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Sentinels of change: divergence in trophic niche of New Zealand sea lions and fur seals from first human contact to today

L. C. Wing[1], S. R. Wing[1,*], R. Kinaston[2], A. J. M. Sabadel[1]

[1]Marine Science Department, University of Otago, PO Box 56, Dunedin 9054, New Zealand
[2]Department of Anatomy, University of Otago, PO Box 56, Dunedin 9054, New Zealand

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ABSTRACT: New Zealand sea lions *Phocarctos hookeri* were once widespread on New Zealand's coasts but were hunted to remnant populations in the Subantarctic islands during expansion of European settlements. In contrast, New Zealand fur seals *Arctocephalus forsteri* maintained their widespread distribution, persisting at remote colonies. The resource niche positions of these species provide insights on structure of underlying food webs and contribution of alternate sources of organic matter to ecosystem function. We measured changes in their resource niche positions with stable isotope analysis (δ^{13}C, δ^{15}N and $\delta^{15}N_{AA}$) of bone collagen from first Māori settlement (1250—1450 CE), middle European expansion (1650—1850 CE) and modern (2016 CE) time periods. Samples from each time period were collected from the Subantarctic islands, central region and from reestablishing sea lion populations on the mainland South Island. In the Subantarctic islands, high trophic positions were maintained through time but divergence in the resource niche of the 2 species between pelagic and benthic food webs occurred in the modern time period, consistent with resource limitation. In the central and mainland regions, both species declined in trophic position during the modern time period. In the central region, the 2 species maintained distinct resource niche discrimination while in the mainland region, they converged in the modern time period, consistent with high overlap on a reduced diversity of low trophic level pelagic prey. These patterns provide a unique view of the long-term changes in trophic relationships between marine top predators during the full history of human occupation in New Zealand.

KEY WORDS: *Phocarctos hookeri* · *Arctocephalus forsteri* · Trophic position · Niche overlap · Zooarchaeology · Stable isotope · Historical ecology

1. INTRODUCTION

Theory predicts that top predators may co-occur when food resources are diverse, plentiful and stable or when the number of potentially competing species remains small (Pianka 1974). In systems with complex predatory guilds, intraspecific resource competition can manifest as avoidance, exploitation, expanded individual specialization or even intraguild predation (Caro & Stoner 2003). Through these key mechanisms for persistence, intact predatory guilds provide important services across a range of ecological systems. For example, in the oceans, intact predatory guilds have been highlighted as key contributors to ecosystem function as they can regulate prey populations, thereby enhancing biodiversity, and can also transport nutrients and organic matter across important concentration gradients (Wing et al. 2014, 2021, Estes et al. 2016). Accordingly, understanding how guilds of predators have persisted in the past and continue to coexist in the face of changing prey fields and environments comprises an important research area.

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*Corresponding author: steve.wing@otago.ac.nz

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Intraguild resource competition and divergence in resource niches have been observed in pinnipeds within a range of marine habitats (Repenning 1975, Hardy et al. 2017, Brault et al. 2019, Salton et al. 2024). For example, observations of increases in individual specialization (Arnould et al. 2011, Riverón et al. 2021) and divergence between coastal and offshore foraging patterns (Pablo-Rodríguez et al. 2016, Aurioles-Gamboa & Szteren 2020) have been observed in sympatric fur seals and sea lions as resources become limiting. Accordingly, understanding how pinnipeds may be able to modify their foraging patterns as they reestablish former ranges and ecological interactions within increasingly degraded and changing ocean ecosystems can be informed by an in-depth understanding of past ecological relationships (Drago et al. 2017, Salton et al. 2024). Unfortunately, information on ecological relationships from the past have been largely lost due to modern patterns in extirpation of species (Collins et al. 2014) and highly modified trophic architecture of potential prey fields (e.g. Durante et al. 2020, 2022). The resulting gap in our knowledge can be partially filled by data gleaned from historic or zooarchaeological samples (Wing & Wing 2001, Erlandson & Rick 2010, Wing et al. 2022a). For example, only ca. 770 yr ago, New Zealand became the last major landmass to be settled by humans (Wilmshurst et al. 2011). The arrival of humans precipitated a dramatic decline in many indigenous vertebrate populations, including top trophic level marine predators (Anderson 1997, Smith 2013) recorded in a concise and remarkably complete archaeological record (Smith & James-Lee 2009, MacDiarmid 2011).

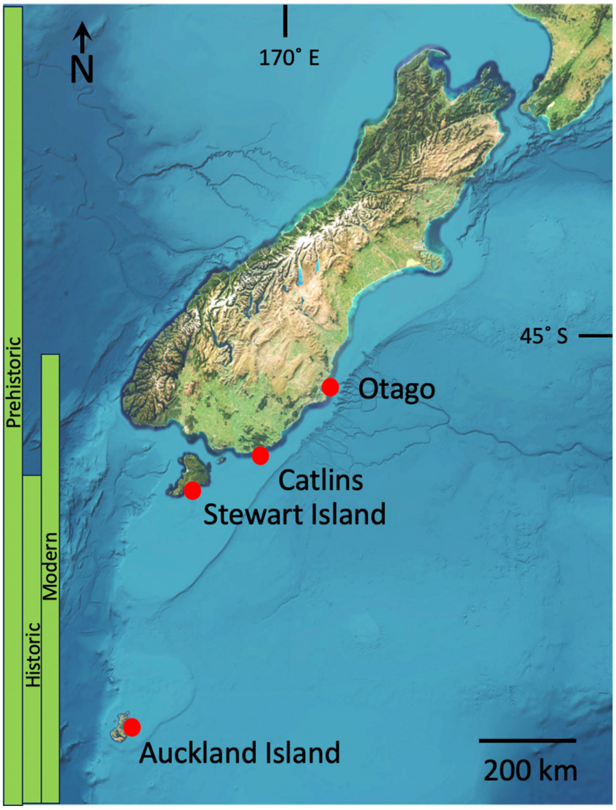

Fig. 1. New Zealand's South Island (Otago and Catlins), Stewart Island and Subantarctic Auckland Island with green bars indicating the approximate latitudinal distribution of New Zealand sea lions during early Māori (prehistoric: 1250–1450 CE), middle European (historic: 1650–1850 CE) and modern (2016 CE) time periods

New Zealand sea lions *Phocarctos hookeri* and New Zealand fur seals *Arctocephalus forsteri* were once ubiquitous on New Zealand coasts, but hunting by Māori from first contact ca. 1250 CE, and Europeans from ca. 1650 CE, reduced colonies of seals to remnant populations at remote locations such as offshore islands, and by the 1700s, extirpated sea lions from the mainland to marginal habitat at the edge of their range in the Subantarctic islands (Childerhouse & Gales 1998, Collins et al. 2014) (Fig. 1). New Zealand sea lions are generalist coastal foragers (Augé et al. 2011), although a wide range of foraging plasticity has been observed among subpopulations (Meynier et al. 2009, Chilvers 2018). Females undertake some of the deepest foraging bouts among the otariids (Chilvers & Wilkinson 2009) and can either display short benthic foraging bouts or longer deeper dive profiles into the mesopelagic zone. Diets of both females and males are plastic and extremely varied, ranging from mesopelagic squid and fishes to benthic fishes including skates and small sharks, octopus and even New Zealand fur seals (Lalas 1997, Bradshaw et al. 1998, Meynier et al. 2009). New Zealand fur seals can forage widely within the coastal zone but in modern times have been observed to particularly rely on mesopelagic fishes and squid at the shelf edge and deep scattering layer offshore (Harcourt et al. 2002, Boren 2010).

