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Divergent Trophic Responses of Sympatric Penguin Species to Historic Anthropogenic Exploitation and Recent Climate Change

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Abstract: The Southern Ocean is in an era of significant change. Historic overharvesting of marine mammals and recent climatic warming have cascading impacts on resource availability, and in turn, ecosystem structure and function. We examined trophic responses of sympatric chinstrap (*Pygoscelis antarctica*) and gentoo (*P. papua*) penguins to nearly 100 years of shared environmental change in the Antarctic Peninsula region using compound-specific stable isotope analyses of museum specimens. A century ago, gentoo penguins fed almost exclusively on low trophic level prey, such as krill, during the peak of historic overexploitation of marine mammals, which was hypothesized to have produced a "krill surplus." In the last 40 years, gentoo penguin trophic position has increased a full level as krill declined in response to recent climate change, increased competition from recovering marine mammal populations, and the development of a commercial krill fishery. A shifting isotopic baseline supporting gentoo penguins suggests a concurrent increase in coastal productivity over this time. In contrast, chinstrap penguins showed no change in trophic position, despite changes in krill availability over the past century. The specialized foraging niche of chinstrap penguins likely makes them more sensitive to changes in krill availability, relative to gentoo penguins, as evinced by their declining population trends in the Antarctic Peninsula over the past 40 years. Over the next century, similarly divergent trophic and population responses are likely to occur among Antarctic krill predators if climate change and other anthropogenic impacts continue to favor generalist over specialist species.

Keywords: Antarctica, Ecogeochemistry, Environmental change, Generalist versus specialist, Historical ecology, Krill surplus, Stable isotopes

Significance Statement: We reveal species-specific changes in penguin trophic responses to historic shifts in krill availability over the last century by applying new molecular isotope techniques to historic penguin museum specimens. Generalist foraging gentoo penguins, whose population increased >75% in the last 40 years, showed adaptive shifts in trophic position in concert with changes in Antarctic krill availability following historic exploitation of marine mammals and recent climate change. In contrast, chinstrap penguins maintained a consistent krill diet despite changes in krill availability and concurrent population declines. These results highlight how responses to shared environmental change can vary substantially among closely related species, supporting ecological niche theory that specialists will be more sensitive to environmental change than their generalist counterparts.

1. Introduction

Ecological responses to shared environmental change can vary substantially among species, even those that are closely related (1-4). Understanding species-specific responses to environmental change is critical to predicting the resilience and adaptation of species to disturbances associated with changes in climate or human-environment interactions. A species' ecological niche, defined as a multi-dimensional hyper-volume that includes axes relating to trophic dynamics, habitat use, and other life-history requirements (5, 6), can be a key predictor of species' responses to changes in their environment (1, 7). For example, specialist species use a narrow window of resources and are thought to be highly sensitive to environmental change (8, 9). In contrast, generalist species have broad or flexible resource use and are predicted to be more resilient to disturbances and/or changes in resource availability associated with environmental change (7, 10).

Chinstrap (*Pygoscelis antarctica*) and gentoo (*P. papua*) penguins co-occur in the Antarctic Peninsula region and provide an opportunity to test explicit hypotheses about sympatric species responses to environmental change. These sympatric species use similar nesting habitats, have similar phenology and breeding biology, are both considered pagophobic (ice-avoiding) unlike their pagophilic congener the Adélie penguin (*P. adeliae*), and strongly overlap in dietary utilization of Antarctic krill (*Euphausia superba*) (11, 12). However, over the last 40 years, chinstrap penguin populations within the Antarctic Peninsula region have decreased by approximately 30 to 53% (13, 14), while those of gentoo penguins have had more than a six-fold increase (14-16). For example, along the South Orkney Islands, South Shetland Islands, and the Western Antarctic Peninsula, chinstrap penguin populations are estimated to have declined from as much as 3.1 million breeding pairs in the 1970s and 1980s to as few as 1.4

million breeding pairs in the 2010s (13), while gentoo penguins in this region increased from approximately 31,312 to 243,316 breeding pairs during this same time period (15, 16). These divergent population trajectories may be, at least partially, explained by key differences in their trophic niches, which are thought to facilitate ecological niche segregation and promote coexistence (5, 17, 18). Chinstrap penguins have a narrow trophic niche with a specialized diet dominated by Antarctic krill (17, 18). Gentoo penguins, conversely, are generalist foragers with a broader and more flexible trophic niche relative to chinstrap penguins (18, 19). Trivelpiece *et al.* (20) proposed a hypothetical framework, invoking dietary reliance on krill, to explain recent population trends in *Pygoscelis* penguins as a function of the synergistic interaction of historic overexploitation of marine mammals, coupled with recent global climate change, on krill availability in the Antarctic Peninsula (Fig. 1).

The sequential over-harvesting of seals, baleen whales, and finfish from the early 19th to the mid-20th century (12, 21, 22) is hypothesized to have resulted in a surplus of Antarctic krill available for the remaining krill predators, such as *Pygoscelis* penguins, (23-25). For example, removal of whales alone in the mid-20th century is calculated to have led to an ~150 million metric ton surplus of krill annually (21, 23). However, over the past 70 yrs, regional climate change, including ocean warming, sea ice decline, and ocean acidification, have acted in concert to negatively impact the abundance, distribution, and recruitment of krill (26-29), though see (30-32). Recent recovery of whale and seal populations (33, 34) and a growing Antarctic krill fishery (35) have likely further removed the prior krill surplus and increased competition among Southern Ocean krill predators, including penguins (Fig. 1).

While compelling, the hypothetical framework proposed by Trivelpiece *et al.* (20) has been challenging to test due to limited data on *Pygoscelis* penguin diets prior to the 1980s. To

test the krill surplus hypothesis and shed light on species-specific responses to recent environmental stressors in the Southern Ocean, this study compares the trophic responses of sympatric chinstrap and gentoo penguins over nearly 100 years of shared environmental change. Accordingly, we applied molecular ecogeochemistry (see SI Appendix for further description) to historic penguin museum specimens dating back to the 1930s. We hypothesized that chinstrap penguins, with their specialized dietary niche and strong reliance on krill, would show little change in trophic position over time regardless of krill availability. In contrast, given the more plastic dietary niche of gentoo penguins, we hypothesized that this species' trophic position has fluctuated over time in response to the proposed climate and harvesting-related changes in the availability of Antarctic krill; i.e. lower trophic positions indicative of higher dietary contribution of krill in the first half of the 20th century during the proposed krill surplus and higher trophic positions reflecting a switch away from krill during the krill decline of the second half of the 20th century.

To test these hypotheses, we analyzed the compound-specific stable nitrogen isotope values of individual amino acids (AAs) in archived penguin feathers to reconstruct the baseline food web nitrogen cycling and penguin trophic positions through time. The source AA phenylalanine $\delta^{15}N$ value ($\delta^{15}N_{Phe}$) exhibits minimal trophic discrimination, providing a proxy for the isotopic signature of nitrogen cycling at the base of the food web, while the trophic AA glutamic acid $\delta^{15}N$ value ($\delta^{15}N_{Glu}$) exhibits strong trophic discrimination (reviewed in McMahon and McCarthy (36)). Together, these differentially fractionating AAs provide a measure of trophic position (TP) that is internally indexed to the nitrogen isotope value of the base of the food web McMahon and McCarthy (36). This approach is particularly valuable for examining

biogeochemical cycling and trophic dynamics in a historical context when it is challenging, if not impossible, to *a priori* characterize the isotopic baseline of past ecosystems.

2. Results and Discussion

We identified divergent trophic responses in two congeneric, sympatric krill-predatory seabirds during nearly 100 years of shared environmental change in the Antarctic Peninsula. Over the past century, gentoo penguins increased a full trophic position, shifting from a nearly exclusive krill diet in the 1930s to a diet with significantly more upper trophic level prey, likely fish and squid, in the modern system. At the same time, the nitrogen isotope baseline supporting the gentoo penguin food web also increased, suggesting that either gentoo penguins have shifted from offshore to inshore foraging over the past 60 years and/or there has been an increase in coastal productivity. In contrast, chinstrap penguins showed no change in trophic dynamics over the past century, indicative of consistent offshore foraging on krill despite the recent decline in krill availability. The timing and direction of these divergent trophic responses support the krill surplus hypothesis and further highlight the sensitivity of specialist chinstrap penguin populations to anthropogenic and climatic forcings that drive changes in krill availability in the Antarctic Peninsula.

