



Long-term stability in the circumpolar foraging range of a Southern Ocean predator between the eras of whaling and rapid climate change

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Assessing environmental changes in Southern Ocean ecosystems is difficult due to its remoteness and data sparsity. Monitoring marine predators that respond rapidly to environmental variation may enable us to track anthropogenic effects on ecosystems. Yet, many long-term datasets of marine predators are incomplete because they are spatially constrained and/or track ecosystems already modified by industrial fishing and whaling in the latter half of the 20th century. Here, we assess the contemporary offshore distribution of a wide-ranging marine predator, the southern right whale (SRW, *Eubalaena australis*), that forages on copepods and krill from ~30°S to the Antarctic ice edge (>60°S). We analyzed carbon and nitrogen isotope values of 1,002 skin samples from six genetically distinct SRW populations using a customized assignment approach that accounts for temporal and spatial variation in the Southern Ocean phytoplankton isoscape. Over the past three decades, SRWs increased their use of mid-latitude foraging grounds in the south Atlantic and southwest (SW) Indian oceans in the late austral summer and autumn and slightly increased their use of high-latitude (>60°S) foraging grounds in the SW Pacific, coincident with observed changes in prey distribution and abundance on a circumpolar scale. Comparing foraging assignments with whaling records since the 18th century showed remarkable stability in use of mid-latitude foraging areas. We attribute this consistency across four centuries to the physical stability of ocean fronts and resulting productivity in mid-latitude ecosystems of the Southern Ocean compared with polar regions that may be more influenced by recent climate change.

isotope ecology | isoscape | environmental change | *Eubalaena australis* | southern right whale

The Southern Ocean is one of the most data-sparse oceanic regions in the world (1) but has nonetheless been subject to massive ecosystem perturbations through industrial sealing, whaling (2), and fishing (3, 4). Ongoing environmental changes of anthropogenic origin, including climate change and the ozone hole, are altering physical and biological conditions in this region (5). Specifically, rapid ocean warming and acidification are affecting the food web of maritime Antarctic and sub-Antarctic ecosystems from phytoplankton (6) to the keystone Antarctic krill [*Euphausia superba* (4, 7, 8)] and top predators (9).

As sentinels of the diverse and productive food webs on which they depend (10), large marine predators are often used to track direct and indirect anthropogenic impacts on ecosystems as they integrate information across the food chain and respond to environmental change or disturbance (11). In recent decades, marine predator populations around the world have shown variation in migratory behavior, distribution, and life history phenology in response to fluctuations in prey availability resulting from climate change (12–17). Most of this research has focused on central place foragers that breed on land (e.g., seabirds and pinnipeds) due to the ease of capture and data collection (9, 10, 18, 19), while comparatively little is known about pelagic cetaceans that spend their entire lives at sea and generally range over larger distances (20, although see ref. 21). Moreover, while many of these studies span decades, they rarely extend to before the onset of the Industrial Revolution (e.g., ref. 18) and thus focus on ecosystems that have already been heavily impacted by humans.

Early whaling records make it possible to characterize the ecology of targeted species prior to large-scale ecosystem changes from industrial whaling and fishing (22–25). In particular, the American whaling fleet operating in the Southern Hemisphere from the

Significance

Assessing change in Southern Ocean ecosystems is challenging due to its remoteness. Large-scale datasets that allow comparison between present-day conditions and those prior to large-scale ecosystem disturbances caused by humans (e.g., fishing/whaling) are rare. We infer the contemporary offshore foraging distribution of a marine predator, southern right whales ($n = 1,002$), using a customized stable isotope-based assignment approach based on biogeochemical models of the Southern Ocean. We then compare the contemporary distributions during the late austral summer and autumn to whaling catch data representing historical distributions during the same seasons. We show remarkable consistency of mid-latitude distribution across four centuries but shifts in foraging grounds in the past 30 y, particularly in the high latitudes that are likely driven by climate-associated alterations in prey availability.

The authors declare no competing interest.

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18th to the early 20th century kept detailed records of where and what species were observed and killed (e.g., ref. 20). Some of the longest commercial records are for southern right whales (SRWs, *Eubalaena australis*), a major consumer of krill and copepods in the Southern Ocean that migrates between coastal winter breeding/nursery grounds and offshore foraging grounds used between spring and autumn (23). An estimated 150,000 SRWs were killed by whalers on a circumpolar scale during the 18th to mid-20th century (26) causing a decline in the global population to as few as 400 individuals before protection enabled the species to moderately recover in parts of its historical range (26, 27). When paired with an understanding of current distribution, whaling records allow the study of a marine predator's foraging range across several centuries.

Knowledge of the current distribution of marine predators such as the SRWs is hindered by our inability to track their wide-ranging movements at a population level and their variable use of different pelagic regions across their range (28, 29). Stable isotope analysis is an effective method to assess the foraging distribution of migratory marine animals (30–32) by comparing carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of their tissues with that of their prey or the baseline isotopic composition of phytoplankton at the base of pelagic food webs (30). This tool has been used extensively to study the ecology of baleen whales (e.g., refs. 17, 33, and 34) as the isotopic composition of skin biopsy samples collected from wintering grounds reflects that of recently visited foraging grounds (33). High-resolution spatial and temporal isoscapes (i.e., models of the distribution of stable isotopic composition) of primary producer (phytoplankton) and primary consumer (zooplankton) isotope values have recently become available across ocean basins (35, 36), allowing us to make accurate geographic assignments for marine predators. This advance is important because the seasonal and annual variability of ocean conditions that influence the isotopic composition of both predators and their prey is not reflected in static isoscapes (30). Recent progress in the development of global biogeochemical ocean models further improves the applicability of isotope assignment to identify foraging patterns of marine predators over large spatiotemporal scales (37).

