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

Solène Derville, Leigh Torres, Seth Newsome, Christopher Somes, Luciano Valenzuela, Hannah Vander Zanden, C. Scott Baker, Martine Bérubé, Geraldine Busquets-Vass, Kris Carlyon, et al.

Main Manuscript

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

Solène Derville*[1,2], Leigh G. Torres[1], Seth D. Newsome[3], Christopher J. Somes[4], Luciano O. Valenzuela[5,6,7], Hannah B. Vander Zanden[8], C. Scott Baker[1,9], Martine Bérubé[10,11], Geraldine Busquets-Vass[3,12], Kris Carlyon[13], Simon J. Childerhouse[14], Rochelle Constantine[15], Glenn Dunshea[16,17], Paulo A. C. Flores[18], Simon D. Goldsworthy[19,20], Brittany Graham[14], Karina Groch[21], Darren R. Gröcke[22], Robert Harcourt[23], Mark A. Hindell[24], Pavel Hulva[25,26], Jennifer A. Jackson[27], Amy S. Kennedy[28], David Lundquist[29], Alice. I. Mackay[19], Petra Neveceralova[25,30,31], Larissa Oliveira[32,33], Paulo H. Ott[32,34], Per J. Palsbøll[10,11], Nathalie J. Patenaude[35], Victoria Rowntree[7,36,6], Mariano Sironi[6,37], Els Vermeuelen[38], Mandy Watson[39], Alexandre N. Zerbini[28,40], Emma L. Carroll*[15]

1. Marine Mammal Institute, Oregon State University, Newport, Oregon, United States
2. UMR Entropie, French Institute of Research for Sustainable Development, Nouméa, New Caledonia
3. Biology Department, University of New Mexico, Albuquerque, New Mexico, United States
4. GEOMAR Helmholtz Centre for Ocean Research Kiel, Kiel, Germany
5. Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Laboratorio de Ecología Evolutiva Humana, FACSO-UNCPBA, Quequén, Buenos Aires Province, Argentina
6. Instituto de Conservación de Ballenas, Buenos Aires, Argentina
7. School of Biological Sciences, University of Utah, Salt Lake City, Utah, United States
8. Department of Biology, University of Florida, Gainesville, Florida, United States
9. Department of Fisheries, Wildlife and Conservation Sciences, Oregon State University, Oregon, United States
10. Marine Evolution and Conservation Group, Groningen Institute of Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands
11. Centre for Coastal Studies, Provincetown, Massachusetts, United States
12. Laboratorio de Macroecología Marina, Centro de Investigación Científica y Educación Superior de Ensenada, Unidad La Paz, La Paz, México
13. Department of Natural Resources and Environment Tasmania, Hobart, Australia
14. Environmental Law Initiative, Wellington, New Zealand
15. School of Biological Sciences, University of Auckland Waipapa Taumata Rau, Auckland, New Zealand
16. Ecological Marine Services Pty. Ltd, Bundaberg, Queensland, Australia
17. Department of Natural History, NTNU University Museum, Norwegian University of Science and Technology, Trondheim, Norway
18. Núcleo de Gestão Integrada ICMBio Florianópolis (NGI ICMBio Florianópolis), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Ministério do Meio Ambiente, Florianópolis, Santa Catarina, Brazil
19. South Australian Research and Development Institute, Primary Industries and Regions South Australia, Adelaide, South Australia, Australia
20. School of Earth and Environmental Sciences, University of Adelaide, Adelaide, South Australia, Australia
21. Instituto Australis, Imbituba, Santa Catarina, Brazil
22. Stable Isotope Biogeochemistry Laboratory (SIBL), Department of Earth Sciences, Durham University, Durham, United Kingdom
23. School of Natural Sciences, Macquarie University, Sydney, NSW, Australia
24. Institute for Marine and Antarctic Studies, University of Tasmania, Tasmania, Australia

25. Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic
26. Department of Biology and Ecology, Faculty of Science, University of Ostrava, Ostrava, Czech Republic
27. British Antarctic Survey, Cambridge, United Kingdom
28. Cooperative Institute for Climate, Ecosystem and Ocean Studies, University of Washington & Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA
29. New Zealand Department of Conservation – Te Papa Atawhai, Wellington, New Zealand
30. Ivanhoe Sea Safaris, Gansbaai, South Africa
31. Dyer Island Conservation Trust, Great White House, Kleinbaai, South Africa
32. Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul, Torres, RS, Brazil
33. Laboratório de Ecologia de Mamíferos, Universidade do Vale do Rio dos Sinos, Sao Leopoldo, RS, Brazil
34. Universidade Estadual do Rio Grande do Sul, Osório, RS, Brazil
35. Collégial International Sainte-Anne, Montreal, Quebec, Canada
36. Ocean Alliance, Massachussetts, United States
37. Diversidad Biológica IV, Universidad Nacional de Córdoba, Córdoba, Argentina
38. Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa
39. Department Environment, Land Water and Planning, Warrnambool, Victoria, Australia
40. Marine Ecology and Telemetry Research & Cascadia Research Collective, United States

*Corresponding authors: Solène Derville and Emma L. Carroll, s.derville@live.fr, e.carroll@auckland.ac.nz

ORCID ID: SD: 0000-0002-0380-7921, LGT: 0000-0002-2643-3950, SDN: 0000-0002-4534-124,2 CJS: 0000-0003-2635-7617, LOV: 0000-0002-5024-6581, HBVZ: 000-0003-3366-5116, CSB: 0000-0003-2183-2036, MB: 0000-0002-1831-2657, GBV: 0000-0003-2867-7614; KC: 0000-0002-8704-684X, SJC: 0000-0002-4161-037X, RC: 0000-0003-3260-539X, GD: 0000-0002-8683-0181, PACF: 0000-0003-3303-1420, SG: 0000-0003-4988-9085, KG: 0000-0002-2034-3444, DRG: 0000-0003-2296-7530, RH: 0000-0003-4666-2934, MAH: 0000-0002-7823-7185, PH: 0000-0002-4968-4859, DL: 0000-0002-7359-7704, AIM: 0000-0002-2837-3760, PN: 0000-0003-0823-3311, LRO: 0000-0002-5735-3697, PHO: 0000-0003-3303-1420, PJP: 0000-0002-4198-7599, VR: 0000-0001-6153-8312, MS: 0000-0003-3647-3355, EV: 0000-0002-3667-1290, MW: 0000-0001-9016-1059, ELC: 0000 0003-3193-7288; ASK: 0000-0002-5282-9676, JAJ: 0000-0003-4158-1924, ANZ: 0000-0002-9776-6605

Author Contributions: ELC, LGT, SDN, LOV, HBVZ, BG and SD designed the research; SD, LGT, CJS and ELC analyzed data; CJS contributed to the baseline model-data analysis; SDN, LOV, CSB, MB, ELC, GBV, KC, SJC, RC, GD, PACF, SDG, KG, DG, RH, MAH, PH, DL, ASK, JAJ, AIM, PN, LRO, PHO, NJP, PJP, VR, MS, EV, MW, and ANZ contributed data; SD, LGT, SDN, LOV, HBVZ and ELC wrote the paper, all authors edited the paper.