Our results provide support for the hypothetical framework proposed by Trivelpiece *et al.* (20), as temporal variation in the dietary generalist gentoo penguins' trophic position was correlated with proposed historic shifts in krill availability. For example, gentoo penguin trophic position was lowest in the 1930s and 1960s during the proposed krill surplus, and highest in the 1980s and 2010s when krill stocks are proposed to have declined (BANOVA all PP>0.99; Fig. 1, Fig. 2). The trophic position of gentoo penguins in the 1930s (median (2.5%-97.5% credible

intervals): TP = 3.4 (3.1-3.6)) and 1960s (TP = 3.1 (2.9-3.3)) was similar to those of the krill

specialist chinstrap penguins (1930s TP = 3.2 (3.1-3.3) [BANOVA PP=0.91], 1960s TP = 3.1

(3.0-3.2) [BANOVA PP=0.42]), indicating a diet dominated by herbivorous zooplankton, such

as Antarctic krill (37). Our data suggest that at the peak of the proposed krill surplus in the early

to mid-20th century, owing to the sequential exploitation and depletion of krill dependent

Antarctic fur seals (*Arctocephalus gazella*), baleen whales, and finfish (Fig. 1 (20, 21), gentoo

and chinstrap penguins both consumed almost exclusively krill.

Between the 1960s (TP = 3.1 (2.9-3.3)) and today (TP = 4.1 (3.9-4.3)), the trophic

position of gentoo penguins in the northern Antarctic Peninsula increased by a full trophic level

(Figs. 2 and 3). Modern gentoo penguin TP equates to a mixed diet of Antarctic krill (~66%) and

fish/squid (~34%), assuming TP = 2.5 for Antarctic krill and TP = 4.1 for common prey fish and

squid (37-39). This predicted modern diet composition agrees with recent studies using stomach

content and bulk tissue stable isotope analyses (18, 19).

The timing of the gentoo penguin trophic shift away from krill dominance aligns with

recent declines in the abundance and recruitment of Antarctic krill since the 1970s (Fig. 1) (20,

27). Since the mid-20th century, the western Antarctic Peninsula has warmed faster than any

region on Earth (6 °C average midwinter temperature increase since 1950 (40)) as a direct result

of anthropogenic climate change (41, 42). Increases in sea surface temperature have led to

substantial declines in the duration, extent, and thickness of sea ice (43, 44), which have been

directly linked to major declines in krill abundance and recruitment since the 1970s (20, 26, 27,

29). Regional ocean acidification due to rising CO_2 levels have further compounded

environmental degradation for krill (45). Over this same time period, the recovery of whale and

seal populations in response to the marine mammal conservation efforts of the International

Convention for the Regulation of Whaling (ICRW) and the development of a commercial krill fishery (32) have likely increased competition for krill among Southern Ocean predators, including penguins. Our results provide long-term historical support for the conclusions drawn from a natural experiment in the western Ross Sea, where a short-term polynya brought penguins and whales together in a confined area, resulting in alterations to Adélie penguin diet and foraging behavior (46). That study concluded that competition for krill between Adélie penguins and minke whales resulted in the switch of penguins' prey from krill to Antarctic silverfish (*Pleuragramma antarctica*), as opposed to a formerly hypothesized seasonal decrease in sea-ice cover (47).

In contrast to the dynamic increase in trophic position of gentoo penguins over the past century, chinstrap penguins exhibited a consistent krill-based trophic position since the 1930s (TP $\cong$ 3.2 (range: 3.1-3.3) [BANOVA all PP<0.99]), despite declines in krill abundance and recruitment in the northern Antarctic Peninsula in recent decades (20, 29, 48). As hypothesized, the divergent trophic responses of specialist-foraging chinstrap and generalist-foraging gentoo penguins aligned with known differences in their respective ecological niches (18, 19). Concurrent with these divergent trophic dynamics were major shifts in penguin population dynamics. Chinstrap penguin populations across the Antarctic Peninsula region decreased by 31% between 1979 and 2010, while gentoo penguin populations increased by >75% during this same time period (14). Our trophic dynamics data, coupled with these recent population trends, agree with ecological theory that predicts climate change favors consumers in generalized niches over specialized niches, meaning that dietary specialists are more severely affected by climate change than generalists (7). We hypothesize that the specialized trophic niche of chinstrap penguins, if it remains static as in the last century, will increasingly negatively impact their

population growth as they remain highly sensitive to declines in the abundance of Antarctic krill (18, 20) and potentially increased competition (49). In contrast, increasing population trends in gentoo penguins and their trophic plasticity relative to shifts in krill availability over the past century highlights this species' ability to adapt to changing environmental conditions. Other life history traits, such as flexible phenology (50) and increased parental investment in chicks (51) may also buffer gentoo penguin populations relative to chinstrap penguin populations.

The rarity of museum specimens often imbues an opportunistic nature to retrospective studies. In this study, the availability of samples from the Antarctic Peninsula region varied both temporary and spatially (e.g. differing years and/or locations within decades for each species; Tables S1 and S2). For example, in the 1980s samples were obtained from two years (1987 and 1989) and two locations (King George Island and Deception Island). Nevertheless, the Chinstrap penguin sample from King George Island in 1987 (TP = 2.9) was within the range of trophic positions found in Chinstrap penguins from Deception Island in 1989 (TP=2.9 to 3.2) and outside the range observed Gentoo penguins from King George Island in 1987 (TP=3.5 to 4.1). Similarly, variation in feather $\delta^{15}N$ values and calculated trophic positions was consistently greater between species and among decades relative to inter-annual or among site variation (Fig. 2; Tables S1 and S2). This is predicted as body feathers synthesized with resources consumed during the post-breeding, pre-molt period (52) represent regional, as opposed to colony specific, resource availability (35, 53). Even so, future analyses that leverage additional opportunstic collections to increase samples sizes, as available, would allow for a more robust assessment of inter-annual and/or spatial variation relative to decadal trends.

Observed shifts in penguin trophic dynamics in the northern Antarctic Peninsula over the last century were overlain on apparent shifts in biogeochemical cycling at the base of the food

web. $\delta^{15}N$ values of the penguin source AA phenylalanine ($\delta^{15}N_{Phe}$), which serve as a proxy for the sources and cycling of nitrogen at the base of the food web (reviewed in McMahon and McCarthy (36)), varied over the ~100-year record for both penguin species, though not in parallel. In the 1930s, both gentoo (median = 4.0‰ (2.5-97.5% credible intervals: 3.5-4.5‰)) and chinstrap penguins (4.4‰ (3.9-5.0‰)) had similarly low $\delta^{15}N_{Phe}$ values indicative of foraging in similar biogeochemical systems (BANOVA PP=0.09). Over the next century, chinstrap penguin $\delta^{15}N_{Phe}$ values oscillated but remained relatively low (between 3.8 and 4.7‰), while gentoo penguin $\delta^{15}N_{Phe}$ values increased significantly between the 1930s (4.0‰ (3.5-4.5‰)) and the 1960s (6.7‰ (6.2-7.2‰)) and then again between the 1980s (6.2‰ (5.7-6.7‰)) and the 2010s (7.4‰ (6.9-7.9‰) [all BANOVAs PP>0.99]). This increase in gentoo penguin $\delta^{15}N_{Phe}$ values over the last century, which was not found in chinstrap penguin $\delta^{15}N_{Phe}$ values, likely reflects changes in gentoo penguin foraging location, nearshore vs. offshore, regional increases in productivity in nearshore waters, or both. A shift in diet alone, from krill in the early to mid-20th century to more fish and squid today, cannot explain the gentoo penguin $\delta^{15}N_{Phe}$ trend alone as the shift in baseline preceded the shift in diet and trophic position (See SI Appendix).