Here, we use these advances to supplement the sparse information available (29, 38, 39) on where many of the SRW populations forage and assess potential distributional shifts since the whaling era. For example, long-term monitoring of the South American SRW population shows that reproductive output and adult survival of SRWs on their breeding grounds in the southwest (SW) Atlantic correlate with climate oscillations that influence the distribution and abundance of their prey on their high-latitude summer foraging grounds (40–42). Such connections between variable environmental conditions and/or prey availability with SRW recovery and fitness are lacking for most populations. Furthermore, the degree to which poor-quality foraging grounds could be responsible for the lack of recovery of some wintering ground populations [e.g., southeast (SE) Australia (43)] cannot be assessed without identifying the foraging grounds used by each population.

Specifically, we address this knowledge gap through the use of a coupled oceanographic biogeochemical isoscape model that accounts for temporal and spatial variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in phytoplankton (37, 44) and a framework that customizes assignment space using prior information on sampling location/date and migratory behavior of SRWs. This approach is used to estimate the circumpolar foraging distributions of SRWs in the late austral summer and autumn through the comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of skin samples ($n = 1,002$) collected from six

genetically distinct populations (45–47). We then investigate the temporal variability of SRW foraging distributions by comparing assignments 1) over three decades (1994 to 2020) using the model output and 2) over four centuries by comparing model outputs directly to whaling data from the late 18th to early 21st century (22, 23) matched to the seasonal window reflected in the skin isotope data. This provides an unprecedented perspective on shifts and stability in the foraging distribution of a Southern Ocean sentinel predator as populations simultaneously recover from exploitation and face rapid climate change.

Results

Foraging Ground Assignments. We compiled 1,002 SRW skin samples from seven different wintering grounds across six genetically distinct populations across the Southern Hemisphere spanning three decades (Fig. 1 and *SI Appendix, Fig. S1*); the New Zealand population is represented by two wintering grounds: New Zealand mainland and Auckland Islands (47). Skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged -26.0 to -16.3‰ and 4.6 to 15.0‰ , respectively (Fig. 1 and *SI Appendix, Tables S1 and S2*). We split samples from Argentina into two groups based on the previously described bimodality in $\delta^{15}\text{N}$ values ($>$ or $<10\text{‰}$), a pattern that was only observed in SRWs sampled from this wintering ground (34). There were statistically significant differences in skin isotope values by decade (Kruskal–Wallis statistics: $\delta^{13}\text{C}$ $\chi^2 = 63.393$, $df = 2$, P value = $1.715\text{e-}14$, and $\delta^{15}\text{N}$ $\chi^2 = 24.121$, $df = 2$, P value = $5.782\text{e-}06$) and wintering ground (Kruskal–Wallis statistics: $\delta^{13}\text{C}$ $\chi^2 = 553.5$, $df = 7$, P value $< 2.2\text{e-}16$, and $\delta^{15}\text{N}$ $\chi^2 = 323.46$, $df = 7$, P value $< 2.2\text{e-}16$) (*SI Appendix, SI1 and Tables S1–S4*). Post hoc Dunn's test further indicated that many of these differences are linked to variation between the south Atlantic and Indo-Pacific wintering grounds (*SI Appendix, Tables S3 and S4*).

We mapped the assigned foraging probability area for each whale using skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and phytoplankton isoscapes from a data-constrained Model of Ocean Biogeochemistry and Isotopes [MOBI (37, 44)] in a bivariate normal probability function (48) (*Materials and Methods*). We used a threshold approach to represent the population-level core and general foraging areas using pixels with highest 50% and 25% probability, respectively (49, 50), per wintering ground (Fig. 2*A*; larger maps of foraging ground assignments for each wintering ground are provided in *SI Appendix, Figs. S2–S9*). Isotopically assigned foraging areas were spread across the circumpolar region. Except for the Auckland Islands, all populations had foraging grounds partially assigned to both mid (around 40°S) and high ($>60^\circ\text{S}$) latitudes (Fig. 2*A*).

To assess interindividual variation in foraging distribution, we also generated summed individual-level maps by wintering ground that depict the percent of individuals whose general foraging areas were assigned to each grid cell (49). Individual-level summary maps of foraging grounds sometimes varied in comparison to maps generated at the population level (Fig. 2*B*). For example, a small proportion of individuals wintering in Argentina and the Auckland Islands was assigned to high-latitude waters, while most individuals from these wintering grounds were assigned to mid-latitude foraging grounds.

Changes in Foraging Grounds at High Latitudes across Decades.

Foraging grounds in the south Atlantic and SW Indian oceans used by SRWs from the Brazilian, South African, and SW Australian wintering grounds showed a marked shift from high to lower latitudes between the 1990s to 2010s (Fig. 3; distribution of data by decade shown in *SI Appendix, Fig. S10*). The modeled