The underlying architecture of food webs supporting top predators is reflected in the trophic positions (TPs; food web height) and relative contributions of alternate sources of basal organic matter (food web breadth) to individuals in the populations (Rooney et al. 2006, Jack & Wing 2011). Both metrics can be estimated from the isotopic values (δ^{15}N and δ^{13}C) within the tissues of consumers and those of the array of basal organic matter sources supporting a food web (Fry 2006). For historic or prehistoric samples for which the baseline values of δ^{15}N and δ^{13}C have likely changed, according to changes in the carbon and nitrogen cycles, information on the isotopic values of specific amino acids ($\delta^{15}N_{AA}$ and $\delta^{13}C_{AA}$) is a useful tool to estimate TP (e.g. Sabadel et al. 2020, Wing et al. 2022a). Thus, isotopic analysis offers a quantitative and repeatable basis for measuring basic changes in food web structure and can be applied to samples of tissues from past time periods in order to reconstruct the chronology of ecosystem change. Accordingly, our approach was to use stable isotopic analysis, both $\delta^{15}N$ and $\delta^{13}C$, as well as $\delta^{15}N_{AA}$, of modern samples, carbon-dated sub-fossils and archived midden remains to precisely track changes in food webs supporting New Zealand fur seals and New Zealand sea lions from first human contact to modern times. Our analysis includes data from 3 discrete time periods including the little ice age when Māori first arrived in New Zealand (ca. 1250–1450 CE) through the middle period including expansion of European settlements (ca. 1650–1850 CE) and extirpation of New Zealand sea lions from New Zealand's South and Stewart Islands, to the modern time period (2016 CE), when New Zealand sea lions have reestablished breeding populations on Stewart Island and the Otago coast on the South Island. These data provide the basis for assessing changes in the resource niche overlap between New Zealand sea lions and New Zealand fur seals during the entire period of human occupation of New Zealand. The unique opportunity provided by these data to understanding the nature of changes through the entire human history in New Zealand is useful for forecasting future human effects on the functioning and resilience of the marine ecosystem and for developing a framework for remediation and restoration of guilds of top predators.

2. MATERIALS AND METHODS

2.1. Sea lion and fur seal tissue sampling

New Zealand has a well-preserved, recent and well-documented collection of archaeological records of New Zealand sea lion and fur seal faunal material. Archaeological collections of sea lion and fur seal bones were sampled from multiple archaeological and subfossil sites from Otago, Catlins in Southland, Stewart Island and the Auckland Islands for early (1250–1450 CE) and middle (1650–1850 CE) time periods (Higham & Horn 2000) (Fig. 1). These samples likely represented a mixture of sexes and ages. Chronology of samples was determined using a combination of radiocarbon dating and stratigraphic associations (Petchey & Higham 2000). TP of modern populations was estimated from fur samples collected from live adult individuals representing a mixture of sexes and ages at 4 sample sites along the extent of their current range (Enderby Island in the Auckland Islands; Port Pegasus on Stewart Island; The Catlins in Southland and the Otago Peninsula; n = 10–20 per site for 2 yr). Additional samples of fur, bone collagen and muscle tissues were sourced from the New Zealand Department of Conservation, which received deceased sea lions and fur seals from the Otago and Southland regions.

2.2. Collagen extraction

We followed standard protocols for obtaining collagen from zooarchaeological faunal material (Newsome et al. 2007). After thorough cleaning with aluminum oxide, 0.2–0.3 g samples of bone material were weighed and dissected into long thin fragments. The samples were demineralized at 20°C in 0.5 M hydrochloric acid, decanted and triple-rinsed with Milli-Q water, yielding collagen. The collagen was immersed in Milli-Q water and hydrochloric acid at pH 3 at 70°C for 48 h. The samples of amber or clear liquid were filtered on an EZZE filter followed by a cleaned Ultrafilter (Millipore Ultra-15 Centrifugal Filters, 30 000 molecular weight cut-off) centrifuge at 2300 rpm (592 × *g*). The resulting solution was pipetted into labelled, sealable, clean plastic tubes. The filter was rinsed twice with Milli-Q water with the rinsing solution also pipetted into the plastic tube, then freeze-dried for 48 h.

2.3. Basal organic matter sources

Suspended particulate organic matter (SPOM) was collected during summertime phytoplankton bloom events to characterize isotopic values of phytoplankton-derived organic matter in each of the study regions (e.g. Durante et al. 2021). Samples were collected by pre-filtering water with a 300 µm mesh to remove zooplankton, followed by filtering on pre-combusted (400°C for 4 h) 0.7 µm GF-F filters and treatment in a sulphurous acid (H_2SO_3) fume for 8 h. In addition, multiple samples (n = 3–5) of common macroalgal species (n = 8) were collected from sites in each of the study regions to characterize isotopic values of kelp-derived organic matter (Cornelisen et al. 2007, Wing et al. 2007, 2022a).

2.4. Stable isotope analysis of whole tissues

From each sample of fur and bone collagen (n = 243), paired samples of fur, bone collagen and muscle tissue (n = 14), a 1 mg subsample was weighed and sealed into a tin capsule for stable isotope analysis. For SPOM samples, whole filters were sealed into larger tin capsules, and for macroalgae samples, a 3 mg subsample was sealed into a tin capsule for stable isotope analysis. Samples were analysed, with replicates every eighth sample, at IsoTrace, Dunedin, by combustion in an elemental analyser (Carlo Erba NA1500) coupled to a Delta Advantage isotope ratio mass spectrometer (IRMS; Thermo-Finnigan) operating in continuous flow mode. Raw delta values were normalized and reported against the international standards for carbon and nitrogen, Vienna Pee Dee Belemnite and atmospheric air, respectively. Normalization was made by 3-point calibration with 2 glutamic acid international reference materials and a laboratory EDTA (Elemental Microanalysis) standard for carbon (USGS-40 = −26.2‰, USGS-41 = 37.8‰, EDTA = −38.52‰) and nitrogen (USGS-40 = −4.52‰, USGS-41 = 47.57‰, EDTA = −0.73‰). Analytical precision based on the replicate analyses of the quality control standard (EDTA, n = 12) was 0.2‰ for δ^{13}C and 0.3‰ for δ^{15}N.