Body feather $\delta^{15}N_{Phe}$ values of the adult penguins sampled in this study (Table S1 and S2) reflect the foraging habitats of penguins during the post-breeding, pre-molt period (52). Foraging migration data from both the breeding and post-breeding periods, including limited data during the pre-molt period, indicate seasonally consistent differences in the foraging habitats of chinstrap and gentoo penguins (17, 35). In the Antarctic Peninsula region, breeding chinstrap penguins typically forage in oceanic waters (>200m depth) off the continental shelf (77% of dives), whereas gentoo penguins primarily forage in nearshore waters (71% of dive locations),

often near the benthos (28% of dives) (54). Outside of the breeding season, gentoo penguins

increase their maximum foraging range but remain in coastal waters (53) regularly returning to

land following 4 to 12-hour bouts of foraging (55). In contrast, during pre-molt chinstrap

penguins forage in offshore, pelagic waters and spend their winter months at sea (35). These

distinct nearshore (gentoo) and offshore (chinstrap) foraging habitats also have distinct baseline

$\delta^{15}N$ values as a function of NO_3^- utilization efficiency (higher utilization in nearshore systems =

higher particulate organic matter (POM) $\delta^{15}N$ values) (56, 57). Modern chinstrap penguin $\delta^{15}N_{Phe}$

values of 4.0‰ (3.6-4.5‰) align well with foraging within the offshore waters of the

northwestern Antarctic Peninsula based on euphausiid-derived nitrogen isoscapes for the region

(4.1 ± 0.8‰) (57). Similarly, modern gentoo penguin $\delta^{15}N_{Phe}$ values (7.4‰ (6.9-7.9‰)) suggest

foraging within nearshore productive waters of the Peninsula (NO_3^- $\delta^{15}N$ = 7 to 10‰ during

periods of maximum NO_3^- drawdown) (58). One possible explanation for the low $\delta^{15}N_{Phe}$ values

of gentoo penguins in the 1930s, relative to later decades, is that during this time period gentoo

penguins foraged further offshore, overlapping with chinstrap penguins. However, this

hypothesis seems less likely, given that past studies support the idea that gentoo penguins are

non-migratory, diurnal foragers that retain the use of near-shore foraging habitats year-round (35,

53, 55).

Alternatively, assuming no changes in foraging distributions, the increasing gentoo

penguin $\delta^{15}N_{Phe}$ values over the past century could reflect an increase in primary productivity in

nearshore waters. As primary productivity increases, the $\delta^{15}N$ value of the residual pool of NO_3^-

increases as NO_3^- is consumed resulting in an increase in the $\delta^{15}N$ value of newly formed

plankton biomass (59). Few data are available for the $\delta^{15}N$ values of POM from nearshore zones

from the first half of the 20th century (60), however, Kim, *et al.* (61) reported increasing

nearshore phytoplankton biomass in the South Shetland Islands and Western Antarctic Peninsula between 1992 and 2016, and Moreau, *et al.* (62) found a strong correlation between the clear increase in summer sea surface temperature from 1990 to 2010 and water column primary production in the same region, likely driven by meltwater stabilization of the water column reducing light limitation (63). If this hypothesis is correct, our data would suggest that modern observations of increasing coastal productivity are part of a longer-term trend of increasing coastal productivity in the northern Antarctic Peninsula since the early-20th century. In contrast, between 1978 and 2006 Chlorophyll a concentrations declined in the offshore, oceanic waters of the northern Antarctic Peninsula (64) where chinstrap penguin typically forage (54), which may explain the observed 0.7‰ decrease in chinstrap penguin $\delta^{15}N_{Phe}$ values over this same time period.

Our comparative trophodynamic approach using molecular geochemistry on museum archived penguins supports the hypothesis that historic anthropogenic exploitation and recent climate change have shifted the availability of Antarctic krill to *Pygoscelis* penguins, and by extension other krill predators, over the past century (20, 65). We predict that the trophic responses of the *Pygoscelis* penguin species in our study are emblematic of a larger ecosystem response to historic shifts in krill availability. For example, Emslie and Patterson (24) observed an abrupt shift in the bulk tissue $\delta^{15}N$ values of radiocarbon dated eggshells from pagophilic Adélie penguins sometime within the last 200 years. While the exact timing of the shift observed by Emslie and Patterson (24) was unclear due to uncertainty in the marine-carbon reservoir effect, we hypothesize that this bulk isotope shift reflects a trophic response of Adélie penguins to changing krill availability, similar to the shift observed in gentoo penguins in our study. Future analyses on Adélie penguin eggshell AA $\delta^{15}N$ values could be used to test this hypothesis.

Regardless, rising temperatures in the Antarctic Peninsula region over the next century, as well as krill harvesting if not managed properly (66), are predicted to continue to negatively impact krill biomass and lead to declines in populations of krill-dependent predators (67, 68). Over the next century the Antarctic Peninsula region will remain a hotspot with respect to multiple, superimposed climate change processes and other anthropogenic impacts (e.g. ocean warming, sea-ice loss, ocean acidification, krill harvesting, tourism, species introductions, etc.) likely creating synergistic challenges for *Pygoscelis* penguins and other specialist and generalist marine predators in Antarctica (68-70).

3. Materials and methods

Chinstrap and gentoo penguin feather samples were obtained from specimens collected from the Antarctic Peninsula region (i.e. the Antarctic Peninsula, including the South Shetland and South Orkney Islands) during historic and more recent Antarctic explorations and curated at natural history museums (Table S1, S2). Five individuals per species were sampled from four discrete time periods (i.e. 1930s, 1960s, 1980s, and 2010s) for a total of 40 specimens.

Three breast feathers per specimen were acid hydrolyzed, derivatized, and analyzed for compound-specific nitrogen (δ^{15}N) stable isotope analysis (CSIA) of twelve individual amino acids (AAs; McMahon, Polito, Abel, McCarthy and Thorrold (71) (see SI Appendix). Feather samples were analyzed in triplicate along with a homogeneous laboratory algal standard (>100 repeat injections) and a mixed AA standard of known isotopic composition (Sigma-Aldrich Co., St. Louis, MO, USA) (mean δ^{15}N reproducibility: ±0.3‰ for laboratory algal standard and mixed AA standard). We calculated individual penguin's trophic position ($TP_{TDF-multi}$) using a multi-TDF equation following McMahon, Polito, Abel, McCarthy and Thorrold (71):

$$TP_{TDF-multi} = 2 + \left[\frac{\delta^{15}N_{(Glu)} - \delta^{15}N_{(Phe)} - TDF_{(Glu-Phe)\ penguin} - \beta}{TDF_{(Glu-Phe)average}} \right]$$

where $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ represent the stable nitrogen isotope values of penguin Glu and Phe, respectively, β represents the difference in $\delta^{15}N$ between Glu and Phe of primary producers (3.4‰ for aquatic microalgae (72-74)), $TDF_{(Glu-Phe)\ average}$ represents an average trophic discrimination factor (TDF) of 6.3‰ ($\Delta^{15}N_{Glu} - \Delta^{15}N_{Phe}$) characteristic of planktonic marine food webs (see meta-analysis by McMahon and McCarthy (36)), and $TDF_{(Glu-Phe)\ penguin}$ represents the *Pygoscelis* penguin-specific $TDF_{Glu-Phe}$ value (3.5‰) derived from a controlled feeding experiment on *Pygoscelis* penguins (71). Alternative methods of calculating TP from AA $\delta^{15}N$ values resulted in similar trends in TP_{CSIA} over time and between species (see SI Appendix, Fig. S1).

The mean and variance of $\delta^{15}N_{Glu}$, $\delta^{15}N_{Phe}$, and $TP_{TDF-multi}$ across each time period were estimated separately using Bayesian Analysis of Variances (BANOVA) for gentoo and chinstrap penguins. Equal variance among time periods and species was assumed for each analysis. Parameter estimates (unbiased) were obtained with Markov chain Monte Carlo (MCMC) and JAGS. Vague priors were used for the mean (normal distributions with a mean of 0 and variance of 1000) and the variance (uniform distribution between 0 and 100). Pairwise comparison among time periods and between species are expressed as Bayesian posterior probabilities (PP > 0.99 as a conservative indication of significant differences) that the posterior distributions of $\delta^{15}N_{Glu}$, $\delta^{15}N_{Phe}$, and $TP_{TDF-multi}$ from one group (time period or species) are different in a one-way comparison with another group. All statistics were performed in R version 3.5.0 (75).