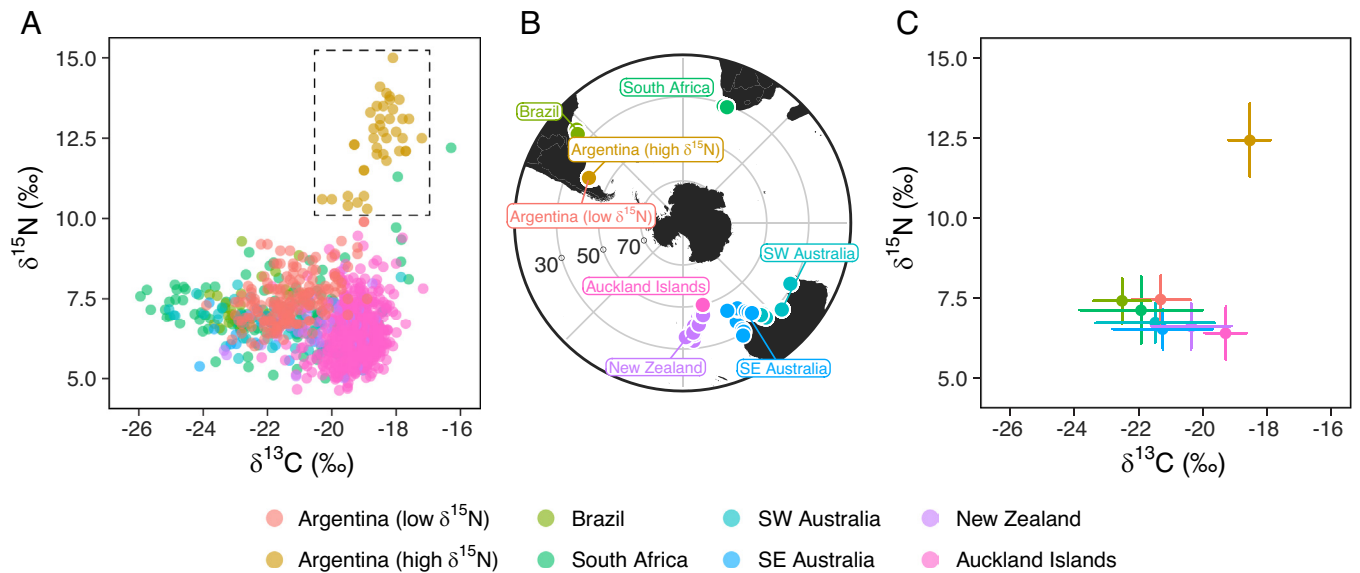


Fig. 1. Distribution of sampling location and stable isotope values for SRW skin samples. (A) Biplot of skin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each wintering ground. The dark gray rectangle delineates the subset of Argentinian samples with high $\delta^{15}\text{N}$ values. (B) Map of sample collection locations by wintering ground; note Australia wintering grounds are divided into SW and SE. (C) Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values summarized by wintering grounds; error bars denote SD.

general foraging areas encompassing waters south of 60°S declined by 13%, 25%, and 19%, respectively, for these three wintering grounds. By contrast, assignment to high-latitude foraging grounds increased in the SW Pacific Ocean by 25% for SE Australia and 10% for New Zealand wintering grounds between the 2000s and the 2010s.

Stability in Foraging Grounds in Mid-latitudes across Centuries.

Foraging ground assignments were compared to 2,614 whaling catch records during the late austral summer and autumn, the seasonal period inferred from $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analyses of skin that accounts for the isotopic incorporation rate of this tissue (33). These data comprised 270 Soviet catches recorded between 1961 and 1968 and 2,344 American catches recorded between 1792 and 1912 (22, 23). Whaling records strongly overlapped with foraging grounds estimated by isotope assignments of samples collected over the last 30 y. Of these records, 2,488 were included in at least one potential foraging range (Fig. 4), with an average of 77% of catch records located within general foraging areas generated at the population level. Discrepancies between catch records and foraging ground assignments from the same seasons mostly occurred in the south Atlantic Ocean in latitudes >50°S. Comparisons at high latitudes to the 18th to 20th century American whaling were not possible as this fleet did not typically hunt >50°S due to notoriously bad weather (22). The late austral summer and autumn Soviet catch records from the 21st century in the south Atlantic Ocean overlapped with foraging grounds assigned to the South African wintering grounds but did not with those of the Argentinian and Brazilian wintering grounds (Fig. 4).

Discussion

We used an isoscape assignment approach to infer the foraging grounds of a marine predator on a circumpolar spatial scale and compare our findings across timescales from decades to centuries. Over the seasons reflected in skin (late austral summer and autumn), SRWs consistently used mid-latitude foraging grounds across four centuries, but there was a decline in the use of some high-latitude foraging grounds in recent decades, particularly in

the south Atlantic Ocean. Our results highlight heterogeneous changes in SRW distribution, suggesting differences in the effects of whaling and climate change across the Southern Ocean. Here, we discuss potential drivers of SRW distribution over time and space, including the availability of their primary prey: krill at high latitudes and copepods at mid-latitudes (23).

In the high latitudes of the Southern Ocean, the distribution of baleen whales and other top predators is typically related to krill availability (e.g., refs. 20 and 51–53). Fluctuations in krill distribution and abundance through time are linked to climate-related shifts in the habitat of this keystone species (e.g., refs. 54 and 55). These spatiotemporal shifts in prey abundance correlate with decadal changes in SRW foraging ground assignments. For example, the Atlantic sector (90°W to 10°W) is subject to faster warming than other regions of the Southern Ocean (56), and the krill stocks within this region have contracted in range and abundance in the past century (7, 57, 58) with implications for krill predators (59). This change coincides with a decrease in high-latitude foraging ground assignments for SRWs that winter in South Africa and Brazil (Fig. 3). In contrast, significant cooling and gains in sea ice may have allowed krill densities to increase in the Pacific sector (150°E to 90°W) since 1930 (55), and this trend is predicted to continue over the coming decades (54). The increase in krill density coincides with a small increase in assignment to high-latitude foraging grounds for SRWs from New Zealand and SE Australia over the past 20 y. Finally, changes in krill distribution over time have not been reported for the Indian sector (10°W to 150°E) due to a sparsity of data (60, 61), limiting our capacity to interpret observed changes in foraging ground assignments of the SW Australian wintering ground.

In contrast to the recent decline in the use of high-latitude foraging areas, we found persistent use of mid-latitude foraging areas across centuries through comparison of isoscape assignment of skin samples and historical whale catch data (Fig. 4). Habitat modeling using historical whaling and satellite track data (24, 25, 38) indicates that the subtropical front (~30 to 40°S) is a key oceanographic feature used as foraging habitat by SRWs and other oceanic predators (62) in the Southern Ocean. The consistent use of this feature

