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What difference does a century make? Shifts in the ecosystem structure of the Ross Sea, Antarctica, as evidenced from a sentinel species, the Weddell seal

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The arrival of humans to Antarctica's Ross Sea (100+ years ago) led to a slow, but sustained increase in human activities in the area. To investigate if human presence has influenced the structure of the ecosystem over the last century, we compared historical (*ca* 100 years old) and modern samples of a sentinel species, the Weddell seal (*Leptonychotes weddellii*), using both bulk tissue and compound-specific stable isotope analysis. The historical isotopic niche of Weddell seals was over five times larger than the modern niche. The isotopic values of individual amino acids showed a clear segregation between historical and modern samples, indicative of differences at the base of the trophic web. Further, we found no significant differences in the trophic position of Weddell seals between the two periods. Our study revealed that the Ross Sea has undergone detectable changes (i.e. in the primary producers community) in the last century, but the presence of humans has not disrupted trophic interactions supporting Weddell seals.

1. Introduction

The continuous expansion of the human population has increasingly impacted the world's oceans and its multiple ecosystems. Activities associated with exploitation of biological resources (e.g. fishing) and, more recently, those inducing climatic change have resulted in major changes to both ecosystems and biogeochemical cycles [1]. Largely due to its relative isolation and the historical challenges in reaching it, the Ross Sea, Antarctica, has remained relatively unaffected by humans [2]. Humans only arrived at the Ross Sea in the mid-1800s, and it was not until the early 1900s that the early Antarctic explorers landed in the southernmost seasonally ice-free area, McMurdo Sound [3]. Since that time, human impacts have remained relatively limited, except perhaps for whaling which, despite not occurring within this system, could have impacted the overall structure of the ecosystem [4].

Today, however, human activities take place in the Ross Sea. Many are related to scientific investigation, as the Ross Sea hosts several research stations, leading to a limited year-round human presence. Furthermore, since the mid-1990s a small but important fishing fleet operates off the continental shelf of the Ross Sea, targeting the Antarctic toothfish (*Dissostichus mawsonii*), with catches of *ca* 3 000 tonnes per year (approx. 0.06% of the total biomass for the Ross Sea) [5,6]. The potential consequences of these activities remain largely unknown, although it has been hypothesized that the removal of toothfish could already have impacted the structure of the ecosystem [7].

Weddell seals (*Leptonychotes weddellii*) are the only yearlong resident air-breathing marine predator of the fast-ice in the Ross Sea. Their piscivorous diet includes Antarctic silverfish (*Pleurogramma antarcticum*) and Antarctic toothfish, among other fish species [8–10]. As top predators, Weddell seals

can offer valuable insight on the structure and dynamics of the Ross Sea, as they integrate information across the entire trophic web [11].

Few studies have used top predators to investigate long-term changes in ecosystems (decadal scale or longer), due to the lack of either baseline information before human intervention, or the availability of time series long enough to address this type of question [12]. Stable isotope analysis (SIA) offers a powerful tool to address these questions on historical and longer time scales, because certain biological materials (e.g. keratin, bone, and teeth) are often well preserved and retain their original isotopic composition [13].

Weddell seals were hunted by the early Antarctic explorers, and pelts from several of these individuals remain inside the huts that were used during these expeditions. These pelts represent a unique archive for the Ross Sea, allowing us to assess the ecology of the species and the ecosystem status, from a time at the onset of human presence in the Ross Sea to the present. Specifically, our aims were (i) to investigate whether the ecology and diet of the Weddell seal has changed in the last century and (ii) to determine potential changes in the structure of the ecosystem (number of trophic levels) between the early 1900s and early 2000s, using stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) measured in fur samples from Weddell seals from both periods of time.

2. Material and methods

Complete details of the isotopic analyses are provided in the electronic supplementary material. Modern samples were collected between 2010 and 2012 from live adult Weddell seals handled in McMurdo Sound and the Victoria Land coast, Ross Sea ($n = 32$) [10] (electronic supplementary material, figure S1). Fur samples were obtained by shaving an area of approximately 4 cm^2 with a commercial razor blade and collecting the hairs in a paper envelope.