Ethics. Field work was conducted via an Antarctic Conservation Act permits (ACA 2006-001 and 2013-007) and animal use approved by WHOI IACUC (27071382).

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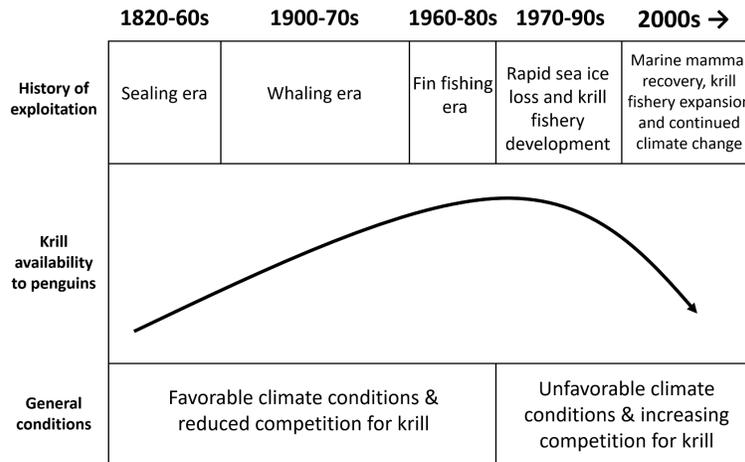
Figure 1. Drivers of krill availability in the Antarctic Peninsula region. a) A conceptual summary of the historic and recent ecosystem perturbations in the Antarctic Peninsula region and their hypothesized implication for the availability of Antarctic krill to penguins in the genus *Pygoscelis* including b) chinstrap (*P. antarctica*) and c) gentoo (*P. papua*) penguins. Adapted from Trivelpiece *et al.* (20).
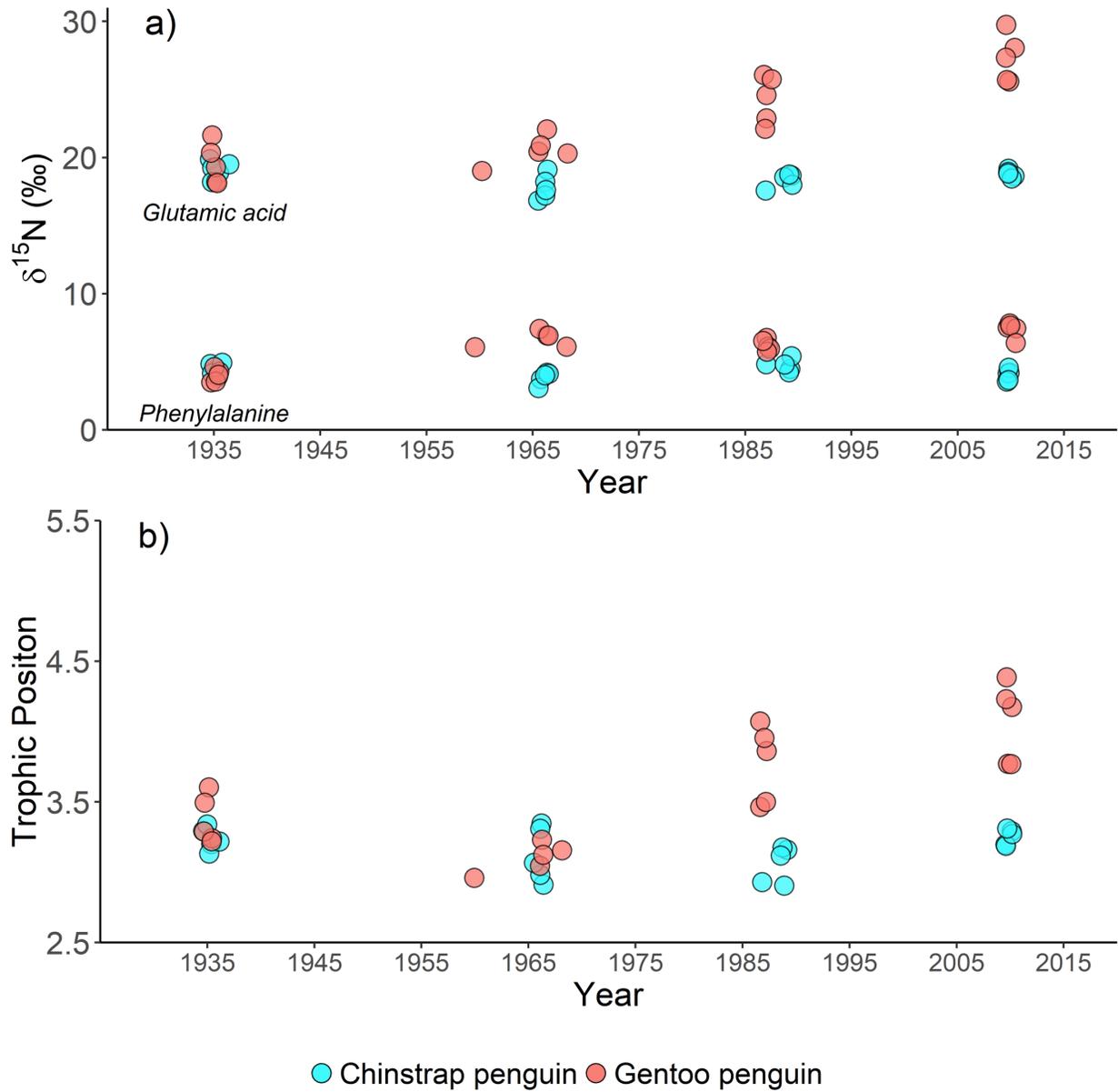
Figure 2. Penguin feather amino acid nitrogen isotope values. a) Feather $\delta^{15}N$ values of phenylalanine and glutamic acid and b) the calculated trophic position of historic, archival museum specimens of chinstrap and gentoo penguins collected in the Antarctic Peninsula region in the 1930s, 1960s, 1980s, and 2010s.
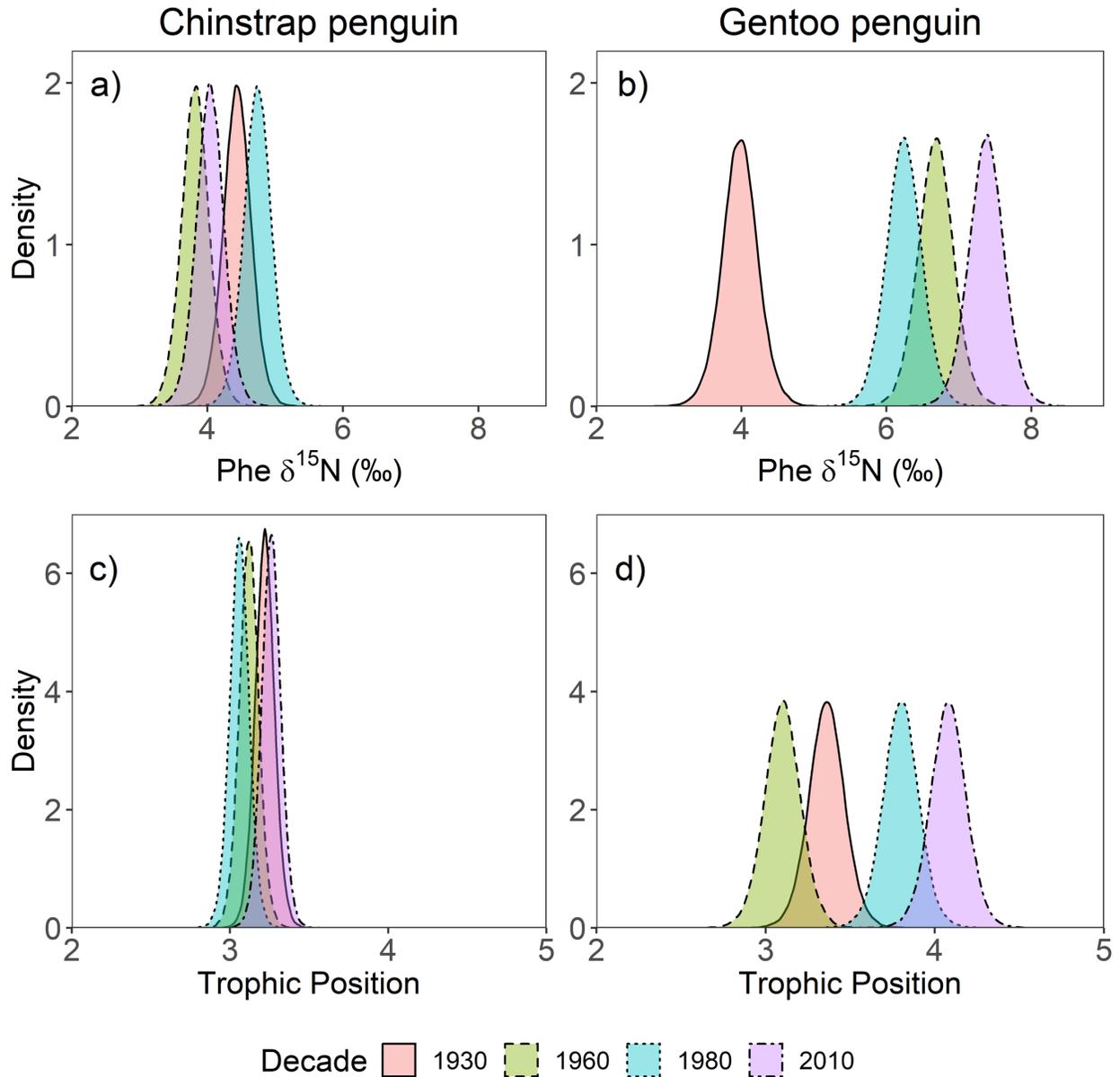
Figure 3. Density distribution of feather isotope parameters. Density distributions, estimated from Bayesian Analysis of Variance (BANOVA) models, of feather $\delta^{15}N$ values of phenylalanine ($\delta^{15}N_{Phe}$) and calculated trophic position ($TP_{TDF-multi}$) of archived historic museum specimens of chinstrap (a,c) and gentoo (b,d) penguins collected in the Antarctic Peninsula region in the 1930s, 1960s, 1980s, and 2010s.