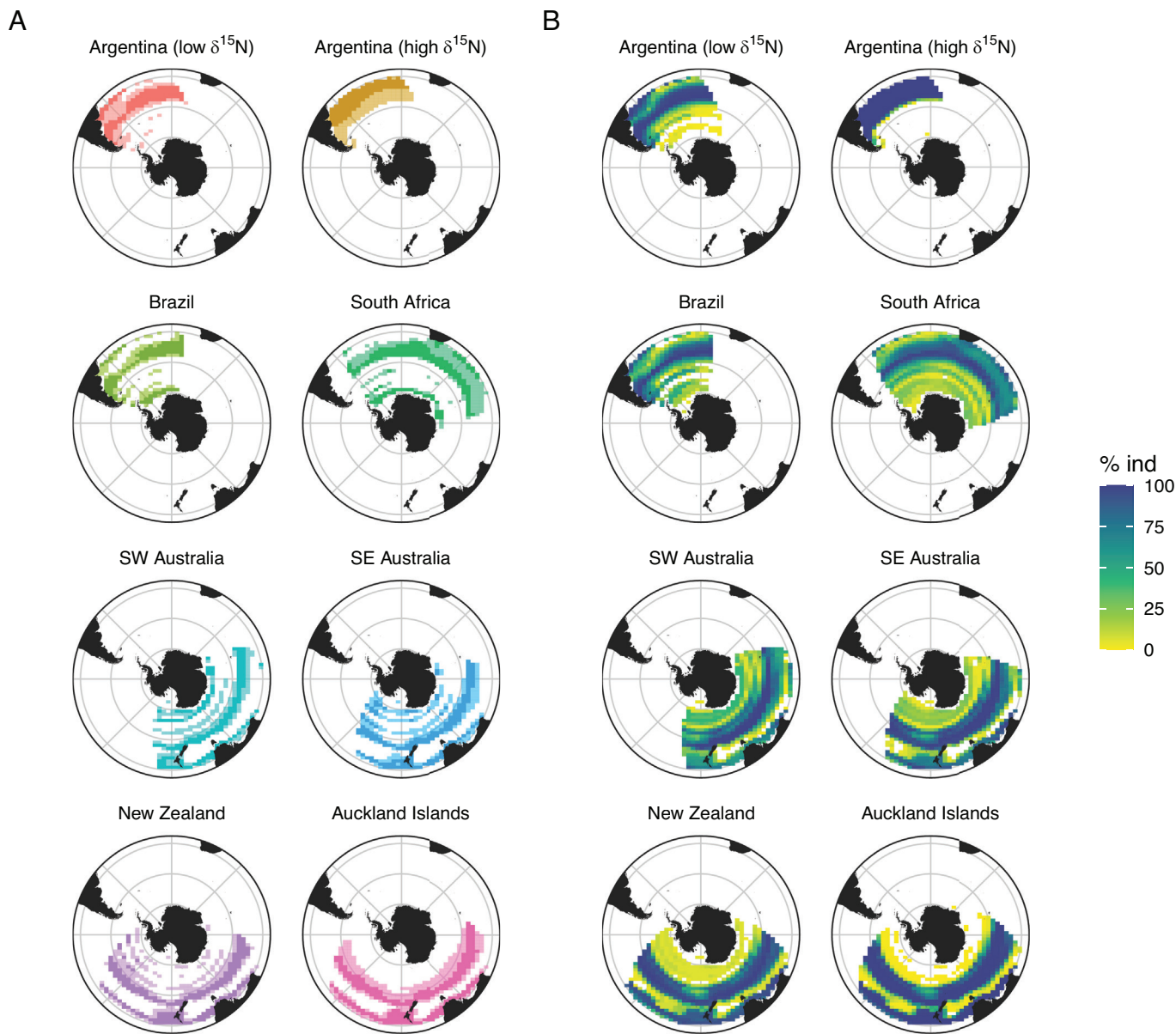


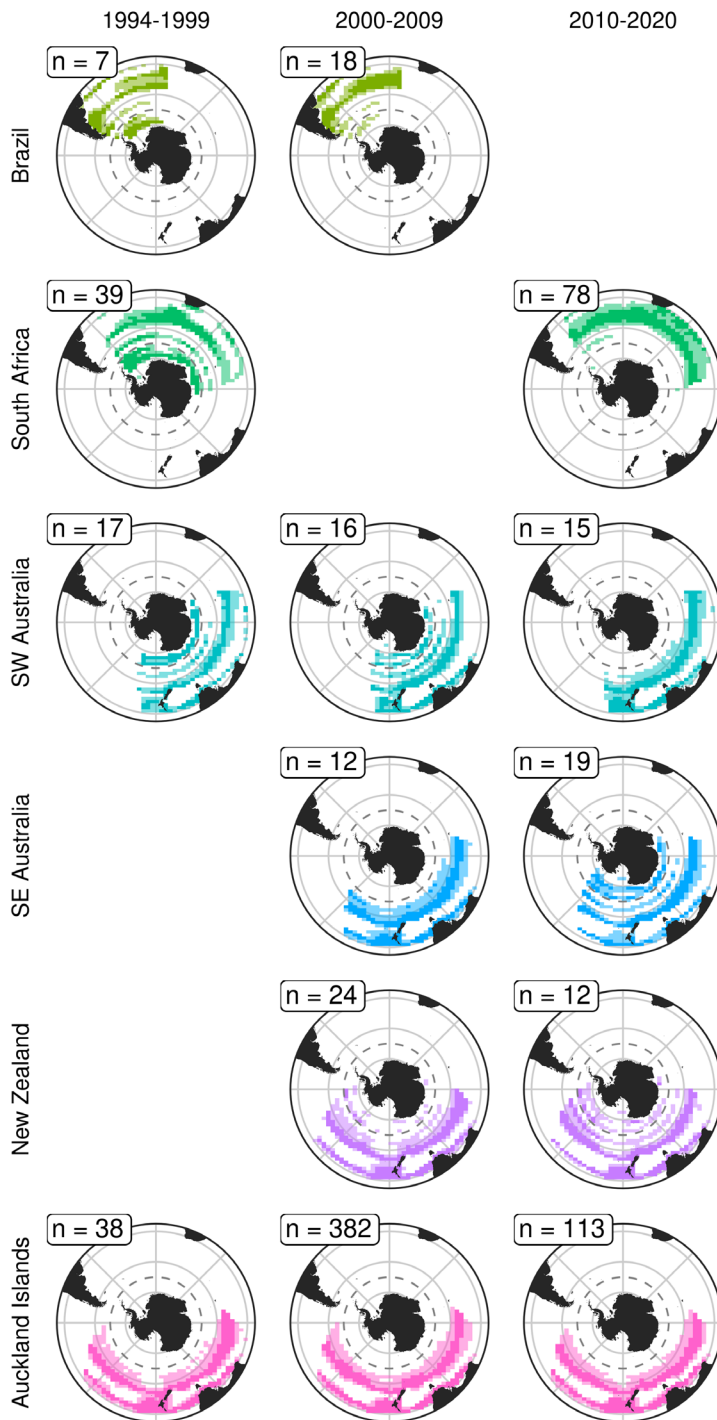
Fig. 2. Isotopically assigned foraging grounds for each SRW wintering ground across all years (sample sizes in Table S1). (A) Population-level average core and general foraging areas in dark and light colors representing the highest 25% and 50% probability pixels, respectively. (B) Individual-level summary of foraging grounds shown with a color scale representing the percent of sampled individuals that was assigned to each grid cell based on binary transformation of the 50% highest probability pixels. Note Australia wintering grounds are divided into SW and SE. Parallels of latitude represented in gray in each map mark 30°S, 50°S, and 70°S.