Competing Interest Statement: The authors have no competing interests to declare.

Classification: Biological Sciences; Ecology

Keywords: isotope ecology; isoscape; environmental change; *Eubalaena australis*; southern right whale

Abstract

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, SRW increased their use of mid-latitude foraging grounds in the south Atlantic and southwest Indian oceans in the late austral summer and autumn, and slightly increased their use of high-latitude (>60°S) foraging grounds in the southwest 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.

Significance Statement

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=1002), using a novel, customized stable-isotope based assignment approach based on biogeochemical models of the Southern Ocean. We then compare the contemporary distributions to whaling catch data representing historical austral summer and autumn distributions. We show remarkable consistency of mid-latitude distribution across four centuries, but shifts in foraging grounds in the past 30 years, particularly in the high latitudes that are likely driven by climate-associated alterations in prey availability.

INTRODUCTION

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 is 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 21). Moreover, while many of these studies span decades, they rarely extend to before the onset of the Industrial Revolution (*e.g.*, (18)) and thus focus on ecosystems that may 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 18th to the early 20th century kept detailed records of where and what species were observed and killed (*e.g.*, (20)). Some of the longest commercial records are for southern right whales (SRW, *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 centuries (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 SRW 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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) 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.*,17, 33, 34), as the isotopic composition of skin biopsy samples collected from wintering grounds reflect 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 are 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 spatio-temporal 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. 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 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 is 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 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 $\delta^{13}C$ and $\delta^{15}N$ in phytoplankton (37, 44), and a framework that customizes assignment space using prior information on sampling location/date and migratory behavior of SRW. This approach is used to estimate the circumpolar foraging distributions of SRWs in the late austral summer and autumn through the comparison of $\delta^{13}C$ and $\delta^{15}N$ values of skin samples (n=1002) 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 (1994–2020) using the model output and (2) over four centuries by comparing model outputs directly to whaling data from the late 18th to early 21st centuries (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 (Figures 1 and S1); the New Zealand population is represented by two wintering grounds: New Zealand mainland and Auckland Islands (47). Skin $\delta^{13}C$ and $\delta^{15}N$ values ranged -26.0‰ to -16.3‰ and 4.6‰ to 15.0‰, respectively (Figure 1 and Tables S1-S2). We split samples from Argentina into two groups based on the previously described bimodality in $\delta^{15}N$ values (> or < than 10 ‰), 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: $\delta^{13}C$ χ^2= 63.393, df = 2, p-value = 1.715e-14, $\delta^{15}N$ χ^2= 24.121, df = 2, p-value = 5.782e-06) and wintering ground (Kruskal-Wallis statistics: $\delta^{13}C$ χ^2= 553.5, df = 7, p-value < 2.2e-16, $\delta^{15}N$ χ^2= 323.46, df = 7, p-value < 2.2e-16: see Supplementary Information material 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 (Tables S3-S4).

We mapped the assigned foraging probability area for each whale using skin $\delta^{13}C$ and $\delta^{15}N$ values and phytoplankton isoscapes from a data-constrained Model of Ocean Biogeochemistry and Isotopes (MOBI (37, 44)) in a bivariate normal probability function (48) (see 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 (Figure 2a); also see Figures S2 to S9 for larger maps of foraging ground assignments for each wintering ground. 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°S) latitudes (Figure 2a).

To assess inter-individual 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 (Figure 2b). For example, a small proportion of individuals wintering in Argentina and the Auckland Islands were 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 southwest Indian oceans used by SRW from the Brazilian, South African and southwest Australian wintering grounds showed a marked shift from high to lower latitudes between the 1990s to 2010s (Figure 3; distribution of data by decade shown in Figure S10). The modelled 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 southwest Pacific Ocean by 25% for southeast 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 $\delta^{13}C$ and $\delta^{15}N$ analysis 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 years. Of these records, 2,488 were included in at least one potential foraging range (Figure 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 18-20th 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 (Figure 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.,* (20, 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.,* (54, 55)). These spatiotemporal shifts in prey abundance correlate with decadal changes in SRW foraging ground assignments. For example, the Atlantic sector (90°W-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 (Figure 3). In contrast, significant cooling and gains in sea ice may have allowed krill densities to increase in the Pacific sector (150°E-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 southeast Australia over the past 20 years. Finally, changes in krill distribution over time have not been reported for the Indian sector (10°W–150°E) due to a sparsity of data (52, 53), limiting our capacity to interpret observed changes in foraging ground assignments of the southwest 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 (Figure 4). Habitat modelling using historical whaling and satellite track data (24, 25, 38) indicate that the subtropical front (~30–40°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 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 18^{th}-20^{th} centuries rarely ventured into the remote and dangerous high-latitudes (>50°S) of the Southern Ocean; thus historical use of these waters by SRW 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 SRW 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) coincided with a decline in body condition (69) and calving rates (70). SRWs wintering in southwest 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 forage in mid-latitudes near the subtropical front (24) and have the best body condition score of any right whale population (65), in addition to having a high population growth rate (73). Use of distinct foraging grounds by other baleen whale sub-populations 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 humpback whale habitat use (75). Therefore future work should investigate regional population dynamics or body condition relative to prey availability, and strength of assignments to, high 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 (Figure 2b) outside the isotopically assigned foraging grounds averaged for the population (Figure 2a), probably due to individual variability in habitat use (76). Part of the Argentinian population is known to feed near South Georgia Island/Islas 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 have also been revealed in this population (Figure 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 (2000–2009, Figure S10). Argentinian SRWs are also known to forage both in high- and mid-latitudes 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 SRW 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.*, (14)) including baleen whales (15, 80).

The novel 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 (SI1). 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) appear to capture the broad-scale patterns of the circumpolar SRW distribution (Figure 4). Critically, this model accounts for annual and seasonal variation of isotopic patterns across the Southern Ocean that may be reflected in the SRW tissue collected at different times (*e.g.*, (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 (Figure 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., southeast 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, Southwest 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 southwest Pacific and southwest Atlantic SRW populations (Figure 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 level 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 is 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 towards 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 the first 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 ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) 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, 583 new values, spanning 1994–2020 (Tables S1and 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 (Table S1). All samples were lipid-extracted prior to isotope analysis; see Table S1 for details about extraction protocols (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 analysis. Precision for $\delta^{13}C$ and $\delta^{15}N$ values was estimated by analysis of internal reference materials and was ≤0.2‰ (SD) for both $\delta^{13}C$ and $\delta^{15}N$ values (Table S1). We also measured the weight percent carbon and

nitrogen concentration of each sample as a control for lipid content; samples had a mean (±SD) [C]:[N] ratio of 3.3±0.3indicative of pure protein.

Whaling Records. We compiled records (catches and sightings) by American (1792–1912) and Soviet (1961–1968) whaling vessels (22, 23). We restricted this dataset to records that occurred at >30°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 acknowledge that it is not fully representative of SRW use of high latitudes.

