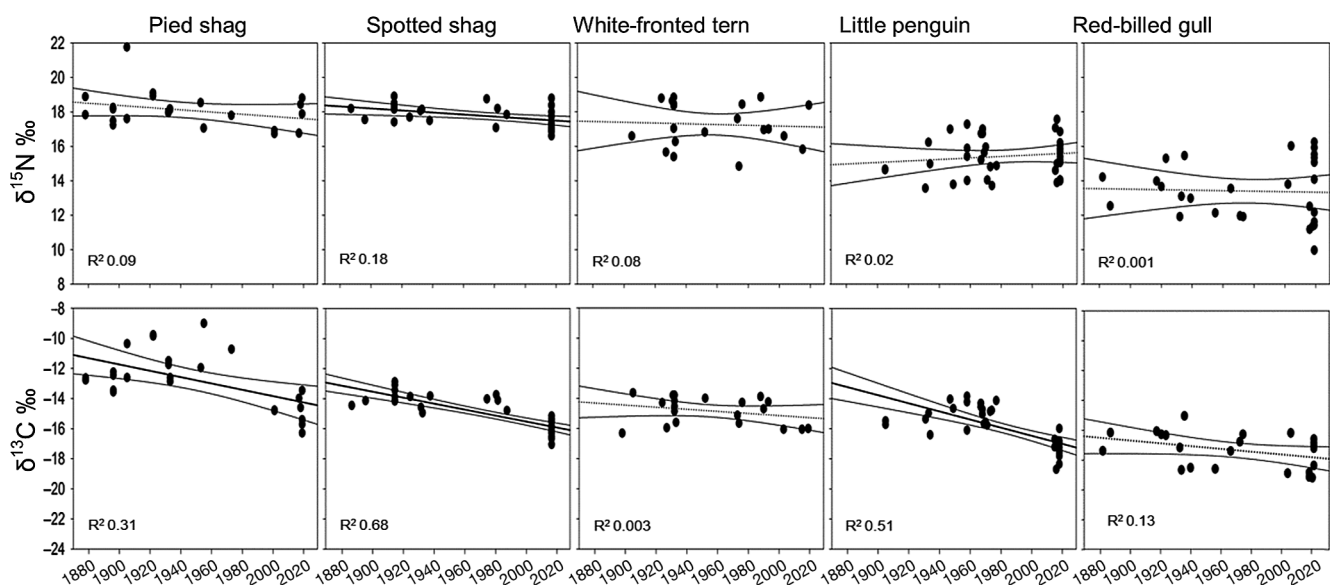


Fig. 3. Nitrogen and carbon stable isotope values of feathers from resident seabirds in the Hauraki Gulf from 1878–2019. Linear regression fit (solid line: significant; dashed line: not significant at $\alpha = 0.05$) shown with 95 % confidence intervals

Little penguins had lower nitrogen isotope values than pied shag, spotted shag and white-fronted tern, with $\delta^{15}\text{N}$ values 4.35‰ above sampled squid and 2.05‰ above fish. Based on a $\delta^{15}\text{N}$ trophic level enrichment factor of 3–5‰ (Mizutani et al. 1992, Post 2002, Cherel et al. 2005), these results suggest a mixed diet of fish and cephalopods when birds accumulate body reserves used for feather growth during their extended moult period onshore in mid- to late summer. This result is consistent with the work of Geurts (2006), who found fish, then cephalopods, dominated the diet of little penguins in the Hauraki Gulf, and is also in accordance with other studies based in New Zealand (Flemming et al. 2013) and Australia (Chiariadia et al. 2003, Preston 2017). The $\delta^{13}\text{C}$ values of penguin feathers were significantly lower than pied shag, spotted shag and white-fronted tern, suggesting a more offshore foraging distribution prior to moult.

