UC Santa Cruz

UC Santa Cruz Electronic Theses and Dissertations

Title

An Examination of the Ecological and Oceanographic Effects of Mid-to-Late Holocene Climate Changes on the Ross Sea Ecosystem

Permalink

https://escholarship.org/uc/item/99s5j3fk

Author

Brault, Emily

Publication Date

2017

Peer reviewed|Thesis/dissertation

eScholarship.org Powered by the California Digital Library
University of California

UNIVERSITY OF CALIFORNIA
SANTA CRUZ

AN EXAMINATION OF THE ECOLOGICAL AND OCEANOGRAPHIC EFFECTS OF MID-TO-LATE HOLOCENE CLIMATE CHANGES ON THE ROSS SEA ECOSYSTEM

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

OCEAN SCIENCES

by

Emily Kristine Brault

December 2017

The Dissertation of Emily Kristine Brault
is approved:

_____
Dr. Paul Koch, chair

_____
Dr. Matthew McCarthy

_____
Dr. Daniel Costa

_____
Dr. Kevin Arrigo

_____
Tyrus Miller
Vice Provost and Dean of Graduate Studies

Copyright © by

Emily K. Brault

2017

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

AN EXAMINATION OF THE ECOLOGICAL AND OCEANOGRAPHIC EFFECTS OF MID-TO-LATE HOLOCENE CLIMATE CHANGES ON THE ROSS SEA ECOSYSTEM

Emily Kristine Brault

Today, West Antarctica has been experiencing some of the most profound and rapid climate change on Earth, affecting biota from phytoplankton to seals. To better predict future changes in Antarctica with continued warming, a clear understanding of this region's biogeochemistry and trophic dynamics is essential. Furthermore, studies of subfossils can reveal how species and their environment responded to past climate events, indicating how anthropogenic climate change might affect them.

The goals of this dissertation are threefold. First, bulk stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$, respectively) analyses of zooplankton were performed to study spatial gradients in West Antarctica's biogeochemistry. These analyses also established isotopic baselines for this area, critical for accurate assessments of animals' movements and foraging behaviors. Second, bulk $\delta^{13}C$ and $\delta^{15}N$ and amino acid $\delta^{15}N$ analyses were conducted on present-day pinnipeds of West Antarctica – crabeater, Weddell, and Ross seals – to thoroughly investigate their foraging ecologies. Third, subfossil specimens of four pinnipeds – crabeater, Weddell, leopard, and southern elephant seals – were analyzed for bulk and amino acid isotope values to discern temporal changes in their foraging strategies and habitats during the Holocene.

We found significant spatial shifts in zooplankton bulk isotope values, which were likely driven by gradients in sea surface temperature and nutrient utilization. Our analyses of modern seals showed that Ross seals forage in a pelagic-based food web isolated from that of crabeater and Weddell seals. Although crabeater and Weddell seals are foraging within a similar food web, the former is likely following sea ice, while the latter targets the most productive areas. Our amino acid $\delta^{15}N$ results revealed a higher trophic position for Ross seals, equivalent to that of Weddell seals, than expected given bulk $\delta^{15}N$ data. Our study of subfossil seal specimens showed that crabeater seals had more diverse diets, incorporating more fish, earlier in the Holocene than in modern times. This suggests the species can show greater flexibility in foraging than might be apparent from modern observations, which may allow them adapt to a changing environment. Furthermore, we found that part of the Ross Sea, habitat for Weddell seals and some southern elephant seals, likely experienced a productivity drop in the recent past, perhaps responding to increasing landfast and sea ice conditions.

This dissertation is dedicated to my friend,

Dr. Rebecca Dickhut,

who supported me in many ways,

taught me to be fearless,

and whose memory I have always carried with me

ACKNOWLEDGEMENTS

I would like to especially thank my advisor, Dr. Paul Koch, for his tremendous guidance in carrying out this dissertation. I am further grateful for his many lessons on science and life, excellent humor, friendship, inspiration, and encouragement. Drs. Matthew McCarthy, Daniel Costa, and Kevin Arrigo have been exceedingly supportive and insightful dissertation committee members and been invaluable in completing my doctoral work. Drs. Rus Hoelzel, Brenda Hall, Luis Hückstädt, Kimberly Goetz, Michael Goebel, Olle Karlsson, Jonas Teilmann, Tero Harkonen, Karin Harding, Valerie Loeb, Kelton McMahon, and Walker Smith Jr have been very helpful in analyzing and interpreting my dissertation data.