Isoscape Assignment Modelling. The baseline phytoplankton isoscapes were acquired from Model of Ocean Biogeochemistry and Isotopes (MOBI (37, 44)) for phytoplankton that include recent improvements to the marine iron cycle (86), see https://andreasschmittner.github.io/Models/MOBI/index.html). Isoscapes consist of $\delta^{13}C$ and $\delta^{15}N$ rasters at 3.6° x 1.8° resolution for the Southern Hemisphere (37, 44). These model outputs consist of monthly $\delta^{13}C$ and $\delta^{15}N$ averages in a hindcast scenario from 1992 to 2021, and the $\delta^{13}C$ predictions incorporate warming from increasing atmospheric CO_2 and input of decreasing atmospheric $\delta^{13}C$ values from anthropogenic emissions (i.e., Suess Effect). The model outputs were corrected with zonal averages derived in latitudinal bins a from a model-data comparison using recently published particulate organic matter datasets (see SI2 (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 six months 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 (Figure S13), as the first two months 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 $\delta^{13}C$ and $\delta^{15}N$ isoscapes in a bivariate normal probability function (48) with a pooled error structure described in SI2 that incorporates uncertainty in trophic discrimination factors (TDFs) and the isoscape rasters. Assignments were made using both $\delta^{13}C$ for $\delta^{15}N$ 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 (SI3, 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 inter-individual 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 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 modelling approach is presented in a schematic Figure S14.

Trophic Discrimination Factor (TDF). We used satellite track data from SRWs to validate $\delta^{13}C$ and $\delta^{15}N$ TDFs used in our isoscape assignment model (See SI4). Briefly, we set a range of TDFs of 2–4‰ for $\delta^{13}C$ and 4–6‰ for $\delta^{15}N$ 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 (SI4, Figure 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 $\delta^{13}C$ and $\delta^{15}N$ 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 (Fig S12).

Temporal Analysis. First, we investigated distributional changes over the last three decades by comparing foraging ground assignments across 1994–1999, 2000–2009 and 2010–2020 (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° 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 (18^{th} to 21^{st} 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.

Acknowledgments

Samples were collected in South Africa as follows; under South African Department of Environmental Affairs research permit (RES2019/19), Cape Nature sample collection permit (CN44-28-5255) and ethical clearance from the University of Pretoria Faculty of Natural and Agricultural Sciences Ethics Committee (NAS271/2019) for the 2018-2019 samples, under permits issued to Peter Best in terms of the South African Sea Fishery Act (no. 12 of 1988), issued 22 February 1995, 9 February 1996 and 9 July 1997 for the 1995-1997 samples; research permits RES2016/99 and RES2017/89 under Charles University Ethical Committee approval for the 2015-2016 samples. Samples were collected in Australia under permits from: Dept. of Environment, (Australia); Dept. of Environment and Heritage (SA); Dept. of Primary Industries, Parks, Water and Environment (Tasmania); Dept. of Natural Resources and Environment (Victoria); Office of Environment and heritage (NSW); Dept. of Environment and Heritage Protection (QLD) sighting ID 49787, Dept. of Conservation and Land Management (WA) and Macquarie University Animal Ethics Committee. New Zealand samples were collected under New Zealand Department of Conservation – Te Papa Atawhai (DOC) Marine Mammal Research permit to CSB (no number) and permit 84845-MAR to ELC and University of Auckland Animal Ethics Committee approved protocols AEC/02/2005/R334 to CSB and 002072 to ELC. Argentina samples were collected under permits from Dirección de Fauna y Flora Silvestres and Subsecretaría de Conservación y Areas Protegidas from Chubut for Argentina and University of Utah IACUC under assigned protocol number 05-01003 and in Brazil under permit Sisbio 16769

from the Brazilian Ministry of the Environment. Sample collection and analysis was funded by Charles University Grant Agency (1140217), Dyer Island Conservation Trust, Great White House, Kleinbaai, ExxonMobil, Total and ENI in South Africa, by the Department Environment, Land Water and Planning Victoria, Department of Natural Resources and Environment Tasmania, and the Australian Marine Mammal Centre (AMMC) in Australia. Sample collection in New Zealand was funded by: 1995–1998 Auckland Islands field seasons – Whale and Dolphin Conservation Society, the U.S. Department of State (Program for Cooperative US/ NZ Antarctic Research), the Auckland University Research Council, and the NZ Marsden Fund; 2006-2009 Auckland Islands field seasons - Winifred Violet Scott Estate Research Grant Fund, Australian Antarctic Division, Marine Conservation Action Fund, Blue Planet Marine NZ Ltd, Holsworth Wildlife Research endowment, New Zealand Ministry of Foreign Affairs, DOC, South Pacific Whale Research Consortium, National Geographic, and Brian Skerry Photography; 2020 Auckland Islands field work - Royal Society Te Apārangi Rutherford Discovery Fellowship to ELC, Live Ocean, Lou and Iris Fisher Charitable Trust, and the University of Auckland – Waipapa Taumata Rau (2020 field season); mainland samples – DOC. Analysis of New Zealand and Australian samples was funded by the AMMC, a Newton Fellowship from the Royal Society of London, Marie Curie Fellowship and the University of Auckland. We thank the Instituto de Conservación de Ballenas for samples from Argentina. Data from satellite tags deployed in Argentina were provided by the project Siguiendoballenas.org. Tag deployment was conducted under permits issued by Dirección de Fauna y Flora Silvestres and Subsecretaría de Conservación y Areas Protegidas, Province of Chubut, and by Secretaria de Ambiente y Desarrollo Sustentable, Province of Rio Negro. Funding for satellite tracking in Argentina was provided by Instituto Aqualie (Brazil), the National Oceanic and Atmospheric Administration of the United States (NOAA), the International Whaling Commission (IWC) and Wildlife Conservation Society (WCS). Data from satellite tags deployed in South Georgia were provided by J. Jackson. Tag deployment was conducted under permit RAP/2019/031 issued by the Government of South Georgia and the South Sandwich Islands (Islas Georgias del Sur y Islas Sandwich del Sur) following review and approval by the BAS Animal Welfare and Ethics Review Board (review #1040). Satellite tracking in South Georgia was funded by Darwin Plus initiative (DPLUS057), with additional funding support from the South Georgia Heritage Trust, Friends of South Georgia Island, WWF UK and EU BEST 2.0 Medium Grant 1594. The Brazilian samples were collected by GEMARS in collaboration with the Projeto Baleia Franca. Isoscape analysis was funded by an International Whaling Commission - Southern Ocean Research Partnership Grant. CJS was supported by the Deutsche Forschungsgemeinschaft (project no. 445549720). PHO was supported by the Brazilian National Research Council (Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq numbers 477611/2004-4 and 144064/98-7) and World Wildlife Fund (WWF-Brazil). LRO was supported by the Brazilian National Council for Scientific and Technological Development (Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq) that provided the Research Productivity grants No. 303813/2011–3, 308650/2014-0, 310621/2017-8 and 315361/2021-2. Thanks to all of our colleagues who have worked on these research projects, to Devi Veytia for advice in manuscript preparation and to Elanor Bell from IWC-SORP for supporting the work.