2.5. Stable isotope analysis of amino acids

Amino acids were extracted from bone collagen (n = 37) and from paired samples of bone collagen and fur (n = 5) by hydrolyzing 2.5 g of each sample with 2 ml 6 M HCl at 110°C for 24 h in an N_2 atmosphere. An internal standard, norleucine (50 µl of 1 mg ml^{-1} solution), was added to monitor the wet chemistry and amino acid stable isotope values. Solutes were then dried under a gentle flow of N_2 at 60°C and subsequently converted into N-acetylisopropyl esters following the protocol described by Sabadel et al. (2016), modified from Styring et al. (2012). Stable isotopes of amino acid N ($\delta^{15}N_{AA}$) were measured by gas chromatography/combustion/IRMS (GC-IRMS), using a Thermo Trace gas chromatograph, the GC combustion III interface, and a Delta^{plus} XP IRMS (Thermo Fisher Scientific). Aliquots (200 µl) of derivatized amino acids were injected, inlet at 270°C in split-less mode, carried by helium at 1.4 ml min^{-1} and separated on a VF-35ms column (0.32 mm ID and a 1.0 µm film thickness). The oxidation reactor was set at 980°C and the reduction reactor at 650°C, and a liquid nitrogen cold trap was employed after the reduction reactor. Samples were analysed in duplicates along with amino acid standards of known isotopic values (measured by element analyzer-IRMS) and calibrated against an international standard, atmospheric N_2. Precision (1 SD) ranged from 0.1 to 1.0‰ with a mean of 0.5‰.

2.6. Isotopic values of multiple tissues and Suess corrections

Differences in isotopic values among tissues can be influenced by differences in turnover rate or tissue-specific differences in trophic enrichment factors (Vanderklift & Ponsard 2003). Accordingly, to enable direct comparisons of isotopic values among tissues, paired fur, bone collagen and muscle samples were collected from modern specimens. Paired frozen tissue samples were sourced from both sea lions and fur seals that had been incidentally caught in modern New Zealand fisheries. The sample archive was made available by Dr. Wendi Rowe (Marine Mammal Pathobiology, Massey University, Palmerston North, New Zealand). Generalized linear models (GLMs) were used to calculate the relationships between paired fur, muscle and bone collagen isotopic values for both sea lions and fur seals (δ^{13}C, δ^{15}N, $\delta^{15}N_{AA}$). Bone collagen was more enriched in ^{15}N than fur by 0.2‰ for $\delta^{15}N_{Pro}$, by 0.4‰ for $\delta^{15}N_{Glx}$ and by 5.3‰ for $\delta^{15}N_{Phe}$. Muscle tissue was more depleted in ^{13}C by 4.74‰ for bone collagen and by 3.58‰ in fur for δ^{13}C, and more enriched in ^{15}N by 1.31‰ and more enriched in ^{15}N by 2.19‰ than fur for δ^{15}N. We then standardized values of $\delta^{15}N_{AA}$ to those of fur to estimate TP (Table S1 in the Supplement at www.int-res.com/articles/suppl/m755p151_supp.pdf). The relationships were then used to convert isotope values based on collagen and fur to corresponding isotopic values of muscle tissue of δ^{13}C to inform mass balance analysis to estimate proportion of organic matter derived from macroalgae in the underlying food webs. Isotopic values (δ^{13}C) were also corrected for the Suess effect using ice core-based estimates of the rate of ^{13}C decrease in the atmosphere (Francey et al. 1999) for historical models. Pre-industrial samples were Suess-corrected by −0.62‰ according to Eide et al. (2017) for the south Pacific region, corroborated by Sabadel et al. (2020) for the coastal fish community in southern New Zealand, for direct comparisons with isotopic values from modern samples (Table S1).

2.7. Isotopic mixing models and trophic level estimates

For $\delta^{15}N_{AA}$ data interpretation, amino acids can be grouped based on their source, trophic or metabolic properties (Whiteman et al. 2019). The primary source amino acid (Src) analysed was phenylalanine (Phe) and trophic amino acids were proline (Pro) and glutamic acid (Glx) (Whiteman et al. 2019). Estimates of TP were calculated from differences in $\delta^{15}N_{AA}$ between the trophic (Tr) amino acid and source amino acids, using:

$$TP = (\delta^{15}N_{Tr} - \delta^{15}N_{Src} - \beta)/TDF_{Tr-Src}) + 1 \quad (1)$$

where β is the isotopic difference between $\delta^{15}N_{AA}$ of Tr and Src amino acids in the primary producers (Chikaraishi et al. 2009), and TDF_{Tr-Src} is the trophic discrimination factor representing the difference in fractionation per TP of $\delta^{15}N_{Tr}$ and $\delta^{15}N_{Src}$ (McMahon et al. 2015). We used the average of $TP_{Pro-Phe}$ and $TP_{Glx-Phe}$ to inform our mass balance mixing model and to estimate changes in TP among species, time periods and regions (Brault et al. 2019).

2.8. Mass balance mixing model

Inputs for individually based 2-source isotopic mixing models based on $\delta^{13}C$ included isotopic values for basal organic matter source pools, an estimation of trophic level (average $TP_{Pro-Phe}$ and $TP_{Glx-Phe}$) of sea lions and fur seals based on $\delta^{15}N_{AA}$ and the trophic discrimination factor $\Delta^{13}C$ (Phillips & Gregg 2001). We characterized isotopic values of phytoplankton by sampling SPOM during the summer bloom period across the study region ($n = 20$; 5 samples per site at 4 sites). We calculated a weighted aggregate isotopic value for common subtidal kelps from samples spatially stratified across the sampling region ($n = 300$; 3–7 species, 5 samples at 3 sub-sites at 4 sites) to calculate an aggregate macroalgal value for $\delta^{13}C$ with variance stratified among species. Average values of $\delta^{3}C$ for phytoplankton (SPOM) ($\delta^{13}C = -23.62 \pm 0.08‰$) and macroalgae ($\delta^{13}C = -16.03 \pm 0.82‰$) were then calculated. For all sea lion and fur seal samples, averages of $TP_{Pro-Phe}$ and $TP_{Glx-Phe}$ were used to inform an individual-based mass balance mixing model (Jack & Wing 2011) using $\delta^{13}C$ to calculate the relative contribution of macroalgae and phytoplankton to underlying food webs. We used the average trophic discrimination factor ($\Delta^{13}C$) of +0.4‰ (SE 0.17) after McCutchan et al. (2003).

2.9. Statistical modelling

We used general linear mixed models in the JMP Pro (Ver 17.0.0, SAS) model fitting platform to test for differences in TP and the proportion of kelp-derived organic matter supporting underlying food webs among species (2 levels, fixed), crossed with time periods (3 levels, fixed) within each of the 3 regions. Pairwise differences among species within and among time periods were then tested with a series of Tukey's post hoc tests.

We used permutational multivariate analysis of variance (PERMANOVA+, Ver 7) to test for differences in niche position of individual sea lions and fur seals based on values of TP and the proportion of kelp-derived organic matter supporting their underlying food webs from the 3 regions and 3 time periods, as well as between preindustrial and the modern time periods. Resemblance matrices were based on Euclidean distances of TP and proportion of kelp-derived organic matter supporting the underlying food webs among samples from individual animals.

3. RESULTS

The estimates of trophic level and contributions of kelp-derived organic matter to the food webs supporting both New Zealand sea lions and New Zealand fur seals enabled us to differentiate the trophic niche of each species in the Subantarctic (Auckland Island), Central (Stewart Island and Catlins), and Mainland (Otago) regions from early (1250–1450 CE), middle (1650–1850 CE) and modern (2016 CE) time periods. Results of the GLM testing for changes in relative TP of sea lions and fur seals by time period within the Subantarctic region revealed no significant differences in the TP of both species through time (Fig. 2a). In contrast, a GLM testing for changes in the contribution of kelp-derived organic matter to the food webs supporting both sea lions and furs seals in the Subantarctic region revealed significant differences during the early time period (1250–1450 CE), no difference during the middle time period (1650–1850 CE) and a general decline and large difference between species in the modern time period (2016 CE) (whole model: $F_{5,122} = 2.83$, $r^2 = 0.10$, $p < 0.01$: effects test Time period: $F = 6.65$, $p = 0.002$: Time period × species: $F = 2.50$, $p < 0.05$: sea lion 1250–1450 CE (ab), fur seal 1250–1450 CE (a), sea lion 1650–1850 CE (ab), fur seal 1650–1850 CE (ab), sea lion 2016 CE (b), fur seal 2016 CE (c)) (Fig. 2b).