Supplemental Information Appendix for:

Divergent Trophic Responses of Sympatric Penguin Species to Historic Anthropogenic Exploitation and Recent Climate Change

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SI 1. Methods for compound-specific stable isotope analysis of amino acids:

Compound-specific stable isotope analyses of penguin feathers followed protocols modified from McMahon et al. (1). Three breast feathers per specimen (~3 mg) were homogenized and acid hydrolyzed in 1 ml of 6 N HCl at 110°C for 20 hrs to isolate the total free amino acids (AAs). Samples were evaporated to dryness under a gentle stream of N_2. The total free AAs were derivatized by esterification with acidified iso-propanol followed by acylation with trifluoroacetic anhydride (2) and brought up in ethyl acetate for stable isotope analysis. The derivatized AAs were injected on column in splitless mode at 250°C and separated on a BPX5 column (60 m x 0.32 mm inner diameter, 1.0 mm film thickness; SGE Analytical Science, Austin, Texas, USA) in a Thermo Trace Ultra gas chromatograph (GC) at the University of California - Santa Cruz, Santa Cruz, California, USA. The separated AA peaks were analyzed on a Finnegan MAT Delta^{Plus} XL isotope ratio monitoring mass spectrometer (irm-MS) interfaced to the GC through a GC-C III combustion furnace (980°C), reduction furnace (650°C), and a liquid nitrogen trap.

We analyzed five individuals per species from four discrete time periods (i.e. 1930s, 1960s, 1980s, and 2010s) for a total of 40 specimens. Feather samples were analyzed in triplicate along with a homogeneous laboratory algal standard (>100 repeat injections) and a mixed AA standard of known isotopic composition (Sigma-Aldrich Co., St. Louis, MO, USA). Standardization of runs was achieved using intermittent pulses of an N_2 reference gas of known isotopic value. Mean reproducibility of the laboratory algal standard and the mixed AA standard across all individual AAs was ±0.3‰.

We analyzed the $\delta^{15}N$ values of twelve individual AAs, accounting for approximately 77% of the total hydrolysable AAs in feathers. We assigned glutamic acid (Glu), aspartic acid

(Asp), alanine (Ala), leucine (Leu), isoleucine (Ile), proline (Pro), and valine (Val) as trophic AAs, and phenylalanine (Phe) and lysine (Lys) as source AAs. Note that glycine (Gly), serine (Ser), and threonine (Thr) do not behave similarly to either of these main groups (3-6) and have not been included in the trophic dynamic calculations. Acid hydrolysis converts glutamine (Gln) and asparagine (Asn) into Glu and Asp, respectively, due to cleavage of the terminal amine group, resulting in the measurement of combined Gln + Glu (referred to hereby as Glu), and Asn +Asp (referred to hereby as Asp).

The mean and variance of $\delta^{15}N_{Glu}$, $\delta^{15}N_{Phe}$, and $TP_{TDF\text{-}multi}$ across each time period were estimated separately using Bayesian Analysis of Variances (BANOVA) for gentoo and chinstrap penguins. Parameter estimates were unbiased for small sample sizes. Equal variance among time periods was assumed for each analysis. Parameter estimates were obtained with Markov chain Monte Carlo (MCMC) and JAGS. Vague priors were used for the mean (normal distributions with a mean of 0 and variance of 1000) and the variance (uniform distribution between 0 and 100). Each analysis was run with three chains, each for 100,000 iterations, a burn in of 10,000 iterations, and thinning of three, producing posterior distributions of 90,000 values. Pairwise comparison between time periods and between species are expressed as Bayesian posterior probabilities (PP) that the posterior distributions of $\delta^{15}N_{Glu}$, $\delta^{15}N_{Phe}$, and $TP_{TDF\text{-}multi}$ from one group (time period or species) are different in a one-way comparison with another group. We consider $PP > 0.99$ as a conservative indication of significant differences in $\delta^{15}N_{Glu}$, $\delta^{15}N_{Phe}$, and $TP_{TDF\text{-}multi}$. All statistics were performed in R version 3.5.0 (7).

SI 2. Overview of CSIA: Disentangling baseline and trophic nitrogen isotope variability

Differential isotopic discrimination of amino acid (AA) nitrogen between diet and consumer allows for the disentanglement of trophic and baseline variability contributing to consumer δ^{15}N values (reviewed in McMahon and McCarthy (8)). Protein AAs are commonly divided into two groups, termed the "trophic" and the "source" AAs, based upon their nitrogen isotope fractionation during trophic transfer (after Popp, *et al.* (9)). The "source" amino acids (e.g. phenylalanine [Phe] and lysine [Lys]) undergo minimal isotopic discrimination between diet and metazoan consumers (10, 11), because N bonds are neither formed nor cleaved during typical metabolic reactions (10, 12, 13). Source AAs (e.g., Phe δ^{15}N [δ^{15}N$_{Phe}$]) provide proxies for the isotopic signature of nitrogen cycling at the base of the food web, without the confounding factor of trophic modification (14-16). Conversely, "trophic" amino acids (e.g. glutamic acid [Glu], aspartic acid [Asp], alanine [Ala], leucine [Leu], isoleucine [Ile], proline [Pro], valine [Val]) exhibit strong isotopic discrimination during metazoan trophic transfer (10, 11) as a result of N-bond cleavage during transamination/deamination reactions (17). Together, these differentially fractionating AAs can be used to assess the trophic position of a consumer while simultaneously controlling for the nitrogen isotope value of the base of the food web (10). This approach is particularly valuable when working in complex or dynamic systems, where multiple different baseline end-members are present (18-20), when working on highly mobile or high trophic level consumers that may integrate across multiple food webs (21-23), and in paleoreconstructive context when it is challenging, if not impossible, to *a priori* characterize the isotopic baseline of past ecosystems (14, 24, 25).