Red-billed gulls had the lowest $\delta^{15}\text{N}$ values of any seabird sampled, which were 4.14‰ above sampled crustaceans. These values are similar to those of common diving petrels *Pelecanoides urinatrix* feeding on marine crustaceans in the outer Hauraki Gulf (Dunphy et al. 2020) (allowing 1‰ for differing tissue nitrogen isotopic fractionation rates between feathers and blood; Quillfeldt et al. 2008). In contrast, carbon isotope values were similar to another common diving petrel population feeding in the inner Hauraki Gulf closer to shore (Dunphy et al. 2020). Together, these results suggest that inshore marine invertebrates are a feature of red-billed gull diet, which is supported by other studies in New Zealand (Mills 1989, Mills et al. 2008). However, red-billed gulls breeding near urban environments can incorporate a range of terrestrially based anthropogenic food sources into their diet (Mills et al. 2008, Auman et al. 2011, Blight et al. 2015). When our $\delta^{15}\text{N}$ isotope values are compared to those of red-billed gulls from contrasting urban and natural habitats in Tasmania, our results were most similar to birds feeding on a mixed diet of terrestrial and marine resources from a non-urban habitat (Auman et al. 2011). The high variance in $\delta^{15}\text{N}$ values from our study also supports the conclusion of a mixed diet for the species during moult, possibly made up of marine and terrestrial invertebrates, but with fewer anthropogenic-based food sources. The exact nature of the red-billed gull diet and how it might change outside of the moult period clearly requires further investigation.

With their low nitrogen isotope values, there is little evidence that salps feature as a dominant component of the diet of the seabird species studied. This result is consistent with studies showing that salps

and jellyfish are often taken as opportunistic low nutrient-value prey items when locally abundant (McInnes et al. 2017, Cavallo et al. 2018). There is no doubt, however, that salps remain a vital component of the Hauraki Gulf marine food web as a prey source for crustaceans, fish and whales (Henschke et al. 2016, Carroll et al. 2019).

We found little evidence for change in the trophic positions of seabird species studied, except for spotted shags, which showed a decrease in $\delta^{15}\text{N}$ values over time. This shift in the nitrogen isotope values of grown feathers (0.78‰) represents approximately one quarter of a trophic level (Mizutani et al. 1992, Post 2002, Cherel et al. 2005), suggesting a possible increase in the exploitation of lower trophic level prey (possibly squid), in a diet otherwise dominated by fish during feather growth. The absence of notable changes in nitrogen isotope values in this study is intriguing, given the significant reductions in trophic position of seabirds observed in pelagic food webs where prey communities are being modified by industrial fishing (Hilton et al. 2006, Wiley et al. 2013, Grecian et al. 2016, Gagné et al. 2018a,b).

The Hauraki Gulf has seen increasing fisheries impacts with the introduction and expansion of commercial fishing from the early 1900s and more recently the growth of a large recreational fishing fleet that exceeds commercial take of popular fish species (Fisheries New Zealand 2020). In conjunction with other factors, such as habitat damage from bottom dredging, overfishing of the gulf has contributed to well documented declines in fish abundance and habitat quality (Pinkerton et al. 2015). Anthropogenically derived nitrogen can elevate baseline nitrogen concentrations and nitrogen stable isotope values (Gaston & Suthers 2004, Dudley & Shima 2010) and conceal meaningful longitudinal trophic level changes in top predators such as seabirds (Elliott et al. 2021).

In order to interpret whether seabird trophic level has changed over time, it is important to know what the baseline $\delta^{15}\text{N}$ values in seabird foraging areas were over the sampling time period. If seabird and baseline $\delta^{15}\text{N}$ values both remained constant over time, then it is reasonable to assume that seabird trophic level did not change, and seabird diet likely remained constant. If, however, there was an increase in $\delta^{15}\text{N}$ baseline over time, and seabird $\delta^{15}\text{N}$ values remained stable, then that would mean an effective decrease in seabird trophic level over that period, as has been observed in other studies (Hilton et al. 2006, Wiley et al. 2013, Grecian et al. 2016, Gagné et al. 2018a,b). In the Hauraki Gulf, nutrient loading from wastewater and river catchment runoff