Results of the GLM testing for changes in relative TP by species and time period within the Central region revealed no significant differences between species within time periods but a significant decline in TP for both species in the modern time period (whole model: $F_{5,30} = 10.93$, $r^2 = 0.65$, $p < 0.0001$: effects test Time period: $F = 25.37$, $p < 0.0001$: 1250–1450 CE (a), 1650–1850 CE (a), 2016 CE (b)) (Fig. 3a). Similarly, a GLM testing for changes in the contribution of kelp-derived organic matter to the food webs supporting both sea lions and furs seals in the Central

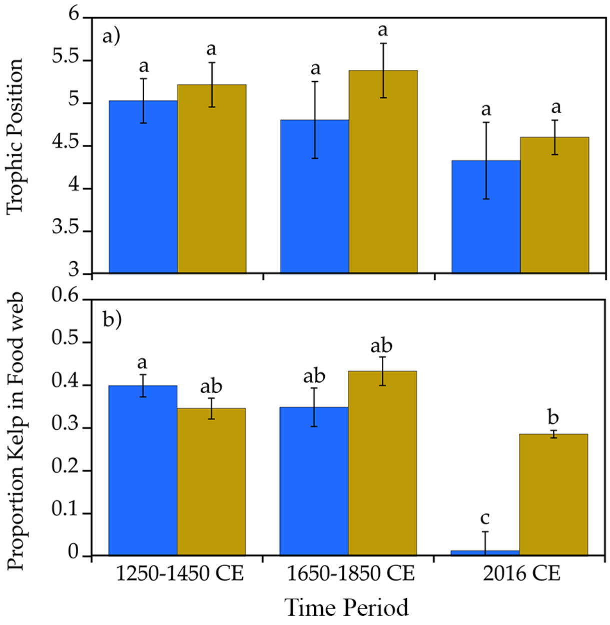

Fig. 2. (a) Trophic position and (b) proportion of kelp-derived organic matter in the underlying food web of New Zealand sea lions (yellow bars) and New Zealand fur seals (blue bars) during early Māori (1250–1450 CE) middle European (1650–1850 CE) and modern (2016 CE) time periods in the Subantarctic Auckland Islands. Error bars indicate ±1 SE; levels not connected by the same letter were significantly different in a Tukey's post hoc test

region revealed significant differences between species in each time period and a general decline in in the modern time period, particularly for fur seals (whole model: $F_{5,165}$ = 23.74, r^2 = 0.42, $p < 0.0001$: effects test Time period × Species: F = 17.65, $p < 0.0001$: sea lion 1250–1450 CE (c), fur seal 1250–1450 CE (ab), sea lion 1650–1850 CE (a), fur seal 1650–1850 CE (bc), sea lion 2016 CE (c), fur seal 2016 CE (d)) (Fig. 3b).

Results of the GLM testing for changes in relative TP by species and time period within the Mainland region revealed significant differences between species in the early time period, none in the middle or modern time periods and a significant decline in TP for both species in the modern time period relative to earlier time periods (whole model: $F_{5,20}$ = 14.84, r^2 = 0.79, $p < 0.0001$: effects test Time period: F = 32.65, $p < 0.0001$: 1250–1450 CE (a), 1650–1850 CE (a), 2016 CE (b)) (Fig. 4a). Similarly, a GLM testing for changes in the contribution of kelp-derived organic matter to the food webs supporting both species in the Mainland region revealed a general decline in the modern time period for both species (whole model: $F_{5,114}$ = 14.92, r^2 = 0.40, $p < 0.0001$: effects test Time period: F = 21.46, $p < 0.0001$: 1250–1450 CE (a), 1650–1850 CE (a), 2016 CE (b)) (Fig. 4b).

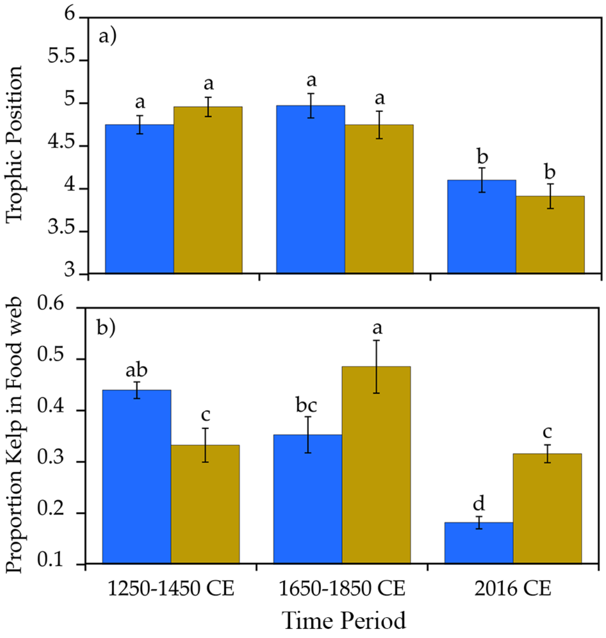

Fig. 3. (a) Trophic position and (b) proportion of kelp-derived organic matter in the underlying food web of New Zealand sea lions (yellow bars) and New Zealand fur seals (blue bars) during early Māori (1250–1450 CE), middle European (1650–1850 CE) and modern (2016 CE) time periods in the Central region including Stewart Island and the northern Catlins coastline. Error bars indicate ±1 SE; levels not connected by the same letter were significantly different in a Tukey's post hoc test

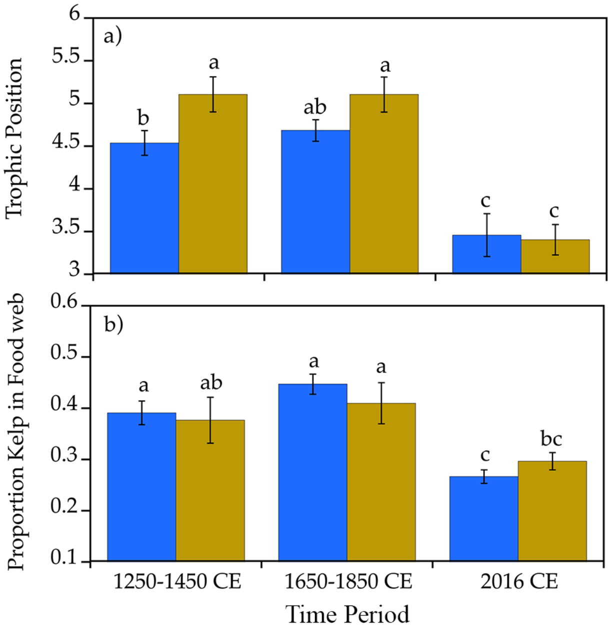

Fig. 4. (a) Trophic position and (b) proportion of kelp-derived organic matter in the underlying food web of New Zealand sea lions (yellow bars) and New Zealand fur seals (blue bars) during early Māori (1250–1450 CE) middle European (1650–1850 CE) and modern (2016 CE) time periods in the Mainland Otago region where New Zealand sea lions reestablished a breeding population in the early 1990s. Error bars indicate ±1 SE; levels not connected by the same letter were significantly different in a Tukey's post hoc test