I thank Dyke Andreasen, Elizabeth Gier, Stephanie Christensen, Brandon Cheney, and Colin Carney for their critical assistance with method development and laboratory analyses. Members of my laboratory groups – Fabian Baptista, Amy Bour, Taylor Broek, Hilary Close, Laura Domingo Martínez, Kwasi Gilbert, Danielle Glynn, Hope Ianiri, Kelton McMahon, Laura Niven, Jon Nye, Lesley Petrie, Rachel Reid, Adrienne Ricker, Aaron Rosenfield, Kevin Salladay, Wilson Sauthoff, John Schiff, Ana Valenzuela Toro, Natasha Vokhshoori, and Jessie Zupcic-Moore – have been encouraging, informative, and helpful throughout my dissertation work. I am indebted to Jon Nye, Aaron Rosenfield, and Kevin Salladay. Without their meticiulous and productive efforts in conducting a multitude of laboratory procedures on thousands of samples this work would not have been feasible. I am exceedingly

grateful to Drs. Rus Hoelzel, Andreanna Welch, and their laboratory group who completed the extensive ancient DNA analyses.

This dissertation was possible via generous financial support. Thank you to the National Science Foundation (NSF ANT-1142108), Cota-Robles Fellowship, and Dr Earl H. Myers and Ethel M. Myers Oceanographic and Marine Biology Trust.

Several collaborators generously contributed numerous samples for carrying out my research. Thank you to: Drs. Daniel Costa, Luis Hückstädt, Kimberly Goetz, Michael Goebel, Olle Karlsson, Jonas Teilmann, Tero Harkonen, Karin Harding, Valerie Loeb, Walker Smith Jr, Heidi Geisz, and Deborah Steinberg. Dr. Brenda Hall, Dr. Paul Koch, Scott Braddock, Audra Norvaisa, Jon Nye, Jill Pelto, and Rachel Reid spent many weeks in the Dry Valleys of Antarctica to sample hundreds of seal mummies. Thank you for your considerable effort during our long and challenging field seasons.

I am grateful to the many friends and family who have given me considerable support during my graduate program. I am especially thankful to: Kim Bernard, Kyle Broach, Corinne Gibble, Britt Henke, Caitlin Kroeger, Regina Radan, Aaron Rosenfield, Wilson Sauthoff, and Catarina Wor Lima. Thank you for your love and encouragement: Dad, Mom, Erin, Pat, Rose, Andrea, Nick, and Pete. I am particularly appreciative of Wilson, who has been with me throughout all of my graduate studies. Thank you, dear little brown dog, for your relentless companionship, adventuresome spirit, and zeal for my presence despite my late night lab sessions and long absences during Antarctic expeditions. - Many thanks to all of you!

INTRODUCTION

West Antarctica is unique for its critical role in ocean primary productivity, biogeochemical cycling, fisheries production, and global climate (Croxall and Nicol 2004, Marinov et al. 2006, Ducklow et al. 2007, 2012, Smith et al. 2014). It lies west of the Transantarctic Mountains and between the Ross and Weddell Seas. Multiple significant polynyas occur along the western Antarctic coast, including the extensive Ross Sea polynya (Arrigo and van Dijken 2003). These open water regions permit high rates of primary production in coastal West Antarctica, which support abundant and diverse upper trophic level biota and contribute to high rates of carbon export (Ducklow et al. 2007, Arrigo et al. 2008, Ducklow et al. 2012, Smith et al. 2014). Substantial sinking of CO_2 occurs in areas of West Antarctica due to winter sea ice formation and Antarctic Bottom Water (AABW) formation (Ducklow et al. 2007, Arrigo et al. 2008, Ducklow et al. 2012, Smith et al. 2014). In recent years, fisheries of krill and Antarctic toothfish (*Dissostichus mawsoni*) have developed in the Ross Sea and around the West Antarctic Peninsula (WAP), respectively (Ainley and Siniff 2009, Trivelpiece et al. 2011). The West Antarctic is presently experiencing some of the most profound and rapid climate change on Earth (Meredith and King 2005, Ducklow et al. 2007, 2012, Stammerjohn et al. 2012). Interestingly, climate trends vary across this region; the WAP has been experiencing decreasing sea ice cover (about 7 % sea ice extent reduction per decade) and duration (by about three months) since the mid-1900s, while the Ross Sea has been undergoing increasing sea ice cover