has increased nitrogen inputs over time (Zeldis & Swaney 2018), and this might be expected to have increased $\delta^{15}\text{N}$ baseline values. However, stable isotope analysis of fish within the Hauraki Gulf ecosystem between 1976 and 2019 (Fig. 4) indicates that $\delta^{15}\text{N}$ baselines may have remained stable over this more recent time period. This finding supports the argument that baseline $\delta^{15}\text{N}$ values have not changed in the regions where seabirds are likely to be feeding, and that the seabird $\delta^{15}\text{N}$ stability we have observed is due to unchanged seabird diet and trophic position over this time.

Analyses of contemporary and historical feather samples indicate changes in the carbon isotopes of Hauraki Gulf seabirds in the period between 1878 and 2019. Three of 5 species studied (pied shag, spot-

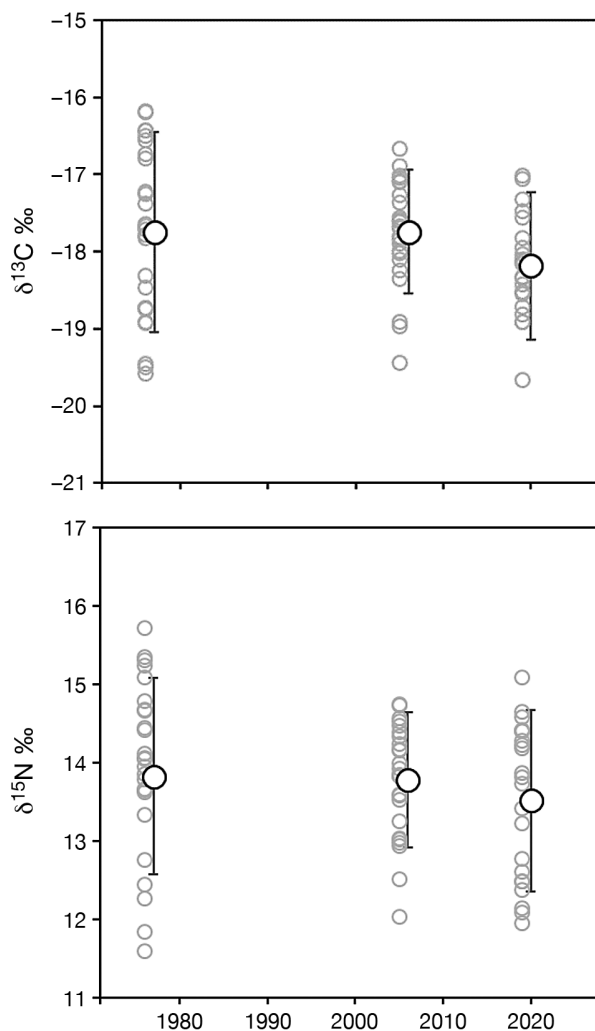


Fig. 4. Carbon and nitrogen stable isotope values of muscle tissue (large circles with error bars show mean \pm SD; grey circles are individual values) from mesopelagic forage fish collected in the Hauraki Gulf in 1976, 2005 and 2019 (see Section 2)