Results of the multivariate PERMANOVA models of multivariate similarity in TP and contribution of kelp-derived organic matter to the food webs supporting sea lions and fur seals revealed distinct patterns of change among time periods within each region. In the Subantarctic region, the niche position of the 2 species overlapped in both the early and middle time periods but significantly diverged in the modern time period with evidence for a shift to a wholly pelagic food web among fur seals (Fig. 5, Table 1). In the Central and Mainland regions, the 2 species occupied significantly different niche positions in the early and modern time periods but not in the middle time period (Figs. 6 & 7, Table 1). The Euclidean distance between centroids of niche position increased with time in the Subantarctic islands and Central regions, but decreased with time in the Mainland region (Fig. 8). Distance between centroids in this case provides a repeatable quantitative measure of resource niche separation.

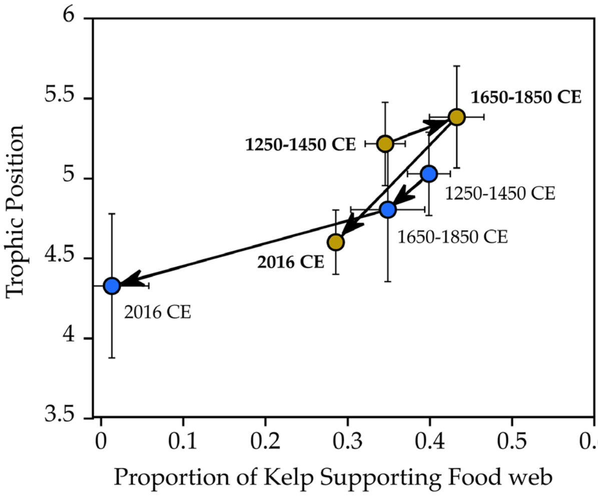

Fig. 5. Trajectories of change in trophic position and proportion of kelp-derived organic matter in the underlying food web for New Zealand sea lions (yellow circles) and New Zealand fur seals (blue circles) from the Subantarctic Auckland Islands. Error bars indicate ±1 SE. Time periods are indicated for sea lions in **bold** and fur seals in normal font

4. DISCUSSION

The data and results presented in the present study provide new insight into the consequences of long-term changes in trophic architecture of marine food webs following human settlement for changing resource niche positions of top predators. Within the ca. 770 yr time frame, we observed consistent patterns in declines in TP in New Zealand sea lions and fur seals during the modern time period at the northern extent of their overlapping ranges in the Central and Mainland regions, where the effects of industrialized fish-

Table 1. Results of a series of permutational multivariate analysis of variance (PERMANOVA) tests for differences in trophic position and the proportion of kelp-based organic matter support the food webs of the New Zealand sea lion *Phocarctos hookeri* and the New Zealand fur seal *Arctocephalus forsteri* from 3 different regions for samples from 3 different time periods: early (1250–1450 CE), middle (1650–1850 CE) and modern period (2016 CE). Significance tests as indicated by permutational p-values (p(perm)) that were <0.05 are highlighted in **bold**; p(perm) for tests with low number of unique permutations were calculated using a Monte Carlo simulation (p(MC))

Region	Test	MS	Test statistic	p(perm)	Unique perms
Subantarctic	Species	0.74	Pseudo-F = 1.51	0.17	9895
	Time	1.58	Pseudo-F = 3.22	0.07	9943
	Species×Time	3.60	Pseudo-F = 0.96	0.13	9925
	1250–1450 CE, Species		t = 1.86	0.09	p(MC)
	1650–1850 CE, Species		t = 1.07	0.39	p(MC)
	2016 CE, Species		t = 1.69	**0.05**	5045
Central	Species	6.87	Pseudo-F = 23.13	**0.0001**	9897
	Time	2.69	Pseudo-F = 9.05	**0.0004**	9958
	Species×Time	0.74	Pseudo-F = 2.49	**0.09**	9958
	1250–1450 CE, Species		t = 2.36	**0.02**	9922
	1650–1850 CE, Species		t = 1.40	0.19	1714
	2016 CE, Species		t = 8.57	**0.0001**	9919
Mainland	Species	4.98	Pseudo-F = 16.2	**0.0001**	9906
	Time	0.22	Pseudo-F = 0.73	0.50	9936
	Species×Time	0.66	Pseudo-F = 2.13	0.12	9954
	1250–1450 CE, Species		t = 2.28	**0.05**	4198
	1650–1850 CE, Species		t = 1.95	0.06	9199
	2016 CE, Species		t = 2.40	**0.02**	9949

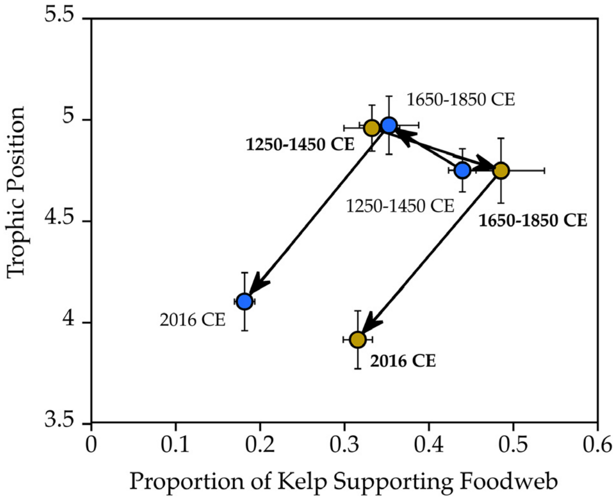

Fig. 6. Trajectories of change in trophic position and proportion of kelp-derived organic matter in the underlying food web for New Zealand sea lions (yellow circles) and New Zealand fur seals (blue circles) from the Central region including Stewart Island and the northern Catlins coastline. Error bars indicate ±1 SE. Time periods are indicated for sea lions in **bold** and fur seals in normal font

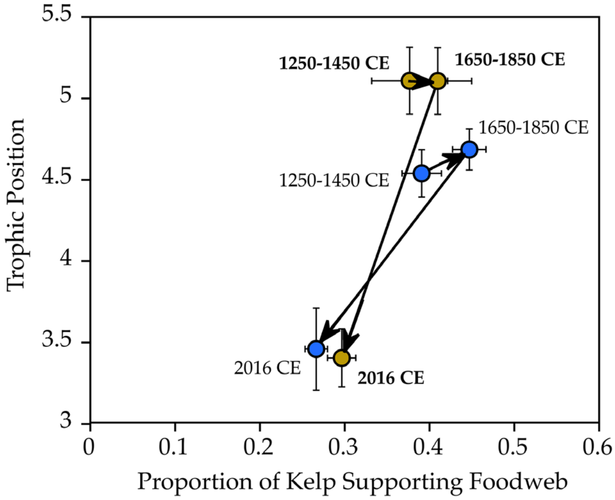

Fig. 7. Trajectories of change in trophic position and proportion of kelp-derived organic matter in the underlying food web for New Zealand sea lions (yellow circles) and New Zealand fur seals (blue circles) from the Mainland Otago region. Error bars indicate ±1 SE. Time periods are indicated for sea lions in **bold** and fur seals in normal font

ing on trophic downgrading have been most severe (Durante et al. 2020, 2022). In the Subantarctic islands, fur seals diverged onto purely pelagic-based food webs while sea lions maintained a mixed benthic—pelagic based food web during the modern period. In the Central region, there was a significant decline in TPs and in the contribution of kelp-derived