Trophic dynamics of consumers can be assessed using a compound-specific trophic position (TP$_{CSIA}$) equation that quantifies trophic transfers and baseline nitrogen isotope

variability from a single sample. Successful application of the TP_{CSIA} equation requires proper parameterization. A recent meta-analysis of controlled feeding experiments examining AA isotopic discrimination across 70 species (88 distinct species-diet combinations) clearly showed that both diet quality and mode of nitrogen excretion significantly affect the trophic discrimination factor (TDF) parameter, the degree of fractionation of individual AAs between diet and consumer (8). In the gentoo and chinstrap penguin food webs, where consumers differ in their mode of nitrogen excretion (e.g., ammonia for krill and fish vs uric acid for penguins) and diet quality (e.g, krill feeding on phytoplankton vs penguins feeding on high protein fish), McMahon, Polito, Abel, McCarthy and Thorrold (1) proposed using a multi-TDF equation ($TP_{TDF-multi}$) with trophic AA Glu and source AA Phe:

$$TP_{TDF-multi} = 2 + \left[\frac{\delta^{15}N_{(Glu)} - \delta^{15}N_{(Phe)} - TDF_{(Glu-Phe)\,penguin} - \beta}{TDF_{(Glu-Phe)average}} \right]$$

where $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ represent the stable nitrogen isotope values of penguin Glu and Phe, respectively, β represents the difference in $\delta^{15}N$ between Glu and Phe of primary producers (3.4‰ for aquatic microalgae) (4, 26, 27), $TDF_{(Glu-Phe)\,average}$ represents an average trophic discrimination factor (TDF) of 6.3‰ ($\Delta^{15}N_{Glu} - \Delta^{15}N_{Phe}$) characteristic of planktonic marine food webs (see meta-analysis by McMahon and McCarthy (8)), and $TDF_{(Glu-Phe)\,penguin}$ represents the *Pygoscelis* penguin-specific $TDF_{Glu-Phe}$ value (3.5‰) derived from a controlled feeding experiment on *Pygoscelis* penguins (1).

Very few studies have used multi-TDF equations to examine consumer trophic dynamics. In fact, of the 60 environmental application studies identified by the meta-analysis of McMahon and McCarthy (8), 92% used a single TDF approach with trophic AA Glu and source AA Phe of either 7 or 7.6‰ $TP_{7.6-TDF}$ *sensu* Chikaraishi, *et al.* (10):

$$TP_{7.6-TDF} = 1 + \left[\frac{\delta^{15}N_{(Glu)} - \delta^{15}N_{(Phe)} - \beta_{Glu-Phe}}{TDF_{7.6}}\right]$$

where $\delta^{15}N_{Glu}$ and $\delta^{15}N_{Phe}$ represent the stable nitrogen isotope values of penguin Glu and Phe, respectively, $\beta_{Glu-Phe}$ represents the difference in $\delta^{15}N$ between Glu and Phe of primary producers (3.4‰ for aquatic microalgae) (4, 26, 27), and $TDF_{7.6}$ represents the commonly used trophic discrimination factor (TDF) of 7.6‰ ($\Delta^{15}N_{Glu} - \Delta^{15}N_{Phe}$) from the seminal paper on TP_{CSIA} by Chikaraishi (10). However, a number of field studies calculating TP_{CSIA} in upper trophic level consumers (including cephalopods, teleost fishes, elasmobranchs, marine mammals, and seabirds) have noted that assuming a constant $TDF_{Glu-Phe}$ value of 7.6‰ often led to substantially underestimated TP_{CSIA} (20-22, 28-30).

Alternatively, several studies have proposed using a single TDF approach but with averaged trophic and source AAs to improve the accuracy and precision of TP_{CSIA} (31-33):

$$TP_{Avg-TDF} = 1 + \left[\frac{\delta^{15}N_{(Avg-TrAA)} - \delta^{15}N_{(Avg-SrAA)} - \beta_{Avg-TrAA - Avg-SrAA}}{TDF_{Avg-TrAA - Avg-SrAA}}\right]$$

where $\delta^{15}N_{Avg-TrAA}$ and $\delta^{15}N_{Avg-SrAA}$ represent the average stable nitrogen isotope values of penguin trophic AAs (Glu, Ala, Leu, Ile, Pro, Val) and source AAs (Phe, Lys), respectively, $\beta_{Avg-TrAA - Avg-SrAA}$ represents the difference in average $\delta^{15}N$ between trophic AAs (Glu, Ala, Leu, Ile, Pro, Val) and source AAs (Phe, Lys) of primary producers (2.8‰ for aquatic microalgae) (4, 27, 32), and $TDF_{Avg-TrAA - Avg-SrAA}$ represents the average trophic discrimination factor (TDF) of 5.4‰ ($\Delta^{15}N_{TrAA} - \Delta^{15}N_{SrAA}$ for pairwise combinations of trophic AAs [Glu, Ala, Leu, Ile, Pro, Val] and source AAs [Phe, Lys]) for aquatic consumers (meta-analysis by McMahon and McCarthy (8). Nielsen, Popp and Winder (33) found that modeled uncertainties in TP_{CSIA} estimates significantly decreased when increasing the number of trophic and source AAs in the calculation.

We found that all three TP_{CSIA} approaches produced similar trends in penguin trophic dynamics (Fig. S1). Chinstrap penguin TP_{CSIA} did not change significantly through time while gentoo penguin TP_{CSIA} increased significantly between the 1960s and 1980s. On average, $TP_{7.6-TDF}$ produced the lowest TP_{CSIA} of any approach (chinstrap 2.4±0.1, gentoo 2.8±0.3), which was not ecologically realistic for consumers foraging on krill (chinstrap penguins) or krill, fish, and squid (gentoo penguins). $TP_{TDF-multi}$ produced the highest and most realistic TP_{CSIA} of any approach (chinstrap 3.2±0.1, gentoo 3.6±0.4). $TP_{Avg-TDF}$ was intermediate between the two other approaches but similar to $TP_{7.6-TDF}$, was often unrealistically low given the known diet patterns of these penguin species (34, 35).

SI 3. Individual amino acid isotope value statistics

Penguin feather $\delta^{15}N_{Phe}$ and $\delta^{15}N_{Glu}$ values differed between species in three of four decades examined (Fig. 2). Bayesian analysis indicated gentoo penguins had higher $\delta^{15}N$ values than chinstrap penguins in the 1960s ($\delta^{15}N_{Phe}$ PP=1.0; $\delta^{15}N_{Glu}$ PP>0.99), 1980s ($\delta^{15}N_{Phe}$ PP>0.99; $\delta^{15}N_{Glu}$ PP=1.0), and 2010s ($\delta^{15}N_{Phe}$ PP=1.0; $\delta^{15}N_{Glu}$ PP=1.0), but not in the 1930s ($\delta^{15}N_{Phe}$ PP=0.09; $\delta^{15}N_{Glu}$ PP=0.68). For each species considered individually over time, we found that chinstrap penguin $\delta^{15}N_{Phe}$ values were lower in the 1960s relative to the 1980s (PP>0.99) and $\delta^{15}N_{Glu}$ values were higher in the 1930s relative to the 1960s (PP>0.99; Fig 3.). Gentoo penguin $\delta^{15}N_{Phe}$ values from the 1930s were lower than all other time periods (PP=1.0), and $\delta^{15}N_{Phe}$ values from the 1980s were lower than the 2010s (PP>0.99; Fig. 3). Gentoo penguin $\delta^{15}N_{Glu}$ values increased over time and differed (all PP<0.99) among all comparisons except those between the 1930s and 1960s (PP=0.84; Fig. 3).

Penguin TPs differed between species in two of four decades examined (Fig. 2). TP did not differ between species in the 1930s (PP=0.91) and 1960s (PP=0.42), while gentoo penguins had higher TP relative to chinstrap penguins in the 1980s (PP=1.0) and 2010s (P=1.0). In addition, Bayesian analysis indicated no difference in chinstrap penguin TP across decades (all PP<0.96; Fig. 3). In contrast, gentoo penguin TP from the 1930s and 1960s were lower than those from the 1980s and 2010s (all PP>0.99; Fig. 3). These shifts in TP resulted in gentoo and chinstrap penguins having similar TPs in the 1930s and 1960s that diverged during the 1980s and 2010s (Fig. 2; Fig. 3).