ted shag and little penguin), showed an average decline in feather $\delta^{13}\text{C}$ values of 2.87‰ over 141 yr, averaging 0.20‰ per decade (having corrected for the Suess effect). This decline in carbon isotope values may be linked to changes in community phytoplankton structure and primary productivity, since experimental studies have demonstrated that phytoplankton carbon fractionation is a function of cell growth rates (Laws et al. 1995, Oczkowski et al. 2018) with lower $\delta^{13}\text{C}$ values tracking reduced primary productivity in marine ecosystems (O'Reilly et al. 2003, Hilton et al. 2006). In the inner Hauraki Gulf, anthropogenic nutrient inputs have increased primary productivity (Chang et al. 2003, Seers & Shears 2015, Zeldis & Swaney 2018) but values have decreased offshore (Pinkerton et al. 2019). Higher productivity would likely produce higher community $\delta^{13}\text{C}$ (Oczkowski et al. 2018) but this was not seen in our data for seabirds and for pelagic fish sampled between 1976 and 2019 (Fig. 4). A further possibility for the observed trend in declining $\delta^{13}\text{C}$ feather values is change in the foraging habitat of moulting birds over time. Studies in the Hauraki Gulf have demonstrated differences in tissue values of seabirds that forage in isotopically enriched near-shore versus ^{13}C -depleted offshore habitats (Lukies 2019, Dunphy et al. 2020) and are consistent with trends observed globally (Hobson et al. 1994, Hobson 1999, Bearhop et al. 2002). Declines in the $\delta^{13}\text{C}$ values of pied shag, spotted shag and penguin feathers in this study may indicate a shift over time away from benthically influenced inshore habitats to more offshore environments driven by anthropogenically mediated factors (declining prey biomass, habitat destruction and disturbance) (Pinkerton et al. 2015).

In conclusion, this study provides nitrogen and carbon stable isotope data for 5 New Zealand coastal seabird species, and attempts to reconstruct their ecological history over 141 yr within an ecosystem increasingly impacted by anthropogenic stressors. Analysis of contemporary stable isotope data confirms trophic level structuring, and supports and expands on existing data on species foraging ecology. Despite significant fisheries and environmental impacts, stable nitrogen isotope values for 4 of the seabirds did not change over time, indicating stability in diet and trophic position, in contrast to similar studies of seabirds from pelagic systems. Despite having some independent baseline nitrogen data indicating baseline stability, due to the low temporal resolution of these data, we cannot rule out the possibility of nitrogen baseline shifts in the foraging areas of the seabirds at other times during the study period. In order to achieve more certainty around

baseline changes and the trophic status of the seabirds over the 141 yr study period, we recommend the use of compound-specific stable isotope analysis of nitrogen in amino acids (CSSIA-AA-N) as an extension of this study. CSSIA-AA-N enables the precise calculation of the trophic position of an organism (Chikaraishi et al. 2009) by analysing the $\delta^{15}\text{N}$ values of amino acids that fractionate substantially between trophic levels (e.g. glutamic acid) and comparing them with those that undergo very little fractionation (e.g. phenylalanine) (Chikaraishi et al. 2009, Chikaraishi 2014, McMahon et al. 2015, Ohkouchi et al. 2017). Employing this isotopic tool would provide more clarity around the trophic status of these seabirds, and enable further insight into potential changes in their foraging strategies over this time period. Carbon isotope values declined significantly in 3 seabird species studied, contrasting well documented increases in primary productivity in the region predicted to drive higher $\delta^{13}\text{C}$ values. We suggest that foraging habitat changes by birds over time may explain this discrepancy. These results demonstrate the value of combining stable isotope analyses of contemporary and archived samples as a cost effective, non-invasive method for long-term monitoring of coastal seabirds in a changing world. Further planned studies refining our understanding of spatial and temporal patterns of carbon and nitrogen flows within the Hauraki Gulf ecosystem can only improve this monitoring potential.