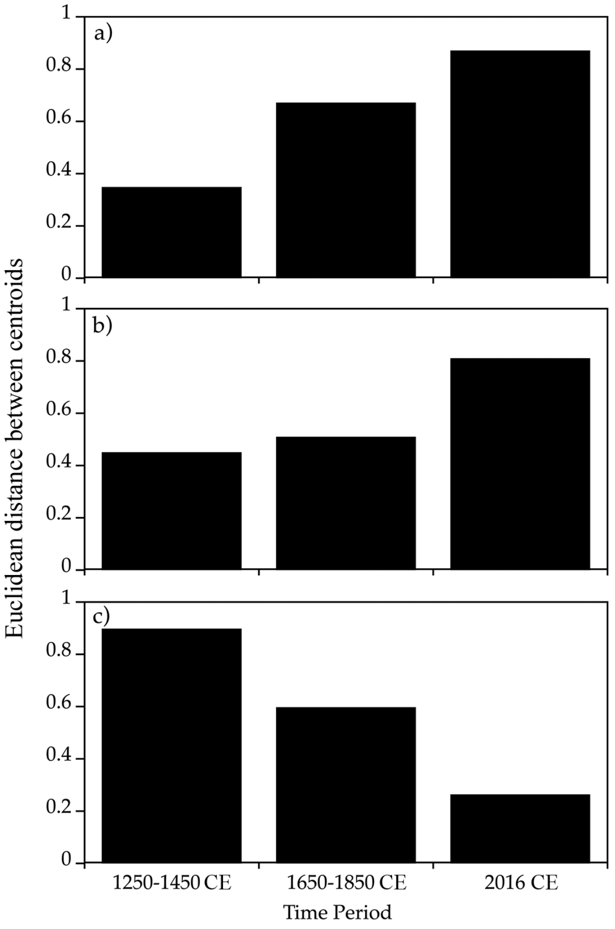

Fig. 8. Average Euclidean distances between multivariate centroids of trophic position and proportion of kelp-derived organic matter in underlying food webs for New Zealand sea lions and New Zealand fur seals as a measure of resource niche divergence or convergence among time periods for the (a) Subantarctic, (b) Central and (c) Mainland regions

organic matter to the food webs supporting both sea lions and fur seals in the modern time period. In the Mainland region, where sea lions have recently reestablished a breeding population, the 2 species have converged onto a very low trophic level resource niche in the modern time period with a consistent decline in the contribution of kelp-derived organic matter to the food web.

Investigation of the archaeological record of ecologically important species, in particular high trophic level predators, represents an important method of documenting long-term changes in community ecology, in particular consequences of shifting trophic architecture in the marine environment. The combination of zooarchaeological and stable isotopic data is an especially powerful approach in this regard. Within the last decade, there has been an expansion of these types of analyses, more recently including compound-specific stable isotope data, representing a significant analytical advance for resolving past changes in TP. Combining these complementary geochemical tools offers high-resolution delineation of food webs in space and time at a new level of precision.

Resource overlap between New Zealand sea lions and New Zealand fur seals likely reflects patterns in resource abundance as well as changes in the base of productivity among time periods reflecting different periods of human occupation and environmental conditions. Our focus on these changes in overlap in resource use between the 2 species among 3 key regions provided the basis for assessing several important contexts for their co-occurrence and reestablishment of connections within coastal food webs. In the Mainland region, New Zealand sea lions were extirpated fully by the 1700s while New Zealand fur seal populations were decimated but persistent during the sealing and whaling period of European expansion (Collins et al. 2016). In 1993, the first New Zealand sea lion to breed on the mainland in ca. 200 yr gave birth to a pup on the Otago coast and the population has now been slowly reestablishing in the region where New Zealand fur seals have persisted (Augé et al. 2011). The potential coastal prey base of fishes has undergone a dramatic decline in both abundance and diversity with the expansion of industrialized fishing from the 1960s and a general gradient in intensity of effects resulting in declining trophic structure from north to south (Durante et al. 2020, 2022). The resulting change in availability of coastal prey for reestablishing sea lion populations presented a distinct challenge in terms of resource niche overlap with fur seals. Our isotopic results indicate that there was a constraint in resource niche and convergence from the middle time period when both species persisted on a relatively high trophic level diet with up to 40% contribution of kelp-derived organic matter in the underlying food web to the modern time period when both species overlap in resource use and rely on a low trophic level, primarily pelagic prey base (Figs. 4 & 7). These results are consistent with observations of historic decline in kelp forest habitats in the region as well as trophic downgrading of the prey base (Durante et al. 2020, Sabadel et al. 2020, Wing et al. 2022a,b).

The Central region was an area that underwent a similar extirpation of New Zealand sea lions in the 1700s and a decline in fur seal colonies. However, colonies of juvenile male sea lions reestablished in the region preceding reestablishment of breeding colonies in the 1990s (Childerhouse & Gales 1998, Collins et al. 2016). Our isotopic data and analyses indicate that the 2 species persisted on a relatively high trophic level diet from the early to middle time periods with clear differentiation of the 2 species between more pelagic and more macroalgal-derived organic matter supply to food webs (Figs. 3 & 6). Resource niche divergence was maintained between middle and modern time periods, but there was a sharp decline in TP and also a decline in the contribution of kelp-derived organic matter to the underlying food web. These data are consistent with both observations of decline in kelp forest habitats and trophic downgrading as observed in the Mainland region. However, maintenance and increases in resource niche divergence indicate that the 2 species have the flexibility to partition available resources, as has been observed in other systems with sympatric populations of fur seals and sea lions (Pablo-Rodríguez et al. 2016, Aurioles-Gamboa & Szteren 2020).

The Subantarctic islands remained as the only one amongst the 3 regions with populations of both species throughout the ca. 770 yr time period of human occupation. In the Subantarctic Auckland Islands, both species have persisted through all 3 time periods, maintaining relatively high trophic levels, and for sea lions, there has been a significant contribution (30–40%) of kelp-derived organic matter to the underlying food web throughout history. During the modern period, there was an apparent large divergence in the resource niche, with sea lions maintaining a relatively small connection to the coastal kelp-based food web while fur seals shifted to a purely pelagic based diet at a lower trophic level. These patterns are consistent with observations of strong resource competition between commercial fisheries around the Auckland Islands and the local sea lion populations (Robertson & Chilvers 2011). As observed in the Central region, resource partitioning by way of divergence in foraging strategies provides an important mechanism for co-occurrence of high trophic level predators.