Historical samples ($n = 34$) were obtained from inside the historical huts in McMurdo Sound. Remains of harvested animals were identified and hair samples were collected using a scalpel blade and scissors, and kept in a paper envelope. While we cannot verify the temporal and spatial extent of the collection of these samples, we assume they are comparable to modern samples given the limited range of individuals (less than 700 km) [14], and the evidence that seal hunts were concentrated between the colonies nearby the huts.

(a) Bulk tissue stable isotope analysis

Bulk tissue samples (fur) were weighed ($0.5 \pm 0.05\text{ mg}$) and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values by combustion in a Carlo Erba Elemental Analyzer interfaced with a Finnigan Delta^{Plus} XP mass spectrometer (Stable Isotope Laboratory, UC Santa Cruz).

(b) Stable isotope analysis of individual amino acids

We focused on a subset of the original hair samples ($n_{\text{historical}} = 10$, $n_{\text{modern}} = 10$). A sample of approximately 2 mg of hair was hydrolysed, followed by amino acid (AA) derivatization and posterior esterification [15]. Samples were then injected into a Gas Chromatography Isotope Ratio Mass Spectrometer (GC-IRMS, Thermo Trace Ultra GC) coupled with an oxidation and reduction furnace, and finally linked to a Finnigan Delta^{Plus} XP mass spectrometer (Stable Isotope Laboratory, UC Santa Cruz). Each sample was injected in triplicate, and we report the average values.

(c) Trophic position of Weddell seals

Bulk $\delta^{15}\text{N}$ values can be used to estimate the trophic position (TP) of consumers. However, this relies on baseline isotopic data (i.e. phytoplankton or primary producer) [16], and as we lack this information for our historical samples, we restricted our comparison of bulk tissue derived-TPs to raw $\delta^{15}\text{N}$ values. $\delta^{15}\text{N}_{\text{AA}}$ data directly use the baseline information retained in Source AAs (AAs that undergo very little or no fractionation with each trophic transfer) and Trophic AAs (AAs that do fractionate with each trophic transfer), providing a robust estimate of TP regardless of baselines [17,18]. We estimated TP using the model proposed in [19]:

$$\text{TP} = 1 + \left[\frac{\delta^{15}\text{N}_{\text{Pro}} - \delta^{15}\text{N}_{\text{Phe}} - \beta_{\text{Pro-Phe}}}{\text{TDF}_{\text{Pro-Phe}}} \right],$$

where $\delta^{15}\text{N}_{\text{Pro}}$ and $\delta^{15}\text{N}_{\text{Phe}}$ represent the values of Proline and Phenylalanine in the samples, $\beta_{\text{Pro-Phe}}$ is the difference between Pro and Phe in marine phytoplankton (3.1‰ [17]) and $\text{TDF}_{\text{Pro-Phe}}$ is the trophic discrimination factor between Pro and Phe across all trophic levels (5.2‰ [20]).

(d) Statistical analysis

The differences in bulk tissue values were investigated using Analysis of Variance (ANOVA). We calculated the isotopic standard ellipses and determined their areas as proxies of niche width (including Bayesian estimates of the confidence intervals, CI), using the package SIBER in R [21]. We also estimated the niche overlap by calculating the intersection between the 95% CI standard ellipses for both historical and modern samples, using the package SIAR in R [22].

We investigated if AAs were significantly different between periods using the *t*-test or Mann–Whitney test, depending on whether the assumptions of the test were fulfilled or not (electronic supplementary material, table S1). For posterior analyses, we retained 11 AAs (electronic supplementary material, table S1) as these were identifiable for all samples used in the study. We used Non-Metric Multidimensional Scaling (NMDS) and Non-Parametric Permutational Multivariate Analysis of Variance (NP-MANOVA) to assess isotopic patterns between historical and modern samples using all $\delta^{13}\text{C}_{\text{AA}}$ and $\delta^{15}\text{N}_{\text{AA}}$ data, as well as focusing only on essential AA $\delta^{13}\text{C}$ and source AA $\delta^{15}\text{N}$ values. NMDS and NP-MANOVA were conducted using the package VEGAN in R [23]. Differences in both bulk (raw $\delta^{15}\text{N}$ data) and AA-derived TP between periods were investigated using a *t*-test.