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LITERATURE CITED

- ✦ Auman HJ, Bond AL, Meathrel CE, Richardson AMM (2011) Urbanization of the silver gull: evidence of anthropogenic feeding regimes from stable isotope analyses. *Waterbirds* 34:70–76
- ✦ Barrett RT, Camphuysen K, Anker-Nilssen T, Chardine JW and others (2007) Diet studies of seabirds: a review and recommendations. *ICES J Mar Sci* 64:1675–1691
- ✦ Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol Biochem Zool* 75:451–458
- Beaumont J, MacDiarmid A, Morrison M, McKenzie A and others (2009) Rocky reef ecosystems — How do they function? Integrating the roles of primary and secondary production, biodiversity, and connectivity across coastal habitats. Final Research Report for Ministry of Primary Industries Project ZBD2005-09. Ministry of Primary Industries, Wellington
- ✦ Blaber SJM, Wassenberg TJ (1989) Feeding ecology of the piscivorous birds *Phalacrocorax varius*, *P. melanoleucos* and *Sterna bergii* in Moreton Bay, Australia: diets and dependence on trawler discards. *Mar Biol* 101:1–10
- ✦ Blight LK, Hobson KA, Kyser TK, Arcese P (2015) Changing gull diet in a changing world: a 150-year stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) record from feathers collected in the Pacific Northwest of North America. *Glob Change Biol* 21: 1497–1507
- ✦ Bräger S (1998) Feeding associations between white-fronted terns and Hector's dolphins in New Zealand. *Condor* 100:560–562
- ✦ Carroll EL, Gallego R, Sewell MA, Zeldis J and others (2019) Multi-locus DNA metabarcoding of zooplankton communities and scat reveal trophic interactions of a generalist predator. *Sci Rep* 9:281
- Cavallo C, Chiaradia A, Deagle BE, McInnes JC, Sánchez S, Hays GC, Reina RD (2018) Molecular analysis of predator scats reveals role of salps in temperate inshore food webs. *Front Mar Sci* 5:381
- ✦ 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. *J Plankton Res* 25:737–758
- ✦ Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar Ecol Prog Ser* 329:281–287
- ✦ Cherel Y, Hobson K, Weimerskirch H (2005) Using stable isotopes to study resource acquisition and allocation in procellariiform seabirds. *Oecologia* 145:533–540
- ✦ Cherel Y, Connan M, Jaeger A, Richard P (2014) Seabird year-round and historical feeding ecology blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values document foraging plasticity of small sympatric petrels. *Mar Ecol Prog Ser* 505:267–280
- ✦ Chiaradia A, Costalunga A, Kerry K (2003) The diet of little penguins (*Eudyptula minor*) at Phillip Island, Victoria, in the absence of a major prey — pilchard (*Sardinops sagax*). *Emu* 103:43–48
- ✦ Chikaraishi Y, Ogawa NO, Kashiya Y, Takano Y, Suga H, Tomitani A (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. *Limnol Oceanogr Methods* 7:740–750
- ✦ Chikaraishi Y, Steffan SA, Ogawa NO, Ishikawa NF, Sasaki Y, Tsuchiya M (2014) High-resolution food webs based on nitrogen isotopic composition of amino acids. *Ecol Evol* 4:2423–2449
- ✦ Dudley BD, Shima JS (2010) Algal and invertebrate bioindicators detect sewage effluent along the coast of Titahi Bay, Wellington, New Zealand. *NZ J Mar Freshw Res* 44:39–51

