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# Divergent trophic responses of sympatric penguin species to historic anthropogenic exploitation and recent climate change

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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 (*Pygoscelis papua*) penguins to nearly 100 y 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 resulted in a krill surplus. In the last 40 y, 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 exhibited no change in trophic position, despite variation in krill availability over the past century. The specialized foraging niche of chinstrap penguins likely renders 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 y. 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.

Antarctica | ecogeochemistry | environmental change | historical ecology | krill surplus

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 multidimensional hypervolume 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 (*Pygoscelis 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 (*Pygoscelis adeliae*), and strongly overlap in dietary utilization of Antarctic krill (*Euphausia superba*) (11, 12). However, over the last 40 y, chinstrap penguin populations within the Antarctic Peninsula region have decreased by ~30 to 53% (13, 14), while those of gentoo penguins have had more than a 6-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 ~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.

## Significance

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 6-fold in the last 40 y, 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.

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(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 region (Fig. 1).

The sequential overharvesting 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 y, 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), although see refs. 30–32. Recent recovery of whale and seal populations (33, 34) and a growing Antarctic krill fishery (35) have likely further decreased the prior krill surplus and increased competition among Southern Ocean krill predators, including penguins (Fig. 1).

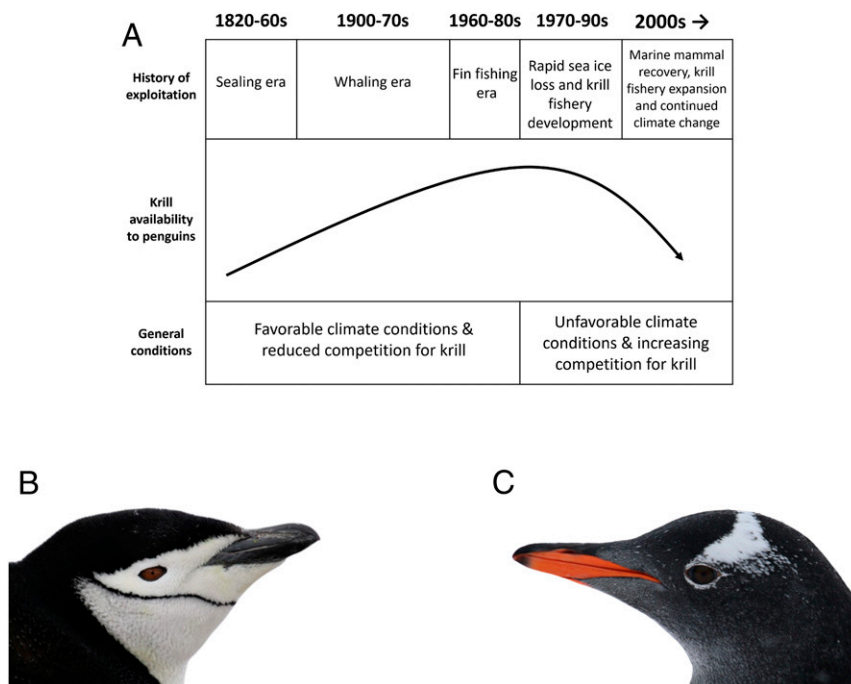
While compelling, the hypothetical framework proposed by Trivelpiece et al. (20) has been challenging to test due to limited data on *Pygoscelis* penguin diets prior to the 1980s. To test the krill surplus hypothesis and shed light on species-specific responses to recent environmental stressors in the Southern Ocean, this study compares the trophic responses of sympatric chinstrap and gentoo penguins over nearly 100 y 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  $\delta^{15}\text{N}_{\text{Phe}}$  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  $\delta^{15}\text{N}_{\text{Glu}}$  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 (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.

## Results and Discussion

We identified divergent trophic responses in two congeneric, sympatric krill-predatory seabirds during nearly 100 y of shared environmental change in the Antarctic Peninsula region. 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 gentoo penguins have shifted from offshore to inshore foraging over the past 60 y 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