Significance for all parametric tests was set at $\alpha = 0.05$. All statistical analyses were conducted in R [24].

3. Results

(a) Bulk tissue

Weddell seals showed significant differences for both bulk hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between historical and modern samples (ANOVAs, $\delta^{13}\text{C}$ $F_{1,64} = 11.55$, $p < 0.01$; $\delta^{15}\text{N}$ $F_{1,64} = 36.5$, $p < 0.01$). Historical samples had lower $\delta^{13}\text{C}$ values ($-24.8 \pm 1.0\text{‰}$) and higher $\delta^{15}\text{N}$ ($14.0 \pm 0.8\text{‰}$) than modern samples ($-23.6 \pm 0.4\text{‰}$ and $13.0 \pm 0.4\text{‰}$, respectively; modern $\delta^{13}\text{C}$ values corrected for the Suess effect) (figure 1; electronic supplementary material, table S1). Both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were more variable in historical samples, as evident from their s.d.s (see above). Accordingly, the isotopic niche of historical samples (posterior distribution mode = 2.6‰^2), was over five times larger than the niche of

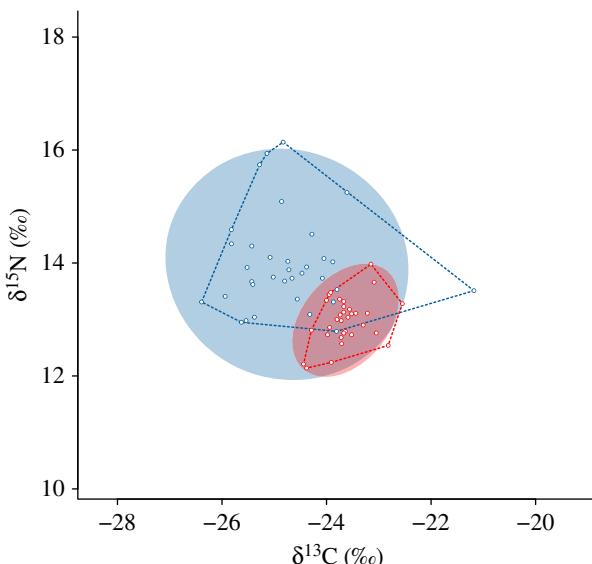


Figure 1. Fur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data of Weddell seals from the Ross Sea, Antarctica. The blue dots represent historical samples ($n = 34$), and red dots correspond to modern samples ($n = 32$). The shaded areas depict the 95% confidence standard isotopic ellipses. The dashed lines correspond to the Minimum Convex Polygons.

modern samples (posterior distribution mode = 0.5‰²; figure 1).

(b) Amino acids

We did not observe a clear pattern in individual AAs between the study periods. Most AAs did not differ between historical and modern samples, except for $\delta^{13}\text{C}_{\text{Ile}}$, $\delta^{13}\text{C}_{\text{Tyr}}$, $\delta^{15}\text{N}_{\text{Pro}}$, and $\delta^{15}\text{N}_{\text{Lys}}$ (electronic supplementary material, table S1).

The NMDS analysis, however, revealed differences when all AAs were considered. Interestingly, $\delta^{13}\text{C}_{\text{AA}}$ data showed more segregation between historical and modern samples than $\delta^{15}\text{N}_{\text{AA}}$, both when all AAs were combined and when AAs were separated per their metabolic groupings (figure 2). The largest segregation was observed at the base of the trophic web (Essential $\delta^{13}\text{C}$ and Source $\delta^{15}\text{N}$), with only 17.6 and 30.5% of the historical NMDS polygons overlapping with modern samples for $\delta^{13}\text{C}_{\text{Essential-AA}}$ and $\delta^{15}\text{N}_{\text{Source-AA}}$ respectively (figure 2; electronic supplementary material, table S2).