References

1. C. C. Chapman, M. A. Lea, A. Meyer, J. B. Sallée, M. Hindell, Defining Southern Ocean fronts and their influence on biological and physical processes in a changing climate. *Nat. Clim. Chang.* **10**, 209–219 (2020).

2. V. J. D. Tulloch, É. E. Plagányi, C. Brown, A. J. Richardson, R. Matear, Future recovery of baleen whales is imperiled by climate change. *Glob. Chang. Biol.* **25**, 1263–1281 (2019).

3. S. Nicol, J. Foster, S. Kawaguchi, The fishery for Antarctic krill - recent developments. *Fish Fish.* **13**, 30–40 (2012).

4. M. McBride, *et al.*, Antarctic krill *Euphausia superba*: spatial distribution, abundance, and management of fisheries in a changing climate. *Mar. Ecol. Prog. Ser.* **668**, 185–214 (2021).

5. J. Dawson, K. Holsman, T. Mustonen, D. Piepenburg, B. Rost, Cross-Chapter Paper 6: Polar Regions. *IPCC WGII Sixth Assess. Rep.*, 66 (2021).

6. M. Montes-Hugo, *et al.*, Recent changes in phytoplankton communities associated with rapid regional climate change along the Western Antarctic Peninsula. *Science (80-.).* **323**, 1470–1473 (2009).

7. A. Atkinson, *et al.*, Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nat. Clim. Chang.* **9**, 142–147 (2019).

8. S. Kawaguchi, *et al.*, Will krill fare well under Southern Ocean acidification? *Biol. Lett.* **7**, 288–291 (2011).

9. H. Weimerskirch, P. Inchausti, C. Guinet, C. Barbraud, Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarct. Sci.* **15**, 249–256 (2003).

10. M. A. Hindell, *et al.*, Tracking of marine predators to protect Southern Ocean ecosystems. *Nature* **580**, 87–92 (2020).

11. E. L. Hazen, *et al.*, Marine top predators as climate and ecosystem sentinels. *Front. Ecol. Environ.*, 1–10 (2019).

12. S. Descamps, H. Strøm, As the Arctic becomes boreal: ongoing shifts in a high-Arctic seabird community. *Ecology* **102**, e03485 (2021).

13. M. Erauskin-Extramiana, *et al.*, Large-scale distribution of tuna species in a warming ocean. *Glob. Chang. Biol.* **25**, 2043–2060 (2019).

14. N. Hammerschlag, *et al.*, Ocean warming alters the distributional range, migratory timing, and spatial protections of an apex predator, the tiger shark (*Galeocerdo cuvier*). *Glob. Chang. Biol.* **28**, 1990–2005 (2022).

15. G. E. Davis, *et al.*, Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data. *Glob. Chang. Biol.* **26**, 4812–4840 (2020).

16. J. C. Bull, *et al.*, Climate causes shifts in grey seal phenology by modifying age structure. *Proc. R. Soc. B Biol. Sci.* **288**, 1–10 (2021).

17. G. L. van den Berg, *et al.*, Decadal shift in foraging strategy of a migratory southern ocean predator. *Glob. Chang. Biol.* **27**, 1052–1067 (2021).

18. L. A. Hückstädt, M. D. McCarthy, P. L. Koch, D. P. Costa, What difference does a century make? Shifts in the ecosystem structure of the Ross Sea, Antarctica, as evidenced from a sentinel species, the weddell seal. *Proc. R. Soc. B Biol. Sci.* **284** (2017).

19. T. Carpenter-Kling, *et al.*, Gentoo penguins as sentinels of climate change at the sub-Antarctic Prince Edward Archipelago, Southern Ocean. *Ecol. Indic.* **101**, 163–172 (2019).

20. S. Bestley, *et al.*, Marine Ecosystem Assessment for the Southern Ocean: Birds and Marine Mammals in a Changing Climate. *Front. Ecol. Evol.* **8** (2020).

21. P. Chambault, *et al.*, Future seasonal changes in habitat for Arctic whales during predicted ocean warming. *Sci. Adv.* **8**, 1–10 (2022).

22. T. D. Smith, R. R. Reeves, E. Josephson, J. N. Lund, Spatial and seasonal distribution of American whaling and whales in the age of sail. *PLoS One* **7**, e34905. doi:10.1371/journal.pone.0034905 (2012).

23. D. Tormosov, *et al.*, Soviet catches of Southern right whales *Eubalaena australis* 1951-1971. *Biol. Conserv.* **86**, 185–197 (1998).

24. L. G. Torres, *et al.*, From exploitation to conservation: habitat models using whaling data predict ditribution patterns and threat exposure of an endangered whale. *Divers. Distrib.* **19**, 1138–1152 (2013).

25. V. González Carman, A. Piola, T. D. O'Brien, D. D. Tormosov, E. M. Acha, Circumpolar frontal systems as potential feeding grounds of Southern Right whales. *Prog. Oceanogr.* **176**, 102123 (2019).

26. J. A. Jackson, N. J. Patenaude, E. L. Carroll, C. S. Baker, How few whales were there after whaling? Inference from contemporary mtDNA diversity. *Mol. Ecol.* **17**, 236–251 (2008).

27. R. Harcourt, J. van der Hoop, S. Kraus, E. L. Carroll, Future directions in *Eubalaena* spp.: Comparative research to inform conservation. *Front. Mar. Sci.* **5**, 530 (2019).

28. P. Best, R. Payne, V. J. Rowntree, J. Palazzo, M. Both, Long-range movements of South Atlantic right whales *Eubalaena australis*. *Mar. Mammal Sci.* **9**, 227–234 (1993).

29. A. N. Zerbini, *et al.*, Satellite tracking of Southern right whales (*Eubalaena australis*) from Golfo San Matías, Rio Negro Province, Argentina. *Rep. SC/67b/CMP17 to Sci. Comm. Int. Whal. Comm. Cambridge, UK. Available from https//iwc.int* (2018).

30. B. S. Graham, L. Koch, Paul, S. D. Newsome, K. W. McMahon, D. Aurioles, "Chapter 14: Using Isoscapes to Trace the Movements and Foraging Behavior of Top Predators in Oceanic Ecosystems" in *Isoscapes: Understanding Movement, Pattern, and Process on Earth Through Isotope Mapping*, J. B. West, Ed. (Springer Science & Business Media, 2010), pp. 299–318.

31. R. Ramos, J. González-Solís, Trace me if you can: The use of intrinsic biogeochemical markers in marine top predators. *Front. Ecol. Environ.* **10**, 258–266 (2012).

32. S. Newsome, M. Clementz, P. Koch, Using stable isotope biogeochemistry to study marine mammal ecology. *Mar. Mammal Sci.* **26**, 509–572 (2010).

33. G. Busquets-Vass, *et al.*, Estimating blue whale skin isotopic incorporation rates and baleen growth rates: Implications for assessing diet and movement patterns in mysticetes. *PLoS One* **12**, e0177880 (2017).