across centuries is supported by climate model predictions and the lack of systematic changes in the locations of subtropical fronts over the past few decades (1). Furthermore, SRWs likely forage on copepods at mid-latitudes (23), which may be less sensitive to shifts in ocean temperature than Antarctic krill (63). Whaling vessels of the 18th to 20th centuries rarely ventured into the remote and dangerous high latitudes (>50°S) of the Southern Ocean; thus, historical use of these waters by SRWs might be underestimated in our analysis in comparison to use of mid-latitude foraging grounds. Nonetheless, there could be a combination of physical and biological factors that promote stability in mid-latitude foraging grounds associated with ocean fronts. Such stability has implications for the resilience of oceanic predators that depend on this productive habitat, such as seabirds (64), marine mammals (65, 66), sharks (67), bony fish, and squids (68), but to our knowledge,

no other studies have examined use of this ecosystem over such a long time period. Accordingly, we recommend that SRWs are integrated into future work to inform marine conservation and management strategies of subtropical front ecosystems in the Southern Ocean (10).

The contrast between changes in foraging at high latitudes and consistent or increasing use of mid-latitude habitat could be related to the differing trajectories of SRW populations. In recent decades, shifts in SRW population demography have been linked with climate variability. For example, there are strong links between reproductive output of SRWs wintering in Brazil and indices of krill abundance (40), highlighting the historical importance of high-latitude foraging areas to SRWs that winter off South America. In South Africa, a suspected climate-driven shift from high-latitude to mid-latitude foraging grounds (17)

A



B

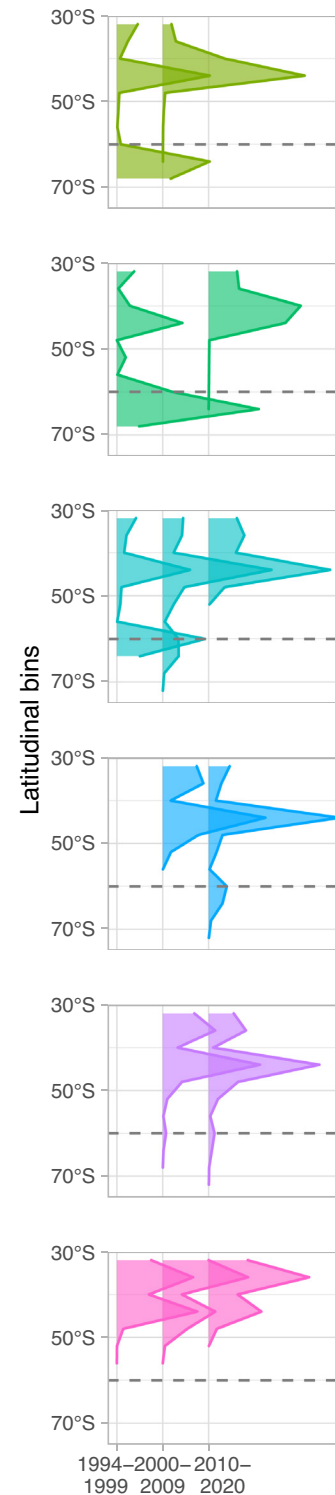


Fig. 3. SRW foraging ground assignments by wintering ground and decade. (A) Maps of assigned general and core foraging areas. Sample size is indicated in each panel. Population-level average core and general foraging areas are represented for each decade by population combination in dark and light colors, respectively. (B) Distribution of the population-level foraging probabilities summed over all pixels (i.e., thresholds) in latitudinal bins of 4° for each decade. Argentinian samples were collected over only one decade (2000 to 2009) and are therefore not represented in this figure. Note Australia wintering grounds are divided into SW and SE. Parallels of latitude represented in gray in each map mark 30°S, 50°S, and 70°S, and the dashed line delineates the 60°S latitude.

coincided with a decline in body condition (69) and calving rates (70). SRWs wintering in SW Australia have also experienced a decline in reproductive output coincident with

latitudinal shifts in foraging grounds (71). In contrast, a large proportion of SRWs wintering in the Auckland Islands consistently forages in mid-latitudes near the subtropical front (24)