The results from the NP-MANOVA confirmed this segregation for both $\delta^{13}\text{C}_{\text{AA}}$ and $\delta^{15}\text{N}_{\text{AA}}$ values. We found no differences between historical and modern samples for $\delta^{13}\text{C}$ when we looked at all AAs ($F_{1,11} = 2.78$, $R^2 = 0.20$, $p = 0.05$) or Non-Essential AAs ($F_{1,11} = 1.52$, $R^2 = 0.12$, $p = 0.20$); however, Essential AAs were significantly different between periods ($F_{1,11} = 4.30$, $R^2 = 0.28$, $p = 0.02$). On the other hand, we did find significant differences when looking at $\delta^{15}\text{N}$ values for all AAs combined ($F_{1,15} = 2.25$, $R^2 = 0.14$, $p = 0.04$), and when focusing only on Source AAs ($F_{1,15} = 4.29$, $R^2 = 0.23$, $p = 0.02$), but no significant differences were found for Trophic AAs ($F_{1,15} = 2.02$, $R^2 = 0.13$, $p = 0.10$).

(c) Trophic position

The historical bulk $\delta^{15}\text{N}$ value was significantly higher than the $\delta^{15}\text{N}$ value of modern samples by 1‰, which would represent a drop of about one third of a trophic level of Weddell seals between both periods [16] (figure 3a). Conversely, AA

data showed no significant differences in the TP of Weddell seals between periods: $\text{TP}_{\text{Historical}} = 3.7$, $\text{TP}_{\text{Modern}} = 3.7$ ($F_{1,15} = 0.12$, $p = 0.74$) (figure 3b). We also found a positive relationship between the average $\delta^{15}\text{N}$ value of Source AA and the $\delta^{15}\text{N}$ value of bulk hair samples ($R^2 = 0.25$, $p < 0.01$) (electronic supplementary material, figure S2).

4. Discussion

It has long been known that Weddell seals feed mostly on fish, particularly Antarctic silverfish and other species of nototheniids and bathydraconiids [8–10]. However, the role of the Antarctic toothfish in the diet of the seals from the Ross Sea has been debated; it has been suggested, based on observational evidence, that Weddell seals consume a larger portion of this species than has been assumed based on direct studies of their diet [25]. Newer isotopic evidence, however, contradicts this hypothesis, as more refined analyses of diet using SIA data have indicated that Antarctic toothfish makes up less than 10% of the diet of Weddell seals [10], similar to previous reports for this population from the late twentieth century [9,26].

Even so, a lingering question is whether the presence of the Ross Sea Antarctic toothfish fishery has resulted in a decrease of toothfish in the diet of modern Weddell seals. Our data show that this is likely not the case. Despite finding differences in the bulk tissue $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between historical and modern samples, these differences were driven by changes in the baseline values, as confirmed by the AA data. The results of our study indicate that the average TP of the Weddell seals from McMurdo Sound has not changed over the past century, in turn indicating that the Antarctic toothfish, a species with an estimated $\text{TP} > 4.5$ [27], was likely not a major component in the historical diet of the species, similar to its low contribution to the diet of Weddell seals today [10].

Ponganis & Stockard [8] and Goetz *et al.* [10] suggested that the Antarctic toothfish could be an important prey item for larger, older, and probably specialized individuals who might seek out this prey item for its high energetic content, despite its large size and potential difficulty to catch. Indeed, an increasing number of studies have reported individual variability and specialization in foraging strategies for other species of pinnipeds, and it is possible that particular individuals prey on Antarctic toothfish at a higher proportion than the overall population. Our data, however, do not support the hypothesis that Antarctic toothfish comprised a larger portion of the diet of the overall Weddell seal population 100 years ago. Further, we found a positive relationship between source amino acids and bulk $\delta^{15}\text{N}$ values, indicating that the differences we observed in bulk values (figure 3a) are due to a decrease at the baseline, not due to a decrease in the TP of the Weddell seals, supporting the conclusions of TP calculation based on $\delta^{15}\text{N}_{\text{AA}}$ values (figure 3b).