**Fig. 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. (A) Adapted with permission from ref. 20.

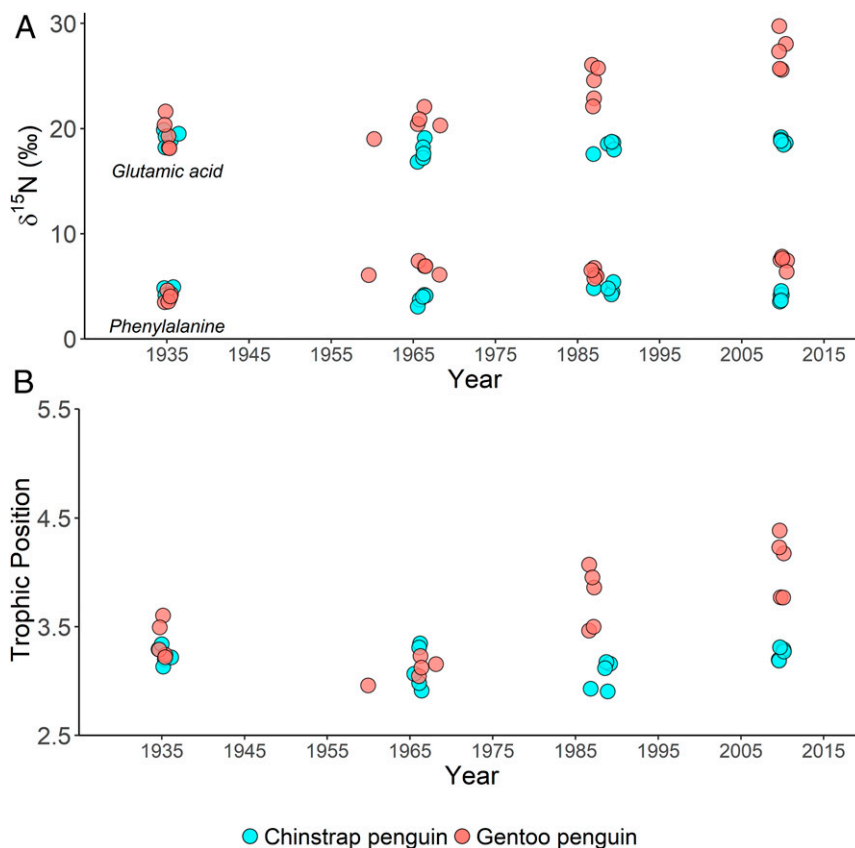
consistent offshore foraging on krill despite the recent decline in krill availability. The timing and direction of these divergent trophic responses support the krill surplus hypothesis and further highlight the sensitivity of specialist chinstrap penguin populations to anthropogenic and climatic forcings that drive changes in krill availability in the Antarctic Peninsula region.

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 (Bayesian analysis of variance [BANOVA] all PP > 0.99; Figs. 1 and 2). The trophic position of gentoo penguins in the 1930s (median [2.5 to 97.5% credible intervals]: TP = 3.4 [3.1 to 3.6]) and 1960s (TP = 3.1 [2.9 to 3.3]) was similar to those of the krill specialist chinstrap penguins (1930s TP = 3.2 [3.1 to 3.3] [BANOVA PP = 0.91], 1960s TP = 3.1 [3.0 to 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 and refs. 20 and 21), gentoo and chinstrap penguins both consumed almost exclusively krill.

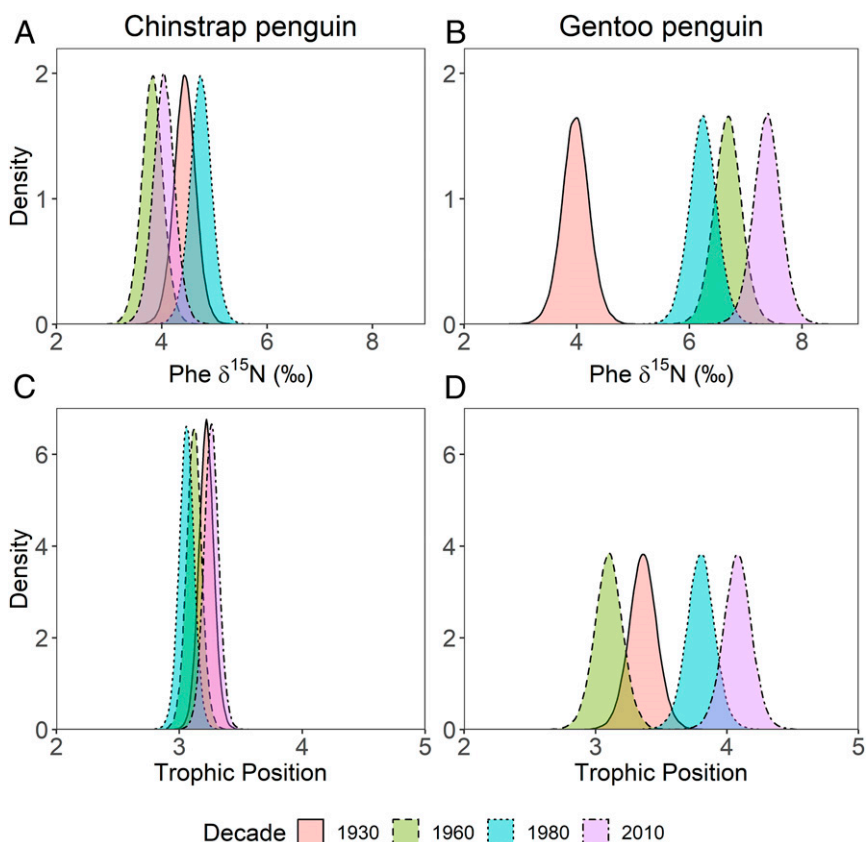
Between the 1960s (TP = 3.1 [2.9 to 3.3]) and today (TP = 4.1 [3.9 to 4.3]), the trophic position of gentoo penguins in the northern Antarctic Peninsula increased by a full trophic level (Figs. 2 and 3). Modern gentoo penguin TP equates to a mixed