SI 4. Alternative hypothesis for variations in $\delta^{15}N_{Phe}$

The observed shifts in penguin trophic dynamics in the northern Antarctic Peninsula over the last 100 years were overlain on apparent shifts in biogeochemical cycling at the base of the food web. The $\delta^{15}N$ values of the source AA phenylalanine ($\delta^{15}N_{Phe}$), which serve as a proxy for the sources and cycling of nitrogen at the base of the food web (reviewed in McMahon and McCarthy (8), varied over the ~100-year record for both penguin species, though trend and magnitude of their values were not in parallel. In the 1930s, both gentoo penguins (median (2.5%-97.5% credible intervals): 4.0‰ (3.5-4.5‰) and chinstrap penguins (4.4‰ (3.9-5.0‰) had similarly low $\delta^{15}N_{Phe}$ values (PP=0.09). Over the next century, chinstrap penguin $\delta^{15}N_{Phe}$ values oscillated but remained relatively low (between 3.8 and 4.7‰), while gentoo penguin $\delta^{15}N_{Phe}$ values increased significantly between the 1930s and the 1960s (median (2.5%-97.5% credible intervals): 6.7‰ (6.2-7.2‰)) and 1980s (6.2‰ (5.7-6.7‰)), and then again by the 2010s (7.4‰ (6.9-7.9‰)) (All PP>0.99).

The divergent shifts in penguin $\delta^{15}N_{Phe}$ values over the last 100 years could reflect temporal shifts in diet among prey items that occupy food webs with different isotopic baselines. In the 1930s, TP data suggest both penguin species were foraging almost exclusively on krill and at this time both gentoo penguins and chinstrap penguins had similar $\delta^{15}N_{Phe}$ values. While chinstrap penguins continued to forage almost exclusively on krill throughout the rest of the century, maintaining relatively low $\delta^{15}N_{Phe}$ values, gentoo penguins shifted their diet to higher trophic level consumers and their $\delta^{15}N_{Phe}$ values also increased. A recent study of food web dynamics in the Scotia Sea found that *Euphausiid* krill, which forage under sea ice, had lower bulk $\delta^{15}N$ values (4.3±1.0‰) than copepods foraging in the water column (5.6±0.9‰) and the myctophid fish (9.2±0.7‰) and *Galiteuthis* squid (8.7±0.1‰) that feed on them (36). However,

this dietary shift is unlikely to be the sole driver of the shift in isotopic baseline recorded in the penguin $\delta^{15}N_{Phe}$ values, as gentoo penguin $\delta^{15}N_{Phe}$ values increased significantly between the 1930s and 1960s, yet their TP did not significantly change until after the 1960s, indicating that the baseline shift began before the trophic shift. This indicates that the underlying driver of changes in penguin $\delta^{15}N_{Phe}$ values between these species is likely a function of shifts in baseline nitrate $\delta^{15}N$ values in their foraging locations as discussed earlier.

SI 5. Literature Cited

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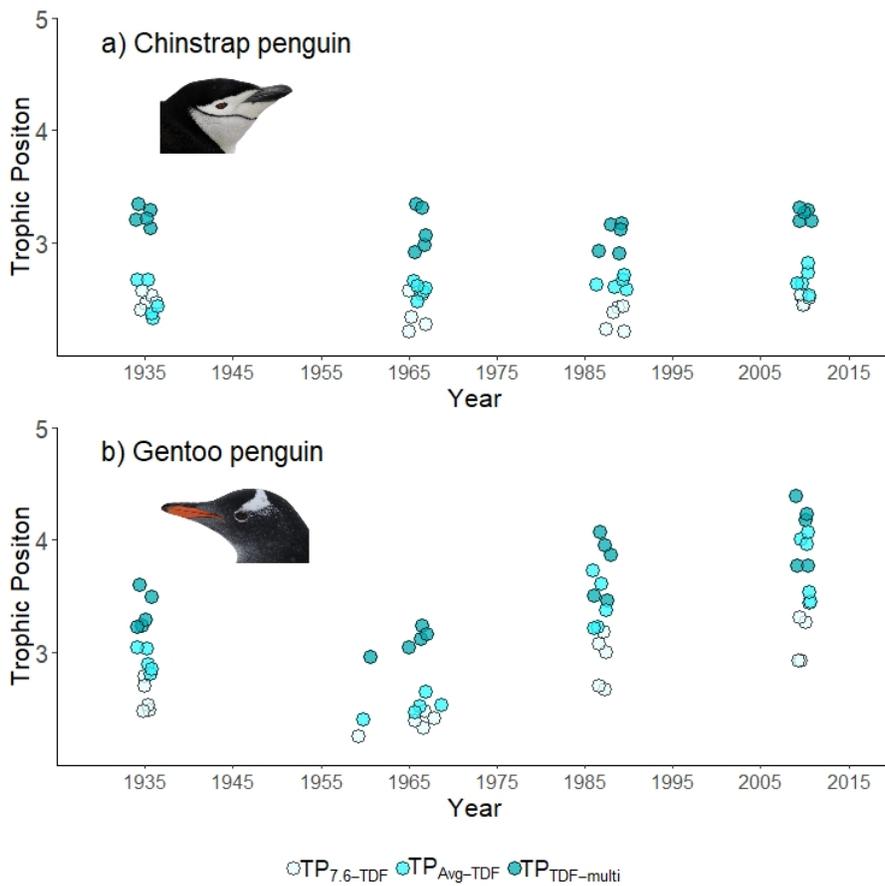
Figure S1. A comparison of the calculated trophic positions of archived historic museum specimens of chinstrap and gentoo penguins collected in the Antarctic Peninsula region in the 1930s, 1960s, 1980s, and 2010s using three compound-specific amino acid nitrogen isotope methods. Each symbol represents one individual penguin (five individuals per species per time periods). $TP_{7.6-TDF}$ used a single TDF approach with trophic AA Glu and source AA Phe, *sensu* Chikaraishi et al. (2007), $TP_{Avg-TDF}$ used a single TDF approach but with averaged trophic and source AAs, *sensu* McCarthy, Benner, Lee and Fogel (31), and $TP_{TDF-multi}$ used a multi-TDF approach that accounted for key transitions in diet quality and consumer mode of nitrogen excretion within the food web supporting penguins *sensu* McMahon, Polito, Abel, McCarthy and Thorrold (1).

Table S1. Collection dates, locations, and δ^{15}N values of individual amino acids from historic, archival museum specimens of adult

chinstrap penguins (*Pygoscelis antarctica*) collected in the Antarctic Peninsula region. 'Trophic' amino acids include glutamic acid

(Glu), aspartic acid (Asp), alanine (Ala), leucine (Leu), isoleucine (Ile), proline (Pro), valine (Val), glycine (Gly), and serine (Ser).

Phenylalanine (Phe) and Lysine (Lys) are classified as a 'source' amino acids and threonine (Thr) as 'metabolic' amino acid following

McMahon and McCarthy (8). Institution codes: American Museum of Natural History (AMNH), National Museum of Natural History

(USNM), Swedish Museum of Natural History (NRM), Royal Belgian Institute of Natural Sciences (RBINS), Natural History

Museum at Tring (NHMUK), and University of North Carolina Wilmington (UNCW).