A striking pattern revealed in our data was that modern Weddell seals in McMurdo Sound had an apparent reduced isotopic niche compared with Weddell seals from 100 years ago, as identified from the standard ellipses in the $\delta^{13}\text{C}$ / $\delta^{15}\text{N}$ bi-space (figure 1; electronic supplementary material, table S2). Indeed, today's mode of the posterior distributions of the standard ellipse of Weddell seals corresponds to only

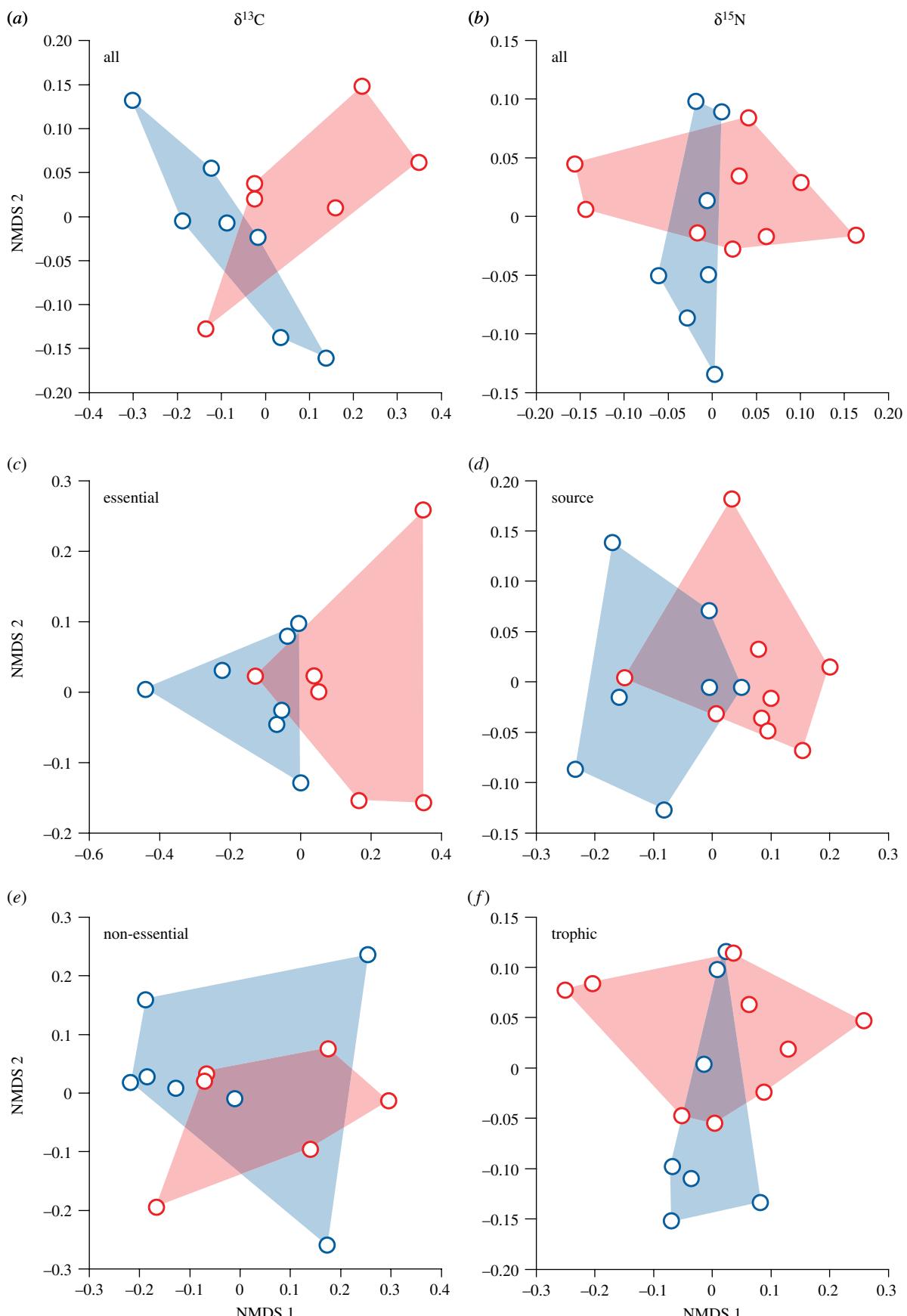


Figure 2. Non-Metric Multidimensional Scaling (NMDS) using individual amino acid stable isotopes values of Weddell seals from the Ross Sea, Antarctica. Panels (a,c,e) correspond to $\delta^{13}\text{C}_{\text{AA}}$ and (b,d,f) $\delta^{15}\text{N}_{\text{AA}}$. (a,b) All amino acids combined, (c,d) Essential $\delta^{13}\text{C}_{\text{AA}}$ and Source $\delta^{15}\text{N}_{\text{AA}}$. (e,f) Non-Essential $\delta^{13}\text{C}_{\text{AA}}$ and Trophic $\delta^{15}\text{N}_{\text{AA}}$.

about 14.7% of what it was a century ago. Two mechanisms could explain this reduction in niche width of the Weddell seal: (i) the McMurdo Sound population could have