34. L. O. Valenzuela, V. J. Rowntree, M. Sironi, J. Seger, Stable isotopes in skin reveal diverse food sources used by southern right whales (*Eubalaena australis*). *Mar. Ecol. Prog. Ser.* **603**, 243–255 (2018).

35. S. Magozzi, A. Yool, H. B. Vander Zanden, M. B. Wunder, C. N. Trueman, Using ocean

models to predict spatial and temporal variation in marine carbon isotopes. *Ecosphere* **8** (2017).

36. C. J. Somes, *et al.*, Simulating the global distribution of nitrogen isotopes in the ocean. *Global Biogeochem. Cycles* **24**, 1–16 (2010).

37. C. J. Somes, A. Schmittner, J. Muglia, A. Oschlies, A three-dimensional model of the marine nitrogen cycle during the last glacial maximum constrained by sedimentary isotopes. *Front. Mar. Sci.* **4**, 1–24 (2017).

38. A. I. Mackay, *et al.*, Satellite derived offshore migratory movements of southern right whales (*Eubalaena australis*) from Australian and New Zealand wintering grounds. *PLoS One* **15**, 1–20 (2020).

39. B. R. Mate, P. B. Best, B. A. Lagerquist, M. H. Winsor, Coastal, offshore, and migratory movements of South African right whales revealed by satellite telemetry. *Mar. Mammal Sci.* **27**, 455–476 (2011).

40. E. Seyboth, *et al.*, Southern Right Whale (*Eubalaena australis*) reproductive success is influenced by krill (*Euphausia superba*) density and climate. *Sci. Rep.* **6**, 1–8 (2016).

41. R. Leaper, *et al.*, Global climate drives southern right whale (*Eubalaena australis*) population dynamics. *Biol. Lett.* **2**, 289–292 (2006).

42. M. Agrelo, *et al.*, Ocean warming threatens southern right whale population recovery. *Sci. Adv.* **7** (2021).

43. K. Stamation, M. Watson, P. Moloney, C. Charlton, J. Bannister, Population estimate and rate of increase of southern right whales *Eubalaena australis* in Southeastern Australia. *Endanger. Species Res.* **41**, 373–383 (2020).

44. A. Schmittner, C. J. Somes, Complementary constraints from carbon (^{13}C) and nitrogen (^{15}N) isotopes on the glacial ocean's soft-tissue biological pump. *Paleoceanography* **31**, 669–693 (2016).

45. E. L. Carroll, *et al.*, Incorporating non-equilibrium dynamics into demographic history inferences of a migratory marine species. *Heredity (Edinb).* **122**, 53–68 (2019).

46. E. L. Carroll, *et al.*, Genetic diversity and connectivity of southern right whales (*Eubalaena australis*) found in the Brazil and Chile-Peru wintering grounds and the South Georgia (Islas Georgias del Sur) feeding ground. *J. Hered.* **111**, 263–276 (2020).

47. E. L. Carroll, *et al.*, Population structure and individual movement of southern right whales around New Zealand and Australia. *Mar. Ecol. Prog. Ser.* **432**, 257–268 (2011).

48. H. B. Vander Zanden, *et al.*, Determining origin in a migratory marine vertebrate: A novel method to integrate stable isotopes and satellite tracking. *Ecol. Appl.* **25**, 320–335 (2015).

49. S. R. Brennan, D. E. Schindler, Linking otolith microchemistry and dendritic isoscapes to map heterogeneous production of fish across river basins: *Ecol. Appl.* **27**, 363–377 (2017).

50. C. N. Trueman, K. M. MacKenzie, K. St John Glew, Stable isotope-based location in a shelf sea setting: accuracy and precision are comparable to light-based location methods. *Methods Ecol. Evol.* **8**, 232–240 (2017).

51. A. Friedlaender, *et al.*, Sympatry and resource partitioning between the largest krill

consumers around the Antarctic Peninsula. *Mar. Ecol. Prog. Ser.* **669**, 1–16 (2021).

52. H. Herr, *et al.*, Horizontal niche partitioning of humpback and fin whales around the West Antarctic Peninsula: evidence from a concurrent whale and krill survey. *Polar Biol.* **39**, 799–818 (2016).

53. L. Riekkola, V. Andrews-Goff, A. Friedlaender, R. Constantine, A. N. Zerbini, Environmental drivers of humpback whale foraging behavior in the remote Southern Ocean. *J. Exp. Mar. Bio. Ecol.* **517**, 1–12 (2019).

54. D. Veytia, *et al.*, Circumpolar projections of Antarctic krill growth potential. *Nat. Clim. Chang.* **10**, 568–575 (2020).

55. G. Yang, *et al.*, Changing circumpolar distributions and isoscapes of Antarctic krill: Indo-Pacific habitat refuges counter long-term degradation of the Atlantic sector. *Limnol. Oceanogr.* **66**, 272–287 (2021).

56. M. P. Meredith, J. C. King, Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. *Geophys. Res. Lett.* **32**, 1–5 (2005).

57. A. Atkinson, V. Siegel, E. Pakhomov, P. Rothery, Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* **432**, 100–103 (2004).

58. A. Atkinson, *et al.*, Stepping stones towards Antarctica: Switch to southern spawning grounds explains an abrupt range shift in krill. *Glob. Chang. Biol.* **28**, 1359–1375 (2022).

59. L. A. Hückstädt, *et al.*, Projected shifts in the foraging habitat of crabeater seals along the Antarctic Peninsula. *Nat. Clim. Chang.* **10**, 472–477 (2020).

60. S. Nicol, T. Pauly, N. L. Bindoff, P. G. Strutton, "BROKE" a biological/oceanographic survey off the coast of East Antarctica (80-150°E) carried out in January-March 1996. *Deep. Res. Part II Top. Stud. Oceanogr.* **47**, 2281–2297 (2000).

61. S. Nicol, J. Kitchener, R. King, G. Hosie, W. K. De la Mare, Population structure and condition of Antarctic krill (*Euphausia superba*) off East Antarctica (80-150°E) during the Austral summer of 1995/1996. *Deep. Res. Part II Top. Stud. Oceanogr.* **47**, 2489–2517 (2000).

62. C. A. Bost, *et al.*, The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J. Mar. Syst.* **78**, 363–376 (2009).

63. G. A. Tarling, P. Ward, S. E. Thorpe, Spatial distributions of Southern Ocean mesozooplankton communities have been resilient to long-term surface warming. *Glob. Chang. Biol.* **24**, 132–142 (2018).

64. T. Carpenter-Kling, *et al.*, A critical assessment of marine predator isoscapes within the southern Indian Ocean. *Mov. Ecol.* **8**, 1–18 (2020).

65. J. Y. Georges, F. Bonadonna, C. Guinet, Foraging habitat and diving activity of lactating Subantarctic fur seals in relation to sea-surface temperatures at Amsterdam Island. *Mar. Ecol. Prog. Ser.* **196**, 291–304 (2000).

66. M. I. Garcia-Rojas, *et al.*, Environmental evidence for a pygmy blue whale aggregation area in the Subtropical Convergence Zone south of Australia. *Mar. Mammal Sci.* **34**, 901–923 (2018).