- ✦ Dunphy BJ, Vickers SI, Zhang J, Sagar RL and others (2020) Seabirds as environmental indicators: foraging behaviour and ecophysiology of common diving petrels (*Pelecanoides urinatrix*) reflect local-scale differences in prey availability. *Mar Biol* 167:53
- ✦ Elliott KH, Braune BM, Elliott JE (2021) Beyond bulk $\delta^{15}\text{N}$: combining a suite of stable isotopic measures improves the resolution of the food webs mediating contaminant signals across space, time and communities. *Environ Int* 148:106370
- ✦ English PA, Green DJ, Nocera JJ (2018) Stable isotopes from museum specimens may provide evidence of long-term change in the trophic ecology of a migratory aerial insectivore. *Front Ecol Evol* 6:14
- Fisheries New Zealand (2020) Fisheries assessment plenary, May 2020: stock assessments and stock status. Compiled by the Fisheries Science and Information Group, Fisheries New Zealand, Wellington
- Flemming SA, Lalas C, van Heezik Y (2013) Little penguin (*Eudyptula minor*) diet at three breeding colonies in New Zealand. *NZ J Ecol* 37:199–205
- ✦ Freeman R, Dennis T, Landers T, Thompson D, Bell E, Walker M, Guilford T (2010) Black petrels (*Procellaria parkinsoni*) patrol the ocean shelf-break: GPS tracking of a vulnerable procellariiform seabird. *PLOS ONE* 5:e9236
- ✦ Frost PGH (2017) Population status and trends of selected seabirds in northern New Zealand. Report to New Zealand Department of Conservation. www.doc.govt.nz/Documents/conservation/marine-and-coastal/marine-conservation-services/reports/int2016-04-status-and-trends-seabirds-peter.pdf
- ✦ Gaglio D, Cook TR, Connan M, Ryan PG, Sherley RB (2017) Dietary studies in birds: testing a non-invasive method using digital photography in seabirds. *Methods Ecol Evol* 8:214–222
- Gagné TO, Hyrenbach KD, Hagemann ME, Bass OL and others (2018a) Seabird trophic position across three ocean regions tracks ecosystem differences. *Front Mar Sci* 5:317
- ✦ Gagné TO, Hyrenbach KD, Hagemann ME, Van Houtan KS (2018b) Trophic signatures of seabirds suggest shifts in oceanic ecosystems. *Sci Adv* 4:eaao3946
- Gaskin C, Rayner MJ (2013) Seabirds of the Hauraki Gulf: natural history, research and conservation. Hauraki Gulf Forum, Auckland
- ✦ Gaston TF, Suthers IM (2004) Spatial variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of liver, muscle and bone in a rocky reef planktivorous fish: the relative contribution of sewage. *J Exp Mar Biol Ecol* 304:17–33
- Geurts J (2006) The feeding and breeding ecology of the little blue penguins (*Eudyptula minor*) from Tiritiri Matangi Island, New Zealand. MSc thesis, Massey University, Auckland
- ✦ Goericke R, Fry B (1994) Variations of marine plankton $\delta^{13}\text{C}$ with latitude, temperature, and dissolved CO_2 in the world ocean. *Global Biogeochem Cycles* 8:85–90
- ✦ González-Bergonzoni I, Vidal N, Wang B, Ning D, Liu Z, Jeppesen E, Meerhoff M (2015) General validation of formalin-preserved fish samples in food web studies using stable isotopes. *Methods Ecol Evol* 6:307–314
- ✦ Grecian WJ, Taylor GA, Loh G, McGill RAR and others (2016) Contrasting migratory responses of two closely related seabirds to long-term climate change. *Mar Ecol Prog Ser* 559:231–242