undergone a process of ecological specialization, thus decreasing the diversity of items that individuals prey upon. This specialization could either be the result of an

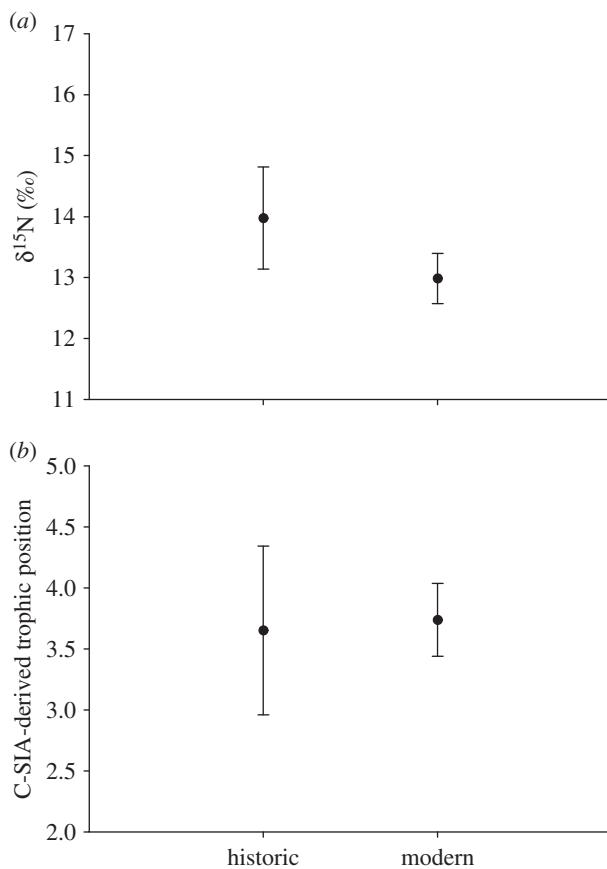


Figure 3. Trophic position (TP) of Weddell seals estimated from bulk tissue (a) and individual amino acid $\delta^{15}\text{N}$ values (b). Bulk tissue $\delta^{15}\text{N}$ values were significantly different between historical and modern samples. AA-derived TP were not significantly different between periods.

increased 'preference' for a few prey species, or a consequence of an increase in the relative abundance and availability of the dominant prey items (e.g. Antarctic silverfish). (ii) Changes at the lower trophic levels of the ecosystem (i.e. phytoplankton community composition and/or lower trophic level consumers) could result in the observed reduced variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, and thus be mistakenly interpreted as a reduction in the niche width of the species.