(more than 5 % sea ice extent expansion per decade) and duration (by about two months) (Kwok and Comiso 2002, Parkinson 2002, Smith et al. 2007, Stammerjohn et al. 2012).

Anthropogenic climate change has affected species at all trophic levels and will continue to do so. Multiple studies have suggested that continued warming would result in increased upper ocean stratification and altered phytoplankton assemblages (Arrigo et al. 2000, Jacobs et al. 2002, Tortell et al. 2008). In the WAP, Montes-Hugo et al. (2009) report a transition from diatoms and large cell phytoplankton species to small cell phytoplankton species in response to warming, a change that has likely affected regional trophic dynamics and carbon export, since larger cell phytoplankton are more important resources to consumers, such as krill, and have higher export rates. Climate change in the WAP appears to be driving a decline in abundance of krill, key prey for numerous species, and, correspondingly, an increase in other zooplankton taxa, especially salps (*Salpa thompsoni*), that have lower nutritional value to predators (Loeb et al. 1997, Atkinson et al. 2004, Ducklow et al. 2007, Schofield et al. 2010). Shifts in abundances of upper trophic level biota have also been observed. The population of Adélie penguins (*Pygoscelis adeliae*), an ice-dependent species, in the WAP has declined by up to 80 % since the 1970s, while Gentoo penguins (*Pygoscelis papua*), a Subantarctic, non-ice-requiring species, have immigrated to and established in this area (Ducklow et al. 2007, Ducklow et al. 2012). The responses of marine mammals to ongoing climate change in West Antarctica are not well known. In regards to pinnipeds, continued warming has been

thought to have net negative effects on ice-dependent species, such as crabeater (*Lobodon carcinophagus*), Weddell (*Leptonychotes weddellii*), Ross (*Ommatophoca rossii*), and leopard (*Hydrurga leptonyx*) seals, while ice-tolerant species, southern elephant seals (*Mirounga leonina*) and Antarctic fur seals (*Arctocephalus gazelle*), will probably experience net positive and net neutral effects, respectively (Siniff 2008).

Given the rapid environmental changes occurring in West Antarctica and the considerable disturbances it has had on the physical environment, biogeochemical cycles, and food web, comprehensive knowledge of the present biogeochemistry and ecologies of biota is critical. This information will anchor future examinations of the impacts of global warming and enable predictions of the responses of the environment and biota to them. Additionally, studies of fossils or subfossils can reveal how species, as well as their environment, responded to past climate events, providing insights into how anthropogenic climate change might affect species and their habitats in the future (e.g., Lorenzen et al. 2011, Alter et al. 2015).

I have developed and conducted this research to further our understanding of the modern biogeochemistry and ecologies of Antarctic seals within the dynamic and rapidly changing region of West Antarctica. Furthermore, I have tried to use subfossils of Antarctic seals to explore changes in their ecologies and habitats to better predict how these species will respond to anthropogenic climate change. In addition, biogeochemic records extracted from pinniped tissues provide insights about the changes that have occurred in the region over the millennia. I accomplished all of

these goals via measurements of nitrogen and carbon isotopes ($\delta^{15}N$ and $\delta^{13}C$, respectively) on bulk material, as well as on amino acids in certain cases, from animal tissues (e.g., blood, hair, bone or tooth collagen).