67. B. Finucci, *et al.*, Ghosts of the deep – Biodiversity, fisheries, and extinction risk of ghost sharks. *Fish Fish.* **22**, 391–412 (2021).

68. J. A. Caccavo, *et al.*, Productivity and change in fish and squid in the Southern Ocean. *Front. Ecol. Evol.* **9** (2021).

69. T. Thavar, Assessing the nutritional state of southern right whales (*Eubalaena australis*) through measurements of body volume and blubber glucocorticoids levels, and investigating the relation to reproductive success. *Master thesis Zool. Univ. Pretoria*, 98 (2021).

70. E. Vermeulen, C. Wilkinson, M. Germishuizen, Report of the southern right whale aerial surveys – 2019. *Rep. Present. to Sci. Comm. Int. Whal. Comm. Cambridge, UK. Available https//iwc.int/en/* (2022).

71. C. Charlton, *et al.*, Southern right whale (*Eubalaena australis*) population demographics at major calving ground Head of Bight, South Australia, 1991–2016. *Aquat. Conserv. Mar. Freshw. Ecosyst.* **32**, 671–686 (2022).

72. F. Christiansen, *et al.*, Population comparison of right whale body condition reveals poor state of the North Atlantic right whale. *Mar. Ecol. Prog. Ser.* **640**, 1–16 (2020).

73. E. L. Carroll, *et al.*, Accounting for female reproductive cycles in a superpopulation capture-recapture framework. *Ecol. Appl.* **23**, 1677–1690 (2013).

74. L. G. Torres, *et al.*, Range-wide comparison of gray whale body condition reveals contrasting sub-population health characteristics and vulnerability to environmental change. *Front. Mar. Sci.* **9**, 1–13 (2022).

75. R. R. Reisinger, *et al.*, Combining regional habitat selection models for large-scale prediction: Circumpolar habitat selection of southern ocean humpback whales. *Remote Sens.* **13** (2021).

76. M. Vighi, *et al.*, Stable isotopes indicate population structuring in the Southwest Atlantic population of right whales (*Eubalaena australis*). *PLoS One* **9** (2014).

77. L. O. Valenzuela, M. Sironi, V. J. Rowntree, J. Seger, Isotopic and genetic evidence for culturally inherited site fidelity to feeding grounds in southern right whales (*Eubalaena australis*). *Mol. Ecol.* **18**, 782–791 (2009).

78. P. Brakes, *et al.*, A deepening understanding of animal culture suggests lessons for conservation. *Proc. R. Soc. B Biol. Sci.* **288** (2021).

79. P. J. Clapham, A. Aguilar, L. T. Hatch, Determining spatial and temporal scales for management: Lessons from whaling. *Mar. Mammal Sci.* **24**, 183–201 (2008).

80. E. L. Meyer-Gutbrod, C. H. Greene, K. T. A. Davies, D. G. Johns, Ocean regime shift is driving collapse of the north atlantic right whale population. *Oceanography* **34**, 22–31 (2021).

81. K. St. John Glew, *et al.*, Sympatric Atlantic puffins and razorbills show contrasting responses to adverse marine conditions during winter foraging within the North Sea. *Mov. Ecol.* **7**, 1–14 (2019).

82. A. Borrell, N. Abad-Oliva, E. Gõmez-Campos, J. Giménez, A. Aguilar, Discrimination of stable isotopes in fin whale tissues and application to diet assessment in cetaceans. *Rapid*

Commun. Mass Spectrom. **26**, 1596–1602 (2012).

83. A. Lorrain, *et al.*, Trends in tuna carbon isotopes suggest global changes in pelagic phytoplankton communities. *Glob. Chang. Biol.* **26**, 458–470 (2020).

84. J. Mestre, *et al.*, Decadal changes in blood δ13C values, at-sea distribution, and weaning mass of southern elephant seals from Kerguelen Islands. *Proc. R. Soc. B Biol. Sci.* **287** (2020).

85. S. Todd, P. Ostrom, J. Lien, J. Abrajano, Use of biopsy samples of humpback whale (*Megaptera novaeangliae*) skin for stable isotope (δ13C) determination. *J. Northwest Atl. Fish. Sci.* **22**, 71–76 (1997).

86. C. J. Somes, *et al.*, Constraining Global Marine Iron Sources and Ligand-Mediated Scavenging Fluxes With GEOTRACES Dissolved Iron Measurements in an Ocean Biogeochemical Model. *Global Biogeochem. Cycles* **35**, e2021GB006948 (2021).

87. M. T. Verwega, *et al.*, Description of a global marine particulate organic carbon-13 isotope data set. *Earth Syst. Sci. Data* **13**, 4861–4880 (2021).

88. K. St John Glew, *et al.*, Isoscape Models of the Southern Ocean: Predicting Spatial and Temporal Variability in Carbon and Nitrogen Isotope Compositions of Particulate Organic Matter. *Global Biogeochem. Cycles* **35** (2021).

89. M. A. Vanderklift, S. Ponsard, Sources of variation in consumer-diet $\delta^{15}N$ enrichment: A meta-analysis. *Oecologia* **136**, 169–182 (2003).

90. J. H. McCutchan, W. M. Lewis, C. Kendall, C. C. McGrath, Variation in trophic shift for stable isotope ratios of carbon, nitrogen, and sulfur. *Oikos* **102**, 378–390 (2003).

91. C. Mompeán, A. Bode, E. Gier, M. D. McCarthy, Bulk vs. amino acid stable N isotope estimations of metabolic status and contributions of nitrogen fixation to size-fractionated zooplankton biomass in the subtropical N Atlantic. *Deep. Res. Part I Oceanogr. Res. Pap.* **114**, 137–148 (2016).

92. S. Caut, E. Angulo, F. Courchamp, Variation in discrimination factors ($\Delta^{15}N$ and $\Delta^{13}C$): The effect of diet isotopic values and applications for diet reconstruction. *J. Appl. Ecol.* **46**, 443–453 (2009).

93. P. Tiselius, K. Fransson, Daily changes in $\delta^{15}N$ and $\delta^{13}C$ stable isotopes in copepods : equilibrium dynamics and variations of trophic level in the field. *J. Plankton Res.* **38**, 751–761 (2016).

94. E. L. Carroll, *et al.*, Satellite tracking and genetic evidence of changing migratory traditions after exploitation. *prep*.

95. A. Kennedy, *et al.*, Photo-ID and satellite tracking connects South Georgia (Islas Georgias del Sur) southern right whales with multiple feeding and calving grounds in the southwest Atlantic. *Mar. Mammal Sci.*

96. A. S. Kennedy, *et al.*, Whales return to the epicentre of whaling ? Preliminary results from the 2020 cetacean survey at South Georgia (Islas Georgias del Sur). *Rep. SC/68B/CMP/22 Present. to Sci. Comm. Int. Whal. Comm. Cambridge, UK* (2020).