- Hauraki Gulf Forum (2020) State of our Gulf 2020. Hauraki Gulf/Tikapa Moana/Te Moananui-ā-Toi State of environment report 2020. Hauraki Gulf Forum, Auckland. <https://www.aucklandcouncil.govt.nz/about-auckland-council/how-auckland-council-works/harbour-forums/docsstateofgulf/state-gulf-full-report.pdf>
- ✦ Henschke N, Everett JD, Richardson AJ, Suthers IM (2016) Rethinking the role of salps in the ocean. *Trends Ecol Evol* 31:720–733
- ✦ 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 rock-hopper penguin *Eudyptes chrysocome*. *Glob Change Biol* 12:611–625
- ✦ Hobson KA (1999) Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120:314–326
- ✦ Hobson KA, Piatt JF, Pitocchelli J (1994) Using stable isotopes to determine seabird trophic relationships. *J Anim Ecol* 63:786–798
- ✦ Imber MJ (1996) The food of Cook's petrel *Pterodroma cookii* during its breeding season on Little Barrier Island, New Zealand. *Emu* 96:189–194
- Jiménez-Uzcátegui G, Vaca L, Cotín J, García C, Costales A, Sevilla C, Pérez-Rosas D (2019) Using referential values of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ to infer the foraging ecology of Galápagos seabirds. *Mar Ornithol* 47:5–10
- ✦ Keeling CD, Mook WG, Tans PP (1979) Recent trends in the $^{13}\text{C}/^{12}\text{C}$ ratio of atmospheric carbon dioxide. *Nature* 277:121–123
- Lalas C (1983) Comparative feeding ecology of New Zealand marine shags (Phalacrocoracidae). PhD thesis, University of Otago
- ✦ Laws EA, Popp BN, Bidigare RR, Kennicutt MC, Macko SA (1995) Dependence of phytoplankton carbon isotopic composition on growth rate and $[\text{CO}_2]_{\text{aq}}$: theoretical considerations and experimental results. *Geochim Cosmochim Acta* 59:1131–1138
- ✦ Lewison R, Oro D, Godley BJ, Underhill L and others (2012) Research priorities for seabirds: improving conservation and management in the 21st century. *Endang Species Res* 17:93–121
- ✦ Lorrain A, Pethybridge H, Cassar N, Receveur A and others (2020) Trends in tuna carbon isotopes suggest global changes in pelagic phytoplankton communities. *Glob Change Biol* 26:458–470
- Lukies K (2019) Kororā/little blue penguins (*Eudyptula minor*) as marine ecosystem indicators—comparing stress physiology and foraging ecology. MSc thesis, University of Auckland
- Marchant S, Higgins PJ (1990a) Handbook of Australasian, Antarctic and New Zealand Birds. 1. Ratites to petrels. Oxford University Press, Melbourne
- Marchant S, Higgins PJ (1990b) Handbook of Australian, New Zealand and Antarctic birds. 3. Snipe to pigeons. Oxford university Press, Melbourne
- ✦ McInnes JC, Alderman R, Lea MA, Raymond B and others (2017) High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. *Mol Ecol* 26:4831–4845
- ✦ McMahon KW, Polito MJ, Abel S, McCarthy MD, Thorrold SR (2015) Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (*Pygoscelis papua*). *Ecol Evol* 5:1278–1290
- Millener PR (1972) The biology of the New Zealand pied cormorant *Phalacrocorax varius varius* Gmelin (1789). MSc thesis, University of Auckland