A consumer's bulk $\delta^{15}N$ and $\delta^{13}C$ values give insights into the conditions of its environment and foraging behavior since these isotopic data are a product of environmental processes and trophic linkages. A number of factors set the $\delta^{15}N$ and $\delta^{13}C$ values of phytoplankton at the base of the marine food web, which are passed on, with modifications from trophic transfers, to upper trophic level consumers (Lorrain et al. 2009, Graham et al. 2010, Jaeger et al. 2010). Phytoplankton $\delta^{15}N$ values are determined by their nutrient source (i.e., nitrate, ammonium, or N_2), the biological transformations (e.g., N_2-fixation and denitrification), and the nutrient pool size (or the extent of nitrogen pool drawdown) in their environment, and isotopic fractionation during the assimilation of nitrogen (reviewed in McMahon et al. 2013). Dissolved CO_2 concentrations, temperature, cell size and geometry, internal biological parameters (e.g., growth rate), and extent of CO_2 drawdown all affect phytoplankton $\delta^{13}C$ values (reviewed in McMahon et al. 2013). Trophic transfers considerably affect a predator's $\delta^{15}N$ values, with animal tissues experiencing ^{15}N-enrichment of about 3 to 5 ‰ with each trophic step (Minagawa and Wada 1984). Thus, bulk $\delta^{15}N$ values are typically indicative of trophic position. In contrast, little trophic level ^{13}C-enrichment occurs in consumer tissues (Minagawa and Wada 1984). Spatial and temporal variations in the driving forces create spatial and temporal

variations in phytoplankton isotope values, patterns that move up a food chain (e.g., Schell et al. 1998).

Measurement of $\delta^{15}N$ values of certain amino acids allow us to disentangle the "trophic" and "source" effects on animal $\delta^{15}N$ values. The $\delta^{15}N$ values of source amino acids, such as phenylalanine (Phe), are minimally ^{15}N-enriched with each trophic step, whereas those of trophic amino acids, such as glutamic acid/glutamine (Glu) or proline (Pro), are heavily ^{15}N-enriched with trophic transfers. As such, $\delta^{15}N$ measurements of these amino acids allow us to tease apart the contributions of a change in phytoplankton $\delta^{15}N$ values from a change in diet on predator $\delta^{15}N$ values (McClelland and Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). Thus, complementing $\delta^{15}N$ and $\delta^{13}C$ analyses of bulk material with $\delta^{15}N$ analysis of amino acids identifies the main force (e.g., change in an animal's habitat or diet) behind an observed bulk isotope pattern.

For Chapter 1, I measured $\delta^{15}N$ and $\delta^{13}C$ values of bulk material from an array of zooplankton taxa to generate the first empirical isoscapes (geospatial maps of isotopic values) for West Antarctica. I found significant spatial variation in baseline isotope values in this region and consider the possible mechanisms behind the patterns. I argued that increasing nitrogen drawdown from pelagic to coastal waters drives a pelagic-to-coastal gradient in baseline $\delta^{15}N$ values, with increasing $\delta^{15}N$ values towards the continent. The $\delta^{13}C$ values decreased with increasing latitude, which I have argued follows spatial patterns in sea surface temperatures. Not only have the isoscapes revealed differences in biogeochemistry across West Antarctica,

they have also been critical for accurate evaluations of species' trophic positions and movements, which were the objectives of Chapter 2.

In Chapter 2, I used bulk isotope analyses, along with amino acid $\delta^{15}N$ analysis, to explore the ecologies of Weddell, crabeater, and Ross seals throughout the West Antarctic. This study has been particularly valuable for the Ross seal, a species that has been one of the least studied marine mammals in the world. My results revealed whether the foraging behaviors of these species vary spatially in this region and further indicated the variation in baseline isotope values observed in Chapter 1. I did not find significant differences in the foraging strategies of Weddell seals throughout West Antarctica, whereas crabeater seals may have slight spatial variation in their diet. Interestingly, I discovered that these seals used different habitats. Ross seals foraged in a pelagic food web, while crabeater and Weddell seals were foraging within similar food webs closer to shore. Yet, crabeater seals were likely following sea ice, while Weddell seals targeted productive continental shelf areas within the western Antarctic. Since the foraging region of Ross seals has a baseline $\delta^{15}N$ value substantially lower than those of Weddell and crabeater seal habitats, prior analyses of the bulk $\delta^{15}N$ values of these three species have underestimated the trophic position of Ross seals. This chapter highlighted the importance of determining spatial variation in phytoplankton isotope values in order to accurately assess the diets, trophic positions, and movements of predators.