Figures

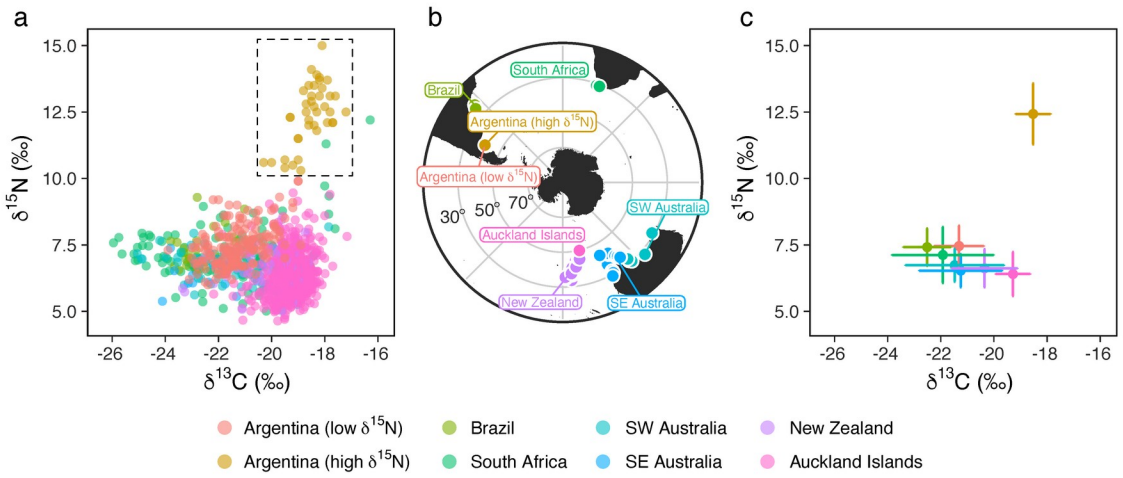
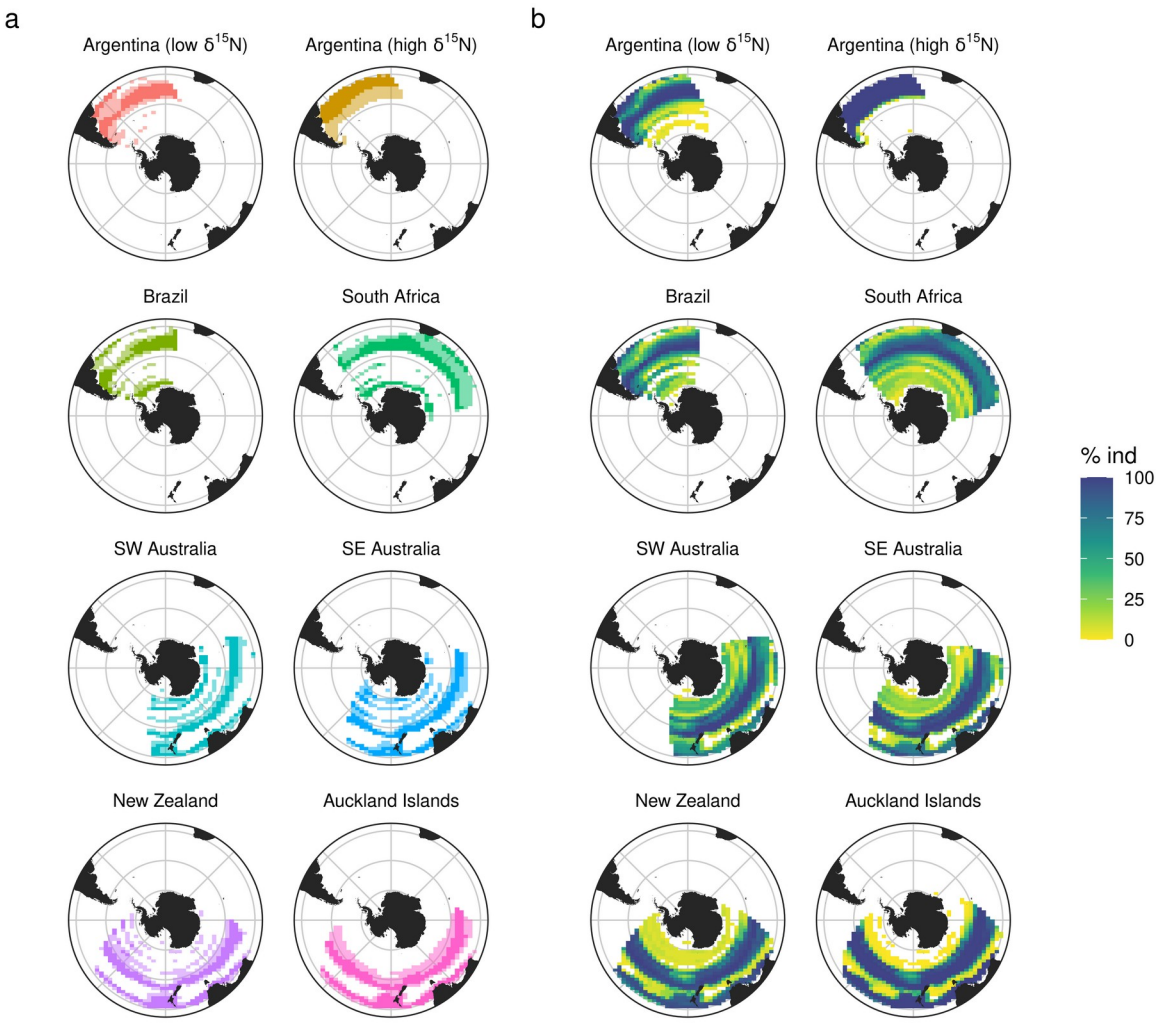


Figure 1. Distribution of sampling location and stable isotope values for southern right whale skin samples. (a) Biplot of skin $\delta^{13}C$ and $\delta^{15}N$ values for each wintering ground. The dark grey rectangle delineates the subset of Argentinian samples with high $\delta^{15}N$ values. (b) Map of sample collection locations by wintering ground; note Australia wintering grounds are divided in southwest (SW) and southeast (SE). (c) Mean $\delta^{13}C$ and $\delta^{15}N$ values summarized by wintering grounds; error bars denote standard deviation.

Figure 2. Isotopically assigned foraging grounds for each southern right whale wintering ground



across all years (see Table S1 for sample sizes). (a) Population-level average core and general foraging areas in dark and light colors representing 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 were assigned to each grid cell based on binary transformation of the 50% highest probability pixels. Note Australia wintering grounds are divided in southwest (SW) and southeast (SE). Parallels of latitude represented in grey in each map mark 30°S, 50°S, and 70°S.