Our estimates of the proportion of kelp-derived organic matter supporting underlying food webs for both the New Zealand sea lion and fur seal were relatively high (33–48%) in each region in the early Māori (1250–1450 CE) and middle (1650–1850 CE) time periods and relatively low (1–31%) in the modern time period, consistent with similar observations for mesopredatory fishes (Wing et al. 2022a). The observed pattern is also consistent with reports of long-term declines in kelp forest habitats in southern New Zealand linked with extensive coastal sedimentation as well as overexploitation of predatory fish and rock lobsters leading to kelp forest declines via trophic cascades in the modern time period (Wing et al. 2022b). Contribution of kelp-derived organic matter to coastal fish communities in regions with extensive kelp forest habitats and pristine forested catchments in New Zealand have been estimated to be 40–60%, while in regions with loss of kelp forest habitats, the contribution falls to below 30% (Udy et al. 2019a,b). These results are consistent with the idea that before widescale land clearances and declines in kelp forest habitats, both New Zealand sea lions and fur seals foraged more coastally on food webs linked more closely with kelp forest production. Within the Subantarctic islands and Central region, there was an increase in the contribution of kelp-derived organic matter to food webs supporting the New Zealand sea lion between the early time period when sea surface temperatures were anomalously cold during the little ice age and the middle time period when surface waters warmed (Lorrey et al. 2014). While we are unable to resolve differences in TP between the sexes within each of the 2 species, our data are consistent with distinct changes in resource niche separation among species through time. The observed differences in resource niche separation were likely driven by changes in resource availability over time, with decline in kelp-based food webs and competition for prey with fisheries as proximate causes. However, large changes in the relative abundance of the 2 species within each region may also have contributed to resource niche divergence.

The average TPs of both New Zealand sea lions and fur seals declined from relatively high and consistent values in the early and middle time periods (4.5–5.1) to low values (3.4–4.1) in the modern time period in the Central and Mainland regions. These patterns are consistent with observations of trophic downgrading in the prey base during the expansion of industrialized fishing in New Zealand (Durante et al. 2020, 2022). Shifts to low trophic level, more pelagic prey are consistent with a directional shift towards more offshore food resources for both sea lions and fur seals in the modern time period as coastal resources become scarce.

The present study quantifies a fundamental but gradual change that has occurred in the structure and function of the coastal marine ecosystem in New Zealand during the full history of human occupation of the islands. The data and results provide an important historical baseline and a glimpse into past ecological relationships in the coastal marine food web. The patterns observed signal some of the important consequences of shifts in trophic structure and particularly loss of kelp forest habitats for maintenance of co-occurring large predators. Sea lions and fur seals function as important ecological sentinels of change in this case and understanding the ecosystem level requirements for co-occurrence is enhanced by long-term ecological data. We demonstrate the value of combining archaeological and ecological research in quantifying previously unknown ecological potential of our native and critically endangered fauna and for developing a framework for remediation and restoration as well as forecasting future human effects on the functioning and resilience of marine ecosystems.

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LITERATURE CITED

Anderson A (1997) Prehistoric Polynesian impact on the New Zealand environment: Te whenua hou. Historical ecology in the Pacific islands. Yale University Press, New Haven, CT

Arnould JPY, Cherel Y, Gibbens J, White JG, Littnan CL (2011) Stable isotopes reveal inter-annual and inter-individual variation in the diet of female Australian fur seals. Mar Ecol Prog Ser 422:291–302

Augé AA, Chilvers BL, Moore AB, Davis LS (2011) Foraging behaviour indicates marginal marine habitat for New Zealand sea lions: remnant versus recolonising populations. Mar Ecol Prog Ser 432:247–256

Aurioles-Gamboa D, Szteren D (2020) Lifetime coastal and oceanic foraging patterns of male Guadalupe fur seals and California sea lions. Mar Mamm Sci 36:246–259

Boren LJ (2010) Diet of New Zealand fur seals (*Arctocephalus forsteri*): a summary. Department of Conservation, Wellington

Bradshaw CJA, Lalas C, McConkey S (1998) New Zealand sea lion predation on New Zealand fur seals. NZ J Mar Freshw Res 32:101–104

Brault EK, Koch PL, Costa DP, McCarthy MD and others (2019) Trophic position and foraging ecology of Ross, Weddell, and crabeater seals revealed by compound-specific isotope analysis. Mar Ecol Prog Ser 611:1–18

Caro TM, Stoner CJ (2003) The potential for interspecific competition among African carnivores. Biol Conserv 110: 67–75

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y and others (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol Oceanogr Methods 7: 740–750

Childerhouse S, Gales N (1998) Historical and modern distribution and abundance of the New Zealand sea lion *Phocarctos hookeri*. NZ J Zool 25:1–16

Chilvers BL (2018) Preliminary assessment of the foraging behaviour and population dynamics of a cryptic population of the endangered New Zealand sea lion. NZ J Ecol 42:48–57

Chilvers BL, Wilkinson IS (2009) Diverse foraging strategies in lactating New Zealand sea lions. Mar Ecol Prog Ser 378:299–308

Collins CJ, Rawlence NJ, Prost S, Anderson CNK and others (2014) Extinction and recolonization of coastal megafauna following human arrival in New Zealand. Proc R Soc B 281:20140097

Collins CJ, Chilvers BL, Taylor M, Robertson BC (2016) Historical population size of the threatened New Zealand sea lion *Phocarctos hookeri*. J Mammal 90:436–443

Cornelisen CD, Wing SR, Clark KL, Bowman MH, Frew RD, Hurd CL (2007) Patterns in the δ^{13}C and δ^{15}N signature of *Ulva pertusa*: interaction between physical gradients and nutrient source pools. Limnol Oceanogr 52:820–832

Drago M, Cardona L, Franco-Trecu V, Crespo EA and others (2017) Isotopic niche partitioning between two apex predators over time. J Anim Ecol 86:766–780

Durante LM, Beentjes M, Wing SR (2020) Shifting trophic architecture of marine fisheries in New Zealand: implications for guiding effective ecosystem-based management. Fish Fish 21:813–830

Durante LM, Smith RO, Kolodzey S, McMullin RM and others (2021) Oceanographic transport along frontal zones forms carbon, nitrogen and oxygen isoscapes on the east coast of New Zealand: implications for food-web studies. Cont Shelf Res 216:104368

Durante L, Wing S, Ingram T, Sabadel A, Shima J (2022) Changes in trophic structure of an exploited fish community at the centennial scale are linked to fisheries and climate forces. Sci Rep 12:4309

Eide M, Olsen A, Ninnemann US, Eldevik T (2017) A global estimate of the full oceanic ^{13}C Suess effect since the preindustrial. Global Biogeochem Cycles 31:492–514

Erlandson JM, Rick TC (2010) Archaeology meets marine ecology: the antiquity of maritime cultures and human impacts on marine fisheries and ecosystems. Annu Rev Mar Sci 2:231–251

Estes JA, Heithaus M, McCauley DJ, Rasher DB, Worm B (2016) Megafaunal impacts on structure and function of ocean ecosystems. Annu Rev Environ Resour 41:83–116

Francey RJ, Allison CE, Etheridge DM, Trudinger CM and others (1999) A 1000-year high precision record of δ^{13}C in atmospheric CO$_2$. Tellus B Chem Phys Meterol 51:170–193