Institution	Catalog no.	Sex	Locality	Year	Glu	Asp	Ala	Leu	Ile	Pro	Val	Gly	Ser	Phe	Lys	Thr	$TP_{7.6\text{-}TDF}$	$TP_{Avg\text{-}TDF}$	$TP_{TDF\text{-}multi}$
AMNH	Skin-442419	Unknown	Deception Island	1935	18.9	12.4	17.2	18.3	18.2	19.3	19.2	6.7	7.9	4.4	4.1	-19.5	2.5	2.6	3.2
AMNH	Skin-442420	Unknown	Deception Island	1935	19.9	13.7	18.6	20.0	18.8	21.3	21.2	7.6	8.2	4.8	5.1	-18.1	2.5	2.7	3.3
AMNH	Skin-442421	Unknown	Deception Island	1935	19.2	13.1	17.8	18.8	18.3	20.8	20.2	8.4	8.2	3.9	3.7	-20.5	2.6	2.8	3.3
AMNH	Skin-442419bis	Unknown	Deception Island	1935	18.2	12.8	17.9	18.0	17.3	20.4	19.1	8.1	8.4	4.2	4.3	-18.2	2.4	2.6	3.1
NHMUK	1938.12.19.137	Male	Deception Island	1936	19.5	12.2	19.1	18.0	17.5	18.8	19.4	8.1	8.6	4.9	5.0	-19.1	2.5	2.5	3.2
USNM	548079	Female	Tower Island	1966	19.1	12.0	16.7	17.6	18.0	17.9	18.2	8.6	9.1	3.7	3.4	-18.3	2.6	2.7	3.3
USNM	548080	Female	Tower Island	1966	16.8	10.7	15.9	15.6	16.9	16.6	17.1	7.7	8.0	4.2	4.1	-17.5	2.2	2.3	2.9
USNM	548078	Male	Tower Island	1966	18.2	12.3	16.5	17.4	17.9	17.7	18.1	9.9	10.1	3.1	3.5	-20.1	2.5	2.7	3.3
USNM	548039	Male	Gaston Island	1966	17.2	10.4	16.1	15.9	16.3	16.8	17.3	8.1	8.4	4.1	3.9	-17.9	2.3	2.4	3.0
USNM	548131	Female	Penguin Island	1966	17.6	11.5	16.1	16.5	16.8	16.5	17.2	8.5	9.1	4.0	3.7	-17.3	2.3	2.4	3.1
RBINS	2	Unknown	King George Island	1987	17.6	13.4	17.9	18.6	18.4	20.7	19.1	9.6	10.5	4.8	4.7	-21.5	2.2	2.6	2.9
NRM	896280	Female	Deception Island	1989	18.7	12.3	16.8	17.6	17.5	20.3	18.1	10.0	10.3	4.5	3.8	-22.2	2.4	2.6	3.2
NRM	896290	Female	Deception Island	1989	18.6	12.6	17.1	18.3	18.9	20.0	18.6	9.0	10.2	4.2	4.0	-23.0	2.4	2.7	3.2
NRM	896291	Female	Deception Island	1989	18.0	13.7	18.1	18.2	18.7	20.6	19.6	9.8	11.0	5.4	5.4	-21.2	2.2	2.5	2.9
NRM	896292	Male	Deception Island	1989	18.8	12.6	17.1	18.3	18.5	21.0	18.9	10.4	10.8	4.8	4.3	-21.4	2.4	2.6	3.1
UNCW	66	Female	King George Island	2010	19.2	12.0	16.2	17.5	17.0	19.8	18.9	9.2	10.0	4.1	3.6	-19.2	2.5	2.6	3.3
UNCW	67	Male	King George Island	2010	18.6	11.9	15.9	17.3	16.8	18.7	19.1	8.1	8.9	4.2	3.3	-18.1	2.5	2.6	3.2
UNCW	68	Female	King George Island	2010	19.0	12.4	16.5	17.6	16.8	20.6	18.7	9.6	10.1	4.6	3.9	-19.5	2.4	2.6	3.2
UNCW	72	Male	King George Island	2010	18.5	11.8	15.4	17.4	17.1	19.2	18.8	8.3	9.1	3.6	3.2	-19.4	2.5	2.7	3.3
UNCW	73	Female	King George Island	2010	18.8	12.6	16.3	18.2	17.3	20.5	19.2	10.2	10.6	3.7	3.7	-19.9	2.5	2.7	3.3

Table S2. Collection dates, locations, and $\delta^{15}N$ values of individual amino acids from historic, archival museum specimens of adult

gentoo penguins (*Pygoscelis papua*) collected in the Antarctic Peninsula region. 'Trophic' amino acids include glutamic acid (Glu),

aspartic acid (Asp), alanine (Ala), leucine (Leu), isoleucine (Ile), proline (Pro), valine (Val), glycine (Gly), and serine (Ser).

Phenylalanine (Phe) and Lysine (Lys) are classified as a 'source' amino acids and threonine (Thr) as 'metabolic' amino acid following

McMahon and McCarthy (8). Institution codes: American Museum of Natural History (AMNH), National Museum of Natural History

(USNM), Royal Belgian Institute of Natural Sciences (RBINS), Texas A&M University (TCWC), and University of North Carolina

Wilmington (UNCW).

Institution	Catalog no.	Sex	Locality	Year	Glu	Asp	Ala	Leu	Ile	Pro	Val	Gly	Ser	Phe	Lys	Thr	$TP_{7.6\text{-}TDF}$	$TP_{Avg\text{-}TDF}$	$TP_{TDF\text{-}multi}$
AMNH	Skin-442413	Unknown	Deception Island	1935	18.2	12.7	19.1	18.8	19.4	18.8	20.1	8.6	9.7	3.5	3.2	-19.4	2.5	2.9	3.2
AMNH	Skin-442414	Unknown	Deception Island	1935	19.3	14.0	20.4	19.2	19.3	20.5	20.1	9.7	10.6	4.3	4.5	-20.0	2.5	2.8	3.3
AMNH	Skin-442415	Unknown	Deception Island	1935	21.6	15.1	21.5	21.7	21.9	21.9	20.9	10.2	11.7	4.6	4.8	-19.9	2.8	3.0	3.6
AMNH	Skin-442416	Unknown	Deception Island	1935	18.1	12.5	18.5	18.5	18.9	18.9	20.3	8.5	10.2	3.5	3.2	-23.1	2.5	2.9	3.2
AMNH	Skin-442418	Unknown	Deception Island	1935	20.4	14.9	20.0	21.2	21.7	20.8	20.6	9.1	10.1	4.0	3.9	-18.3	2.7	3.0	3.5
AMNH	SKIN-775712	Female	Brabant Island	1960	19.0	13.2	18.5	18.4	19.0	20.4	20.5	14.3	16.8	6.1	6.3	-17.2	2.3	2.4	3.0
USNM	548097	Male	Laurie Island	1966	20.4	14.9	19.8	20.2	20.6	21.5	22.3	16.0	18.0	6.9	6.7	-17.6	2.3	2.5	3.0
USNM	548098	Female	Laurie Island	1966	22.1	16.9	21.6	21.5	22.2	23.2	23.5	17.3	19.5	7.4	7.5	-18.3	2.5	2.7	3.2
USNM	547952	Female	Anvers Island	1966	20.9	15.7	19.7	20.3	20.6	21.4	22.0	16.2	17.9	6.9	7.3	-17.8	2.4	2.5	3.1
TCWC	13447	Unknown	Hope Bay, Palmer Peninsula	1968	20.3	14.7	19.3	19.3	20.1	20.8	22.2	15.2	17.1	6.1	6.6	-16.7	2.4	2.5	3.2
RBINS	69799	Female	King George Island	1987	25.8	21.9	25.6	26.7	27.2	28.6	28.9	13.1	14.5	6.5	6.2	-22.1	3.1	3.6	4.0
RBINS	3	Unknown	King George Island	1987	22.9	18.6	23.7	24.4	24.9	25.9	26.0	12.5	12.9	6.8	5.8	-20.9	2.7	3.2	3.5
RBINS	4	Unknown	King George Island	1987	26.1	21.6	26.8	27.1	27.5	27.7	29.7	10.7	12.5	6.1	5.9	-23.1	3.2	3.7	4.1
RBINS	7	Unknown	King George Island	1987	24.6	19.8	24.8	25.0	25.5	26.6	26.7	11.6	11.9	6.0	6.5	-21.4	3.0	3.4	3.9
RBINS	9	Unknown	King George Island	1987	22.1	17.8	24.3	23.6	24.4	25.0	25.3	11.1	13.0	5.8	6.1	-23.3	2.7	3.2	3.5
UNCW	43	Female	King George Island	2010	25.6	21.4	27.0	26.8	27.7	28.7	28.9	12.5	13.1	7.5	7.4	-22.1	2.9	3.5	3.8
UNCW	48	Male	King George Island	2010	29.7	26.3	28.7	31.3	32.0	32.3	33.4	11.7	12.2	7.8	7.6	-24.9	3.4	4.0	4.4
UNCW	50	Male	King George Island	2010	28.1	24.5	29.3	30.1	30.7	31.6	31.6	11.0	12.6	7.5	6.8	-22.3	3.3	4.0	4.2
UNCW	51	Male	King George Island	2010	25.7	22.9	26.7	27.7	28.7	29.0	30.0	11.2	13.2	7.7	7.3	-22.2	2.9	3.5	3.8
UNCW	58	Female	King George Island	2010	27.3	24.3	29.1	30.0	30.3	30.6	31.2	11.3	12.6	6.4	5.8	-23.2	3.3	4.1	4.2