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<sub>2</sub> levels has 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 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



**Fig. 2.** Penguin feather amino acid nitrogen stable isotope values. (A) Feather  $\delta^{15}\text{N}$  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.



**Fig. 3.** Density distribution of feather stable isotope parameters. Density distributions, estimated from BANOVA models, of feather  $\delta^{15}\text{N}$  values of phenylalanine ( $\delta^{15}\text{N}_{\text{Phe}}$ ) and calculated trophic position (TP<sub>DF-multi</sub>) of archived historic museum specimens of (A and C) chinstrap and (B and D) gentoo penguins collected in the Antarctic Peninsula region in the 1930s, 1960s, 1980s, and 2010s.

(*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  $\approx$  3.2 [range: 3.1 to 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 30 to 53% between 1979 and 2010, while gentoo penguin populations increased 6-fold during this same time period (13–16). 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 highlight 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; *SI Appendix, Tables S1 and S2*). For example, in the 1980s samples were obtained from 2 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 in gentoo penguins from King George Island in 1987 (TP = 3.5 to 4.1). Similarly, variation in feather  $\delta^{15}\text{N}$  values and calculated trophic positions was consistently greater between species and among decades relative to interannual or among site variation (Fig. 2 and *SI Appendix, Tables S1 and S2*). This is predicted as body feathers synthesized with resources consumed during the postbreeding, premolt period (52) represent regional, as opposed to colony-specific, resource availability (35, 53). While obtaining additional historic museum samples is unlikely, future studies collecting feathers from current breeding populations at higher samples sizes over time could provide a more robust assessment of interannual and/or spatial variation.

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.  $\delta^{15}\text{N}$  values of the penguin source AA phenylalanine ( $\delta^{15}\text{N}_{\text{Phe}}$ ), 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-y record for both penguin species, although not in parallel. In the 1930s, both gentoo (median = 4.0‰ [2.5 to 97.5‰, credible intervals: 3.5 to 4.5‰]) and chinstrap penguins (4.4‰ [3.9 to 5.0‰]) had similarly low  $\delta^{15}\text{N}_{\text{Phe}}$  values indicative of foraging in similar biogeochemical systems (BANOVA PP = 0.09). Over the next century, chinstrap penguin  $\delta^{15}\text{N}_{\text{Phe}}$  values oscillated but remained relatively low (between 3.8 and 4.7‰), while gentoo penguin  $\delta^{15}\text{N}_{\text{Phe}}$  values increased significantly between the 1930s (4.0‰ [3.5 to 4.5‰]) and the 1960s (6.7‰ [6.2 to 7.2‰]) and then again between the 1980s (6.2‰ [5.7 to 6.7‰]) and the 2010s (7.4‰ [6.9 to 7.9‰]) [all BANOVAs PP > 0.99]. This increase in gentoo penguin  $\delta^{15}\text{N}_{\text{Phe}}$  values over the last century, which was not found in chinstrap penguin  $\delta^{15}\text{N}_{\text{Phe}}$  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  $\delta^{15}\text{N}_{\text{Phe}}$  trend as the shift in baseline preceded the shift in diet and trophic position (SI Appendix).