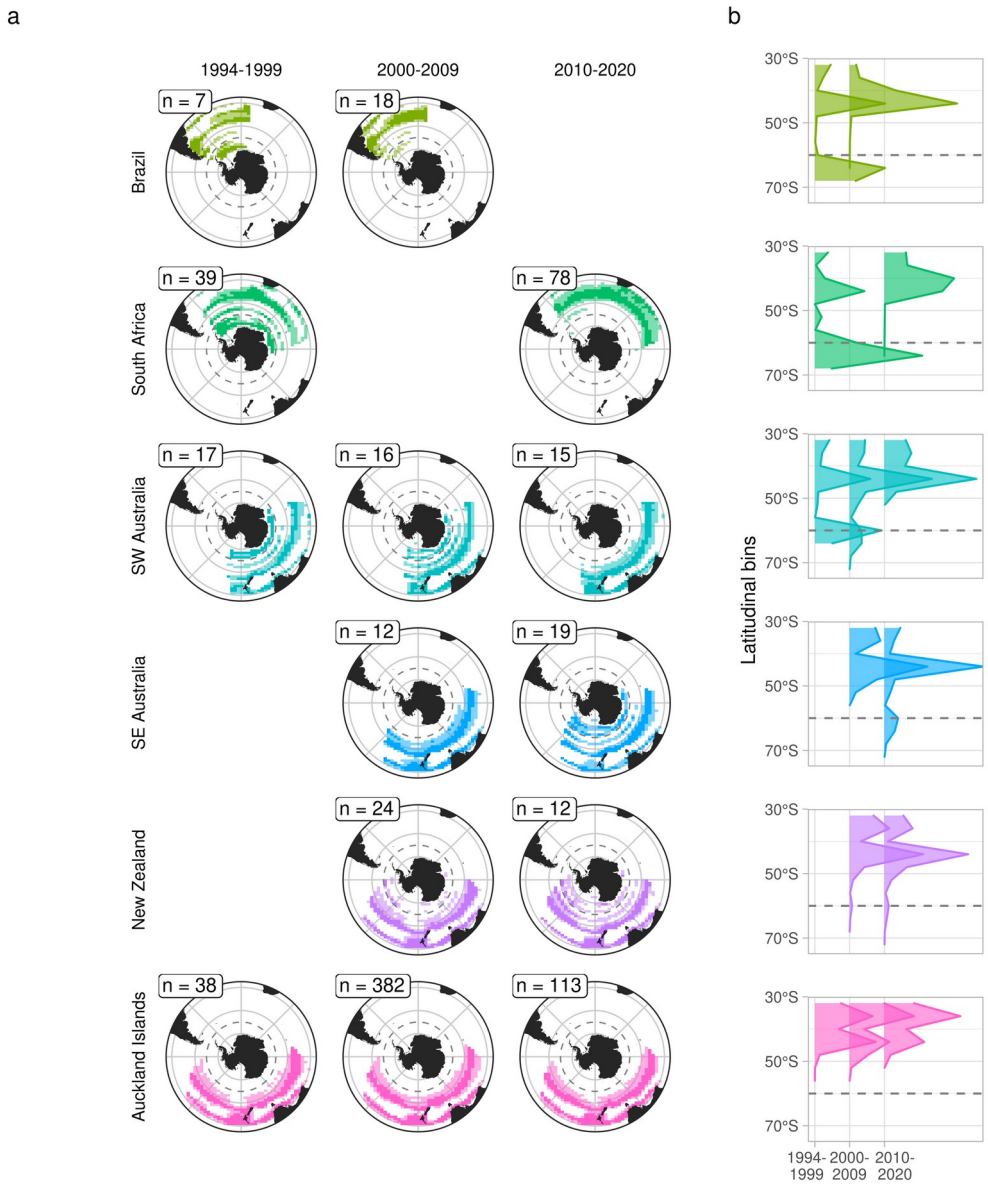


Figure 3. Southern right whale foraging grounds assignments by wintering ground and decade. (a) Maps of assigned general and core foraging areas. Sample size is indicated in each panel. Population-level average core and general foraging areas are represented for each decade by population combination 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 (2000-2009) and are therefore not represented in this figure. Note Australia wintering grounds are divided in southwest (SW) and southeast (SE). Parallels of latitude represented in grey in each map mark 30°S, 50°S, and 70°S, and the dashed line delineates the 60°S latitude.

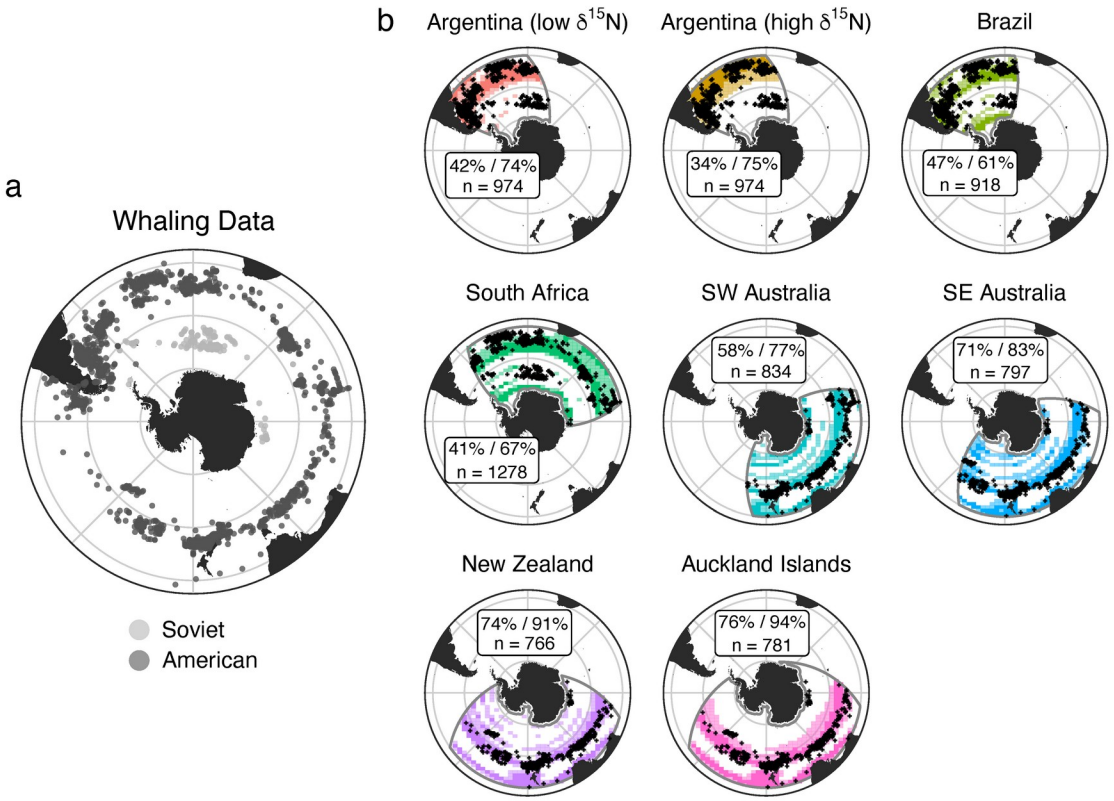


Figure 4. Geographic positions of (a) American and Soviet southern right whale whaling records, and (b) overlap with foraging grounds isotopically assigned to each wintering ground. In panel b, only the whaling records occurring within the foraging bubble (outlined in grey) set for each wintering ground 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 are indicated over each panel (core % / general %). Note Australia wintering grounds are divided in southwest (SW) and southeast (SE). Parallels of latitude represented in grey in each map mark 30°S, 50°S, and 70°S.