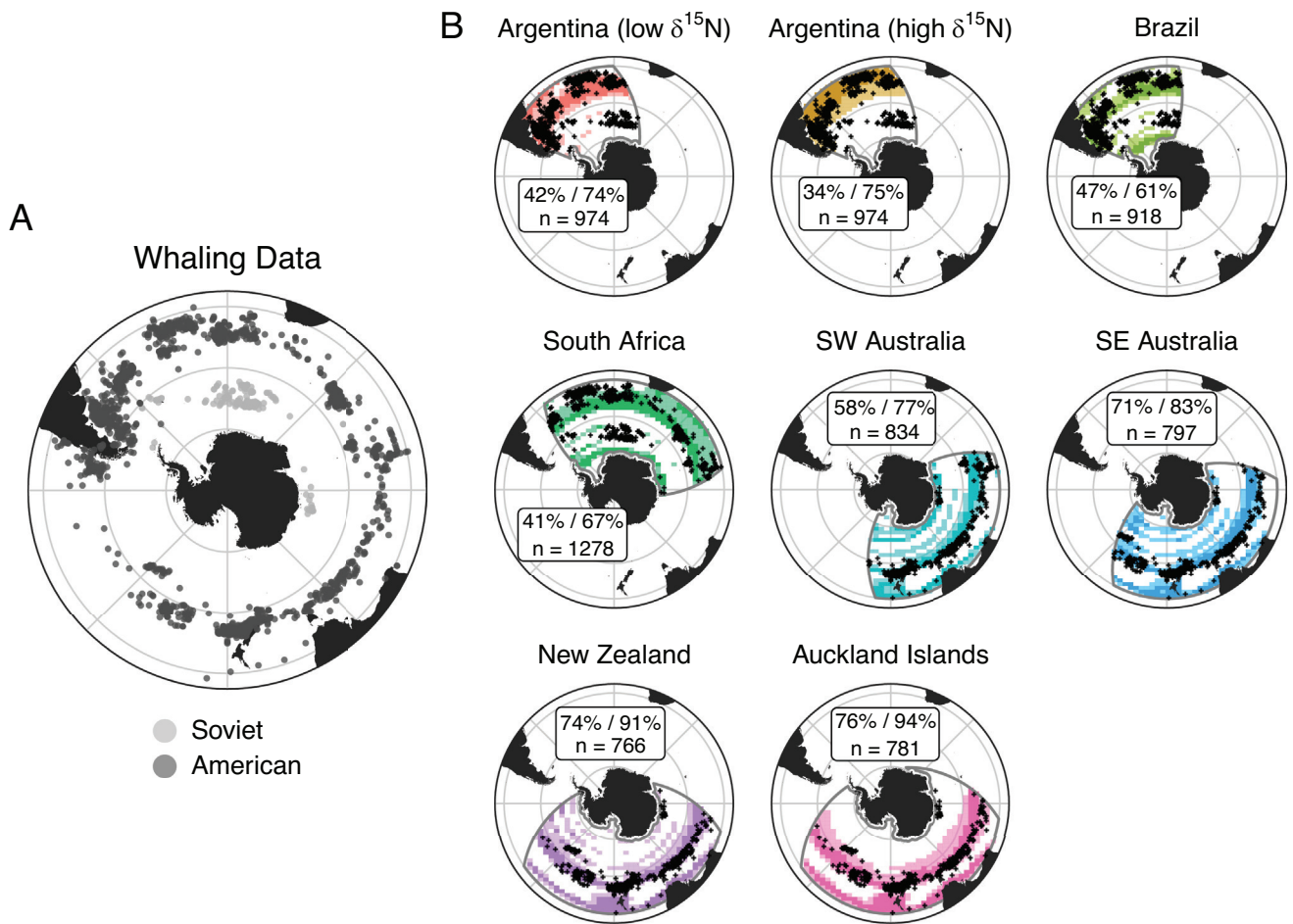


Fig. 4. Geographic positions of (A) American and Soviet SRW whaling records, and (B) overlap with foraging grounds isotopically assigned to each wintering ground. In panel B, only the whaling records occurring within the foraging bubble (outlined in gray) set for each wintering ground are mapped (indicated by n in each panel). Population-level average core and general foraging areas are shown in dark and light colors, respectively. The percent of whaling records overlapping with the core and general foraging grounds is indicated over each panel (core %/general %). Note Australia wintering grounds are divided into SW and SE. Parallels of latitude represented in gray in each map mark 30°S, 50°S, and 70°S.

and has the best body condition score of any right whale population (72) in addition to having a high population growth rate (73). Use of distinct foraging grounds by other baleen whale subpopulations has been associated with significant differences in body condition that likely impacts survival (74). Similarly, we hypothesize that SRW populations that are more dependent on mid-latitude foraging grounds may have steadier recovery trajectories than those with significant use of high-latitude habitat. Such regional heterogeneity has been shown as important to understand large-scale patterns in habitat use by humpback whales (75). Therefore, future work should investigate regional population dynamics or body condition relative to prey availability and the strength of assignments to high-latitude and mid-latitude foraging grounds.

High-latitude waters are generally considered to be the prime foraging grounds for the Argentinean SRW population (34), but our analysis unexpectedly revealed that this population largely uses mid-latitude foraging grounds during the late austral summer and autumn. A few individuals wintering in Argentina were assigned to high-latitude waters (Fig. 2B) outside the isotopically assigned foraging grounds averaged for the population (Fig. 2A), probably due to individual variability in habitat use (76). Part of the Argentinian population is known to feed near South Georgia Island/Islands Georgias del Sur around

54°S (29, 77), where anomalously warm temperatures can negatively impact calving success in the following year (40, 41). Furthermore, a marked increase in adult female mortality rates was detected following El Niño events (42), however, individual variability in foraging distribution has also been revealed in this population [Fig. 1A; (34, 77)]. As with South Africa and Brazil, SRWs wintering in Argentina may have shifted to forage more in mid-latitudes, at least over the seasonal time window covered by this study, but decadal changes could not be investigated for this population due to the restricted sampling period from 2000 to 2009 (*SI Appendix, Fig. S10*). Argentinian SRWs are also known to forage in both high latitude and mid-latitude of the south Atlantic Ocean, and the isotopic signal from the former may be masked by the latter as foraging continues over the Patagonian Shelf during the northward migration in late autumn. In support of the latter hypothesis, historical stable isotope analysis from bone samples of SRWs (76) and satellite tracking demonstrated intensive use of the outer continental shelf and slope between 35°S and 52°S (29), where these whales likely encounter exceptionally productive conditions as they migrate during the late austral autumn.

We found long-term, persistent use of mid-latitude foraging grounds over several centuries despite SRWs being reduced by whaling to less than 1% of their historic population size (26, 27).