- Mills JA (ed) (1989) Lifetime reproduction of the red-billed gull. Academic Press, London
- ✦ Mills JA, Yarrall JW, Bradford-Grieve JM, Uddstrom MJ, Renwick JA, Merilä J (2008) The impact of climate fluctuation on food availability and reproductive performance of the planktivorous red-billed gull *Larus novaehollandiae scopulinus*. *J Anim Ecol* 77:1129–1142
- ✦ Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: further evidence and the relation between $\delta^{15}\text{N}$ and animal age. *Geochim Cosmochim Acta* 48:1135–1140
- ✦ Mizutani H, Fukuda M, Kabaya Y (1992) ^{13}C and ^{15}N enrichment factors of feathers of 11 species of adult birds. *Ecology* 73:1391–1395
- ✦ O'Reilly CM, Alin SR, Plisnier PD, Cohen AS, McKee BA (2003) Climate change decreases aquatic ecosystem productivity of Lake Tanganyika, Africa. *Nature* 424:766–768
- ✦ Oczkowski A, Taplin B, Pruell R, Pimenta A, Johnson R, Grear J (2018) Carbon stable isotope values in plankton and mussels reflect changes in carbonate chemistry associated with nutrient enhanced net production. *Front Mar Sci* 5:43
- ✦ Ohkouchi N, Chikaraishi Y, Close HG, Fry B and others (2017) Advances in the application of amino acid nitrogen isotopic analysis in ecological and biogeochemical studies. *Org Geochem* 113:150–174
- ✦ Oro D (2014) Seabirds and climate: knowledge, pitfalls, and opportunities. *Front Ecol Evol* 2:79
- ✦ Paleczny M, Hammill E, Karpouzi V, Pauly D (2015) Population trend of the world's monitored seabirds, 1950–2010. *PLOS ONE* 10:e0129342
- ✦ Paul D, Skrzypek G, Fórizs I (2007) Normalization of measured stable isotopic compositions to isotope reference scales—a review. *Rapid Commun Mass Spectrom* 21:3006–3014
- Pinkerton M, Macdiarmid A, Beaumont J, Bradford-Grieve J and others (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
- Pinkerton M, Sutton P, Wood S (2019) Satellite indicators of phytoplankton and ocean surface temperature for New Zealand. Rep CR387. Ministry of Environment, Wellington
- ✦ Post DM (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83:703–718
- Powlesland RG, Sharp S, Smith A (2008) Aspects of the breeding biology of the pied shag (*Phalacrocorax varius*) at Makara Beach, Wellington, New Zealand. *Notornis* 55:69–76
- Preston TJ (2017) Relationships between foraging behaviour, diet and reproductive success at an urban colony of little penguins (*Eudyptula minor*). St Kilda, Australia. PhD dissertation, Monash University, Melbourne
- ✦ Quillfeldt P, McGill RAR, 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. *Mar Ecol Prog Ser* 295:295–304
- ✦ Quillfeldt P, McGill RAR, Masello JF, Weiss F, Strange IJ, Brickle P, Furness RW (2008) Stable isotope analysis reveals sexual and environmental variability and individual consistency in foraging of thin-billed prions. *Mar Ecol Prog Ser* 373:137–148
- ✦ Quillfeldt P, Masello JF, McGill RAR, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? *Front Zool* 7:15
- ✦ Rawlence NJ, Rayner MJ, Lovegrove TG, Stoddart D and others (2019) Archival DNA reveals cryptic biodiversity within the spotted shag (*Phalacrocorax punctatus*) from New Zealand. *Condor* 121:duz029
- ✦ Rayner MJ, Hauber ME, Clout MN, Seldon DS, Van Dijken S, Bury S, Phillips RA (2008) Foraging ecology of the Cook's petrel *Pterodroma cookii* during the austral breeding season: a comparison of its two populations. *Mar Ecol Prog Ser* 370:271–284
- ✦ Rayner MJ, Hauber ME, Steeves TE, Lawrence HA and others (2011) Contemporary and historic separation of trans-hemispheric migration between two genetically distinct seabird populations. *Nat Commun* 2:332
- ✦ Rayner MJ, Carlile N, Priddel D, Bretagnolle V and others (2016) Niche partitioning by three *Pterodroma* petrel species during non-breeding in the equatorial Pacific Ocean. *Mar Ecol Prog Ser* 549:217–229
- ✦ Rayner MJ, Taylor GA, Gaskin CP, Dunphy BJ (2017) Seasonal activity and unpredicted polar front migration of northern New Zealand common diving petrels (*Pelecanoides urinatrix*). *Emu* 117:291–298
- ✦ Roman L, Hardesty BD, Hindell MA, Wilcox C (2019) A quantitative analysis linking seabird mortality and marine debris ingestion. *Sci Rep* 9:3202
- ✦ Seers B, Shears N (2015) Spatio-temporal patterns in coastal turbidity—long-term trends and drivers of variation across an estuarine-open coast gradient. *Estuar Coast Shelf Sci* 154:137–151
- Turbott EG (1956) Notes on the plumages and breeding cycle of the spotted shag *Phalacrocorax (Stictocarbo) punctatus punctatus* (Sparman, 1786). *Rec Auckl Inst Mus* 4:343–363
- Webster ME (2017) The extended specimen: emerging frontiers in collections-based ornithological research. CRC Press, Boca Raton, FL
- ✦ Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res II* 54:211–223
- ✦ Weiss F, Furness RW, McGill RAR, Strange IJ, Masello JF, Quillfeldt P (2009) Trophic segregation of Falkland Islands seabirds: insights from stable isotope analysis. *Polar Biol* 32:1753–1763
- ✦ Wiley AE, Ostrom PH, Welch AJ, Fleischer RC and others (2013) Millennial-scale isotope records from a wide-ranging predator show evidence of recent human impact to oceanic food webs. *Proc Natl Acad Sci USA* 110:8972–8977
- ✦ 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. *Estuar Coast* 41:2240–2259