Fry B (2006) Stable isotopic ecology. Springer, New York, NY

Harcourt RG, Bradshaw CJA, Dickson K, Davis LS (2002) Foraging ecology of a generalist predator, the female New Zealand fur seal. Mar Ecol Prog Ser 227:11–24

Hardy N, Berry T, Kelaher BP, Goldsworthy SD and others (2017) Assessing the trophic ecology of top predators across a recolonisation frontier using DNA metabarcoding of diets. Mar Ecol Prog Ser 573:237–254

Higham TFG, Horn PL (2000) Seasonal dating using fish otoliths: results from the Shag River Mouth site, New Zealand. J Archaeol Sci 27:439–448

Jack LC, Wing SR (2011) Individual variability in trophic position and diet of a marine omnivore is linked to kelp bed habitat. Mar Ecol Prog Ser 443:129–139

Lalas C (1997) Prey of Hooker's sea lions, *Phocarctos hookeri*, based at Otago Peninsula, New Zealand. In: Hindell M, Kemper C (eds) Marine mammal research in the Southern Hemisphere. Surrey Beatty, Chipping Norton, p 130–136

Lorrey A, Fauchereau N, Stanton C, Chappell P and others (2014) The Little Ice Age climate of New Zealand reconstructed from Southern Alps cirque glaciers: a synoptic type approach. Clim Dyn 42:3039–3060

MacDiarmid A (2011) Large isolated late-settled islands: potential tests of human impacts on marine ecosystems. MS31 Part A. Report to New Zealand Ministry of Fisheries, Wellington

McCutchan JH Jr, Lewis WM, Kendall C, McGrath CC (2003) Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102:378–390

McMahon KW, Thorrold SR, Elsdon TS, McCarthy MD (2015) Trophic discrimination of nitrogen stable isotopes in amino acids varies with diet quality in a marine fish. Limnol Oceanogr 60:1076–1087

Meynier L, MacKenzie DDS, Duignan PJ, Chilvers BL, Morel PCH (2009) Variability in the diet of New Zealand sea lion (*Phocarctos hookeri*) at the Auckland Islands, New Zealand. Mar Mamm Sci 25:302–326

Newsome SD, Etnier MA, Gifford-Gonzalez D, Phillips DL and others (2007) The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. Proc Natl Acad Sci USA 104:9709–9714

Pablo-Rodríguez N, Aurioles-Gamboa D, Montero-Muñoz JL (2016) Niche overlap and habitat use at distinct temporal scales among the California sea lions (*Zalophus californianus*) and Guadalupe fur seals (*Arctocephalus philippii townsendi*). Mar Mamm Sci 32: 466–489

Petchey F, Higham T (2000) Bone diagenesis and radiocarbon dating of fish bones at the Shag River Mouth site, New Zealand. J Archaeol Sci 27:135–150

Phillips DL, Gregg JW (2001) Uncertainty in source partitioning using stable isotopes. Oecologia 127:171–179

Pianka ER (1974) Niche overlap and diffuse competition. Proc Natl Acad Sci USA 71:2141–2145

Repenning CA (1975) Otarioid evolution. Rapp P-V Reùn Cons Int Explor Mer 169:27–33

Riverón S, Raoult V, Baylis AMM, Jones KA, Slip DJ, Harcourt RG (2021) Pelagic and benthic ecosystems drive differences in population and individual specializations in marine predators. Oecologia 196:891–904

Robertson BC, Chilvers BL (2011) The population decline of the New Zealand sea lion *Phocarctos hookeri*: a review of possible causes. Mammal Rev 41:253–275

Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. Nature 442:265–269

Sabadel AJM, Woodward EM, Van Hale R, Frew RD (2016) Compound-specific isotope analysis of amino acids: a tool to unravel complex symbiotic trophic relationships. Food Webs 6:9–18

Sabadel AJM, Durante LM, Wing SR (2020) Stable isotopes of amino acids from reef fishes uncover Suess and nitrogen enrichment effects on local ecosystems. Mar Ecol Prog Ser 647:149–160

Salton M, Raoult V, Jonsen I, Harcourt R (2024) Niche partitioning and individual specialisation in resources and space use of sympatric fur seals at their range margin. Oecologia 204:815–832

Smith I (2013) Pre-European Māori exploitation of marine resources in two New Zealand case study areas: species range and temporal change. J R Soc NZ 43:1–37

Smith I, James-Lee T (2009) Data for archaezoological analysis of marine resource use in two New Zealand study areas. Archaeology Department, University of Otago, Dunedin

Styring AK, Kuhl A, Knowles TDJ, Fraser RA, Bogaard A, Evershed RP (2012) Practical considerations in the determination of compound-specific amino acid δ^{15}N values in animal and plant tissues by gas chromatography-combustion-isotope ratio mass spectrometry, following derivatisation to their N-acetylisopropyl esters. Rapid Commun Mass Spectrom 26:2328–2334

Udy JA, Wing SR, O'Connell-Milne SA, Durante LM, McMullin RM, Kolodzey S, Frew RD (2019a) Regional differences in supply of organic matter from kelp forests drive trophodynamics of temperate reef fish. Mar Ecol Prog Ser 621:19–32

Udy JA, Wing SR, O'Connell-Milne SA, Kolodzey S, McMullin RM, Durante LM, Frew RD (2019b) Organic matter derived from kelp supports a large proportion of biomass in temperate rocky reef fish communities: implications for ecosystem-based management. Aquat Conserv 29:1503–1519

Vanderklift MA, Ponsard S (2003) Sources of variation in consumer-diet δ^{15}N enrichment: a meta-analysis. Oecologia 136:169–182

Whiteman JP, Smith EAE, Besser AC, Newsome SD (2019) A guide to using compound-specific stable isotope analysis to study the fates of molecules in organisms and ecosystems. Diversity 11:8

Wilmshurst JM, Hunt TL, Lipo CP, Anderson AJ (2011) High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. Proc Natl Acad Sci USA 108:1815–1820

Wing SR, Wing ES (2001) Prehistoric fisheries in the Caribbean. Coral Reefs 20:1–8

Wing SR, Leichter JJ, Perrin CM, Rutger SM, Bowman MH, Cornelisen CD (2007) Topographic shading and wave exposure influence morphology and ecophysiology of *Ecklonia radiata* (C. Agardh 1817) in Fiordland, New Zealand. Limnol Oceanogr 52:1853–1864

Wing SR, Jack L, Shatova O, Leichter JJ, Barr D, Frew RD, Gault-Ringold M (2014) Seabirds and marine mammals redistribute bioavailable iron in the Southern Ocean. Mar Ecol Prog Ser 510:1–13

Wing SR, Wing LC, O'Connell-Milne SA, Barr D, Stokes D, Genovese S, Leichter JJ (2021) Penguins and seals transport limiting nutrients between offshore pelagic and coastal regions of Antarctica under changing sea ice. Ecosystems 24:1203–1221

Wing SR, Durante LM, Connolly AJ, Sabadel AJM, Wing LC (2022a) Overexploitation and decline in kelp forests inflate the bioenergetic costs of fisheries. Glob Ecol Biogeogr 31:621–635

Wing SR, Shears NT, Tait LW, Schiel DR (2022b) The legacies of land clearance and trophic downgrading accumulate to affect structure and function of kelp forests. Ecosphere 13:e4303

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