We hypothesize that social or behavioral factors could contribute to maintaining SRW distributions, notably maternally directed fidelity to foraging grounds. When conserved across generations, this fidelity is termed “migratory culture” (78) and has been inferred in SRWs from correlations between isotopic and genetic data (77). A number of species of baleen whales are known to have lost the knowledge of migratory destinations when the population that used the area was extirpated by commercial whaling (79). In contrast, the potential shift away from high-latitude foraging grounds observed here for SRWs suggests behavioral flexibility, perhaps through experience or social transmission from conspecifics (78). Such flexibility in response to climatic shifts has been demonstrated in other marine predators (e.g., ref. 14) including baleen whales (15, 80).

The isoscape assignment approach used in this study provides unprecedented knowledge about SRW foraging grounds. This approach allows us to investigate foraging ground assignments across broad spatial and temporal scales compared with traditional multivariate statistical analyses that are limited to tests of significant differences in the distribution of skin isotope values between sample partitions (*SI Appendix, S11*). In the past, process-based isotope models have generally not been used to geolocate animals due to their inherently high levels of uncertainty (35), but the newest generation of data-constrained, process-based phytoplankton isoscapes used here (37) appears to capture the broad-scale patterns of the circumpolar SRW distribution (Fig. 4). Critically, this model accounts for annual and seasonal variation of isotopic patterns across the Southern Ocean that may be reflected in SRW tissue collected at different times (e.g., ref. 81), provided that the estimated isotopic incorporation rates of skin tissue are accurate (33, 82). The resulting foraging ground assignments showed clear latitudinal discrimination but less ability to delineate the longitudinal limits of foraging ranges. Therefore, we used the maximum migratory distance observed in satellite tracks of SRWs departing from the Auckland Islands as prior knowledge to estimate putative foraging ranges (*SI Appendix, Fig. S11*). Individual SRWs almost certainly show migratory specialization and might be foraging closer to their respective wintering grounds, while other individuals may also forage beyond the maximum distance assumed here.

Several limitations must be considered prior to expanding this approach to other species or regions. While this work was based on all available samples at the time of analysis, we acknowledge that some regional datasets are small but actually represent a sizable proportion of the total population size in some cases; e.g., SE Australian dataset ($n = 46$) is ~20% of the total population size (43). Our findings are also supported by the identification of regional trends observed in more than one wintering ground, such as in Brazil, SW Australia, and South Africa. Additionally, while our approach was able to account for abiotic factors influencing isoscape variability such as the Suess effect and oceanographic processes, it is not able to account for potential biotic drivers such as changes in food web structure. Such factors can influence plankton isotope values and in turn the isotope values of higher trophic level predators (83, 84). Factors unrelated to the isoscape analysis could also be contributing to the observed changes, such as increased competition from other krill predators at higher latitudes. A caveat in using isotope analyses to study the distribution of large, endangered, or elusive species is uncertainty in trophic discrimination factors (TDFs) needed to directly compare consumer tissues with baseline isoscapes. Here, we were able to constrain

this variable through analysis of an independent satellite tracking dataset to validate foraging locations. Since we focused on investigating circumpolar-scale patterns, we selected TDFs to enable comparison across wintering grounds. We acknowledge different populations could forage at slightly different trophic levels (34), which would impact TDFs used to directly compare whale and phytoplankton isotope values, and possibly explain the difference in TDFs estimated for SW Pacific and SW Atlantic SRW populations (*SI Appendix, Fig. S12*). We believe our circumpolar perspective and approach that incorporates temporal variation in isoscapes and tracking data to estimate range and TDFs is robust and should inspire future research in isoscape geographic assignments.

Long-term distributional changes of pelagic predators are notoriously difficult to assess due to flexible use of their large range that impedes direct observation, particularly in the remote waters of the Southern Ocean. We surpassed these challenges by using an isotope-based approach to assign SRWs at both the individual and population levels to circumpolar foraging grounds. We show that this mobile predator displays short-term (decadal) flexibility in its latitudinal foraging distribution, perhaps driven by impacts of rapid climate change, but long-term (century-scale) consistency in the use of mid-latitude foraging grounds as it recovers from commercial whaling. A southward range shift and decreased availability of suitable habitat are predicted to occur at mid-latitudes by the end of the century for SRWs (24). However, SRW populations seem to have had diverging responses to global warming over the past few decades, potentially shifting toward increased reliance on the subtropical front located in mid-latitudes. Overall, SRWs appear stable in their use of the mid-latitude foraging grounds, despite potential loss of cultural migratory memory after the whaling era. In addition to showing potential shifts in distribution, this work represents a useful global assessment of SRW foraging habitat use. These findings can be applied to the identification of high-priority areas for SRW protection, assessment of offshore anthropogenic threats, inference of the stock identity of whales exploited by commercial whaling, and understanding the drivers of variable recovery of SRW populations around the Southern Ocean.

Materials and Methods

Stable Isotope Analysis. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of adult SRW skin collected during the austral winter/spring (July–October) were compiled from the literature or generated for this study: 419 published values and 583 new values, spanning 1994 to 2020 (*SI Appendix, Tables S1 and S5*). Most samples came from skin biopsy or sloughed skin samples from living whales, except for one sample from a whale killed by a ship strike in Queensland, Australia, and two stranded adult whales from Argentina (*SI Appendix, Table S1*). All samples were lipid-extracted prior to isotope analysis; details about extraction protocols are provided in *SI Appendix, Table S1* (33, 85). Isotope values were normalized using internal reference materials calibrated to internationally accepted standards for carbon (Vienna Pee Dee Belemnite) and nitrogen (atmospheric N_2) isotope analyses. Precision for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was estimated by analysis of internal reference materials and was $\leq 0.2\%$ (SD) for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (*SI Appendix, Table S1*). We also measured the weight percent carbon and nitrogen concentrations of each sample as a control for lipid content; samples had a mean (\pm SD) [C]:[N] ratio of 3.3 ± 0.3 indicative of pure protein.