Owing to the lack of historical isotopic data and information on population trends for the prey community of the Ross Sea, we cannot dismiss the hypothesis that this reduction in the isotopic niche does, indeed, reflect a more specialized diet in modern Weddell seals. Yet, such a dramatic reduction in the niche size of the Weddell seal over the last 100 years therefore seems improbable, particularly considering the similarity in the degree of diversity of prey items in the diets of different populations of Weddell seals across its distributional range [10,28,29], and wide range of prey items consumed by the Ross Sea population today [10].

Instead, the reduction in variability of both isotopes could be associated with changes at the ecosystem baseline rather than changes in the niche width of the species. The arrival of humans to the Ross Sea occurred close to the end of the Little Ice Age (LIA), the most recent neoglacial period (approx. AD 1500–1900), when global temperatures were colder than during the twentieth century [30]. Polito *et al.* [31] argued that this colder environment during the LIA could have resulted in the decrease of Antarctic silverfish in the diet of Adélie penguins (*Pygoscelis adeliae*) from the colonies in the same study area, as evidenced from sediment

samples. However, unlike Weddell seals, these penguins congregate in colonies during the breeding period (Antarctic summer), when their movements are restricted due to the limitations imposed by incubation and chick-rearing, so the silverfish reduction indicated by sediment records could be explained by local conditions and not necessarily reflect the environment in the Ross Sea.

During the LIA the Ross Sea presented lower air temperatures (1.6°C cooler than during the twentieth century) and enhanced katabatic winds (descending from the high-altitude Antarctic continent) that created a more persistent and larger polynya (an area of open water in the sea ice), which resulted in higher biological productivity and the prevalence of open water diatoms over sea-ice-associated diatoms [32,33]. It is possible that the divergent baseline values that our AA data indicate are, at least in part, a result of the differences in the phytoplankton community composition and primary productivity. As noted above, depending on the element (C or N), certain AA groups retain the isotopic values from the primary producers, with little or no fractionation across trophic levels: Essential AA $\delta^{13}\text{C}$ and Source AA $\delta^{15}\text{N}$. It has been shown on other ocean regions that widespread shifts in both N supply and plankton community composition associated with climatic change since the end of the LIA has resulted in major coupled baseline changes in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of primary producers [18,34]. The change in these primary producer-derived AA groups between the historic and modern samples, suggests that climatic changes in the Antarctic since the LIA have led to shifts in baseline isotope values, likely associated with widespread change in upwelled nutrient supply, productivity rates, and possibly assemblages of primary producers over the last century.

Because top predators integrate ecological information, they can be used to obtain insights into the status of marine ecosystems. Using stable isotope data from Weddell seals, our study revealed little indication of major alterations in the structure of the trophic web of the Ross Sea due to the presence of humans during the last 100 years. On the other hand, our results revealed that detectable changes have occurred at the base of the trophic web (i.e. primary producers community) between these periods, likely linked to environmental changes. Recently, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) announced the establishment of a 1.55 million km² Marine Protected Area (MPA) in the Ross Sea [35]. This MPA, the largest in the world, is the result of the international interest in protecting the Ross Sea and regulating human activities. Considering the results from this study, this protection effort is particularly important as this ecosystem continues to be largely unaffected by humans, especially in comparison to the rest of the world's oceans.

Ethics. Animal handling was approved by the University of California Santa Cruz Institutional Animal Care and Use Committee (IACUC). Research was conducted under NMFS permit No. 87-1851, and approved by the Antarctic Conservation Act and Antarctic Heritage Trust New Zealand.

Data accessibility. The raw isotopic data are presented in the electronic supplementary material.

Authors' contributions. L.A.H., P.L.K., and D.P.C. designed the study. L.A.H. and D.P.C. collected the samples. L.A.H. and M.D.M. analysed the samples. All authors wrote the manuscript.

Competing interests. We have no competing interests.

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