Body feather  $\delta^{15}\text{N}_{\text{Phe}}$  values of the adult penguins sampled in this study (SI Appendix, Table S1 and S2) reflect the foraging habitats of penguins during the postbreeding, premolt period (52). Movement data from both the breeding and postbreeding periods, including limited data during the premolt 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 (>200 m 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-h bouts of foraging (55). In contrast, during premolt, 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  $\delta^{15}\text{N}$  values as a function of  $\text{NO}_3^-$  utilization efficiency (higher utilization in nearshore systems = higher particulate organic matter [POM]  $\delta^{15}\text{N}$  values) (56, 57). Modern chinstrap penguin  $\delta^{15}\text{N}_{\text{Phe}}$  values of 4.0‰ (3.6 to 4.5‰) align well with foraging within the offshore waters of the northwestern Antarctic Peninsula based on euphausiid-derived nitrogen isoscapes for the region ( $4.1 \pm 0.8\text{‰}$ ) (57). Similarly, modern gentoo penguin  $\delta^{15}\text{N}_{\text{Phe}}$  values (7.4‰ [6.9 to 7.9‰]) suggest foraging within nearshore productive waters of the Antarctic Peninsula ( $\text{NO}_3^- \delta^{15}\text{N} = 7$  to 10‰ during periods of maximum  $\text{NO}_3^-$  drawdown) (58). One possible explanation for the low  $\delta^{15}\text{N}_{\text{Phe}}$  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 nonmigratory, diurnal foragers that retain the use of nearshore foraging habitats year-round (35, 53, 55).

Alternatively, assuming no changes in foraging distributions, the increasing gentoo penguin  $\delta^{15}\text{N}_{\text{Phe}}$  values over the past century could reflect an increase in primary productivity in nearshore waters. As primary productivity increases, the  $\delta^{15}\text{N}$  value of the residual pool of  $\text{NO}_3^-$  increases as  $\text{NO}_3^-$  is consumed, resulting in an increase in the  $\delta^{15}\text{N}$  value of newly formed plankton biomass (59). Few data are available for the  $\delta^{15}\text{N}$  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  $\delta^{15}\text{N}_{\text{Phe}}$  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  $\delta^{15}\text{N}$  values of radiocarbon-dated eggshells from pagophilic Adélie penguins sometime within the last 200 y. 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  $\delta^{15}\text{N}$  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 hot spot with respect to multiple, superimposed climate change processes and other anthropogenic impacts (e.g., ocean warming, sea ice loss, ocean acidification, krill harvesting, tourism, and species introductions) likely creating synergistic challenges for *Pygoscelis* penguins and other specialist and generalist marine predators in Antarctica (68–70).

## 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 (SI Appendix, Tables S1 and 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 ( $\delta^{15}\text{N}$ ) stable isotope analysis (CSIA) of 12 individual AAs [McMahon et al. (71)] (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.) (mean  $\delta^{15}\text{N}$  reproducibility:  $\pm 0.3\text{‰}$  for laboratory algal standard and mixed AA standard). We calculated individual penguins' trophic positions (TP<sub>TDF-multi</sub>) using a multi-trophic discrimination factor (TDF) equation following McMahon et al. (71):

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

where  $\delta^{15}\text{N}_{\text{Glu}}$  and  $\delta^{15}\text{N}_{\text{Phe}}$  represent the stable nitrogen isotope values of penguin Glu and Phe, respectively;  $\beta$  represents the difference in  $\delta^{15}\text{N}$  between Glu and Phe of primary producers [3.4‰ for aquatic microalgae (72–74)];  $TDF_{\text{Glu-Phe average}}$  represents an average TDF of 6.3‰ ( $\Delta^{15}\text{N}_{\text{Glu}} - \Delta^{15}\text{N}_{\text{Phe}}$ ) characteristic of planktonic marine food webs [see metaanalysis by McMahon and McCarthy (36)]; and  $TDF_{\text{Glu-Phe penguin}}$  represents the *Pygoscelis* penguin-specific TDF<sub>Glu-Phe</sub> value (3.5‰) derived from a controlled feeding experiment on *Pygoscelis* penguins (71). Alternative methods of calculating TP from AA

$\delta^{15}\text{N}$  values resulted in similar trends in  $\text{TP}_{\text{CSIA}}$  over time and between species (SI Appendix, Fig. S1).

The mean and variance of  $\delta^{15}\text{N}_{\text{Glu}}$ ,  $\delta^{15}\text{N}_{\text{Phe}}$ , and  $\text{TP}_{\text{TDF-multi}}$  across each time period were estimated separately using 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 and Just Another Gibbs Sampler (JAGS). Vague priors were used for the mean (normal distributions with a mean of 0 and variance of 1,000) and the variance (uniform distribution between 0 and 100). Pairwise comparison among time periods and between species are expressed as Bayesian posterior probabilities ( $\text{PP} > 0.99$  as a conservative indication of significant differences) that the posterior distributions of  $\delta^{15}\text{N}_{\text{Glu}}$ ,  $\delta^{15}\text{N}_{\text{Phe}}$ , and  $\text{TP}_{\text{TDF-multi}}$  from one group (time period or species) are different in a 1-way comparison with another group. All statistics were performed in R version 3.5.0 (75).

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