Whaling Records. We compiled records (catches and sightings) by American (1792 to 1912) and Soviet (1961 to 1968) whaling vessels (22, 23). We restricted this dataset to records that occurred at $>30^\circ\text{S}$ during the late austral summer and autumn (from February to July) to match with the temporal and spatial window

of the isoscape assignment. Due to the scarcity of whaling data south of 50°S (specifically the American whaling data), we acknowledged that it is not fully representative of SRW use of high latitudes.

Isoscape Assignment Modeling. The baseline phytoplankton isoscapes were acquired from MOBI (37, 44) for phytoplankton that include recent improvements to the marine iron cycle (86) (<https://andreasschmittner.github.io/Models/MOBI/index.html>). Isoscapes consist of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ rasters at $3.6^\circ \times 1.8^\circ$ resolution for the Southern Hemisphere (37, 44). These model outputs consist of monthly $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ averages in a hindcast scenario from 1992 to 2021, and the $\delta^{13}\text{C}$ predictions incorporate warming from increasing atmospheric CO_2 and input of decreasing atmospheric $\delta^{13}\text{C}$ values from anthropogenic emissions (i.e., Suess effect). The model outputs were corrected with zonal averages derived in latitudinal bins from a model data comparison using recently published particulate organic matter datasets [SI Appendix, S12 (87, 88)].

To compare the isotope value of whale skin to the MOBI isoscape to enable the identification of foraging grounds, we accounted for both the isotopic incorporation rate and trophic discrimination. The isotopic incorporation rate reflects the time period over which dietary inputs are incorporated into consumer tissue, which for skin is estimated to be up to 6 mo prior to sampling for baleen whales (33, 82). For each whale, we provided a custom isoscape by averaging the MOBI isoscape across the third to fifth months prior to sampling (33), ranging from the late austral summer to autumn (SI Appendix, Fig. S13), as the first 2 mo prior to sampling were removed from the isoscapes to exclude the migratory period. Trophic discrimination adjusts for the difference in trophic level between the MOBI (phytoplankton) isoscape and SRW skin and was determined using a validation process described below.

Likely foraging area origins were determined using skin isotope values and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isoscapes in a bivariate normal probability function (48) with a pooled error structure described in SI Appendix, S12 that incorporates uncertainty in TDFs and the isoscape rasters. Assignments were made using both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values to estimate the likelihood that each raster cell in the isoscape represents the foraging area origin. The geographical scope of assignment was constrained to a 6,500-km radius “potential foraging range” from each wintering ground to reflect prior information on swimming distances and migration behavior of SRWs (SI Appendix, S13 and Fig. S12). For each whale, a posterior probability of origin map within this potential foraging range was generated and rescaled so that all pixel values summed to one. Then, individual assignment maps were pooled in two different ways to estimate population-level foraging grounds and individual-level foraging grounds that allowed us to explore interindividual variation in movement (49). For the population-level summary, rescaled individual maps were averaged per wintering ground. We mapped the probability distribution of the pixels in the potential foraging range and used a threshold approach to determine general (pixels with the highest 50% probability) and core (highest 25%) foraging areas (49, 50). For the individual-level summary, rescaled individual maps were binned into binary maps with a threshold corresponding to the 50% contour of the probability distribution. The resulting individual foraging areas were summed by wintering ground, and we calculated the percent of individuals whose foraging areas were assigned to each cell. For clarity, the assignment modeling approach is presented in a schematic SI Appendix, Fig. S14.

TDF. We used satellite track data from SRWs to validate $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDFs used in our isoscape assignment model (SI Appendix, S14). Briefly, we set a range of TDFs of 2 to 4% for $\delta^{13}\text{C}$ and 4 to 6‰ for $\delta^{15}\text{N}$ based on the literature to account for the ~2 trophic levels between SRW and phytoplankton (33, 82, 89–93). We then compiled movement data from 49 individuals tagged with Argos-linked satellite tags (Wildlife Computers) in two winter breeding grounds [south Atlantic: Argentina, $n = 31$ (29), and Indo-Pacific: Auckland Islands, $n = 16$ (94)] and one summer foraging ground [south Atlantic: South Georgia, $n = 2$ (95)] associated with the Argentinian wintering ground (96). State space models were used to define area-restricted search (ARS) behavior indicative of foraging (SI Appendix, S14 and Fig. S15). ARS positions were aggregated over a grid that matched in resolution and extent with the MOBI model (37, 44) for phytoplankton. We then iterated the isoscape assignment

model (described above) for each combination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ TDFs (at 0.5‰ increments). The TDF values that produced the geographic assignments with the highest percentage overlap with the ARS data were identified for the south Atlantic and Indo-Pacific and then averaged to generate a value to apply across the circumpolar dataset (SI Appendix, S14 and Fig. S12).

Temporal Analysis. First, we investigated distributional changes over the last three decades by comparing foraging ground assignments across 1994 to 1999, 2000 to 2009, and 2010 to 2020 (SI Appendix, S14 and Fig. S10). We produced separate probability of origin maps for samples collected in each wintering ground and each time period. We assessed distributional changes in the Southern Ocean by calculating the percent change of the general foraging surface area assigned by decade to waters $>60^\circ$ latitude. Decadal changes were further analyzed by comparing the distribution of the population-level summed probabilities of foraging assigned to each pixel in assignment maps of each wintering ground by latitudinal bins. No probability threshold was applied in this case, in contrast to the population level summaries, to ensure that we captured all available information (49).

Second, we investigated distributional changes over four centuries (18th to 21st century) through comparison to whaling catch records. We selected catch records that occurred within the foraging bubbles assigned to each wintering ground that occurred during the late austral summer and autumn and calculated the proportion of catches spatially overlapping with predicted core and general foraging areas quantified as percent overlap.

Data, Materials, and Software Availability. All study data are made publicly available in the SI Appendix. Codes can be downloaded from <https://github.com/SoleneDerville/SRW-isoscape-assignment>.

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