Lastly, in Chapter 3 I have presented bulk and amino acid isotope data for subfossil specimens of crabeater, Weddell, southern elephant, and leopard seals,

spanning the last several thousand years. These results have shown how environmental conditions in the Ross Sea changed over the mid-to-late Holocene, and how pinniped species responded to their altered environments. From their isotopic results, Weddell seals and some southern elephant seals likely foraged within productive, coastal regions of the Ross Sea up to the latest Holocene. This habitat changed over the last 1,000 years, experiencing reduced productivity and less nitrogen drawdown relative to the earlier Holocene. In contrast, the foraging area of crabeater seals likely encompassed a less productive region of the Ross Sea, perhaps the pack ice zone, which has not experienced changes in productivity or nitrogen drawdown during the Holocene. Intriguingly, crabeater seal isotope results revealed a considerable shift in their diets, which was not found for any other species of pinniped. Fish composed a greater portion, substantially larger in some cases, of the crabeater seal diet for much of the Holocene than has been observed in the present day (Hückstädt et al. 2012). Thus, crabeater seals appeared to have only recently shifted to diets composed almost exclusively of krill, which may have been driven by changes in harvesting and climate (Trivelpiece et al. 2011). Southern elephant seals, likewise, had variable foraging behaviors throughout the Holocene, undergoing an array of migrations to capture prey. Some animals appear to have fed in the same highly productive shelf sites as Weddell seals, whereas other individual seem to have foraged pelagically much further north, perhaps in the circumpolar current systems. Elephant seals decreased and ultimately disappeared from the Ross Sea beginning around 1,000 years ago, as conditions became icier. I have concluded that crabeater

and southern elephant seals likely have higher adaptive capacities than Weddell seals since they historically exhibited flexibility in diet and foraging routes, correspondingly, whereas Weddell seals showed no alterations in their foraging behavior despite considerable changes in their environment during the last 5,000 years.

REFERENCES

Alter SE, Meyer M, Post K, Czechowski P, Gravlund P, Gaines C, Rosenbaum HC, Kaschner K, Turvey ST, Plicht J, Shapiro B (2015) Climate impacts on transocean dispersal and habitat in gray whales from the Pleistocene to 2100. Mol Ecol 24:1510-1522

Arrigo KR, DiTullio GR, Dunbar RB, Robinson DH, VanWoert M, Worthen DL, Lizotte MP (2000) Phytoplankton taxonomic variability in nutrient utilization and primary production in the Ross Sea. J Geophys Res, C, Oceans 105:8827-8846

Ainley DG, Siniff DB (2009) The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. Antarct Sci 21:317-327

Arrigo KR, van Dijken GL (2003) Phytoplankton dynamics within 37 Antarctic coastal polynya systems. J Geophys Res, C, Oceans 108:3271

Arrigo KR, van Dijken G, Long M (2008) Coastal Southern Ocean: A strong anthropogenic CO_2 sink. Geophys Res Lett 35:L21602

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the southern ocean. Nature 432:100-103

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y, Suga H, Tomitani A, Miyashita H, Kitazato H, Ohkouchi N (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol Oceanogr: Methods 7:740-750

Croxall JP, Nicol S (2004) Management of Southern Ocean fisheries: global forces and future sustainability. Antarct Sci 16:569-584

Ducklow, HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC (2007) Marine pelagic ecosystems: The West Antarctic Peninsula. Philos Trans R Soc Lond B Biol Sci 362:67-94

Ducklow HW, Clarke A, Dickhut R, Doney SC, Geisz H, Huang K, Martinson DG, Meredith MP, Moeller HV, Montes-Hugo M, Schofield O, Stammerjohn SE, Steinberg D, Fraser W (2012) The marine system of the Western Antarctic Peninsula. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) Antarctic ecosystems: an extreme environment in a changing world, Blackwell Publishing LTD, Hoboken, New Jersey, USA, p 121-159

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes. Springer, Netherlands, p 299-318

Hückstädt LA, Burns JM, Koch PL, McDonald BI, Crocker DE, Costa DP (2012a) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287-301

Jacobs SS, Giulivi CF, Mele PA (2002) Freshening of the Ross Sea during the late 20th century. Science 297:386-389

Jaeger A, Connan M, Richard P, Cherel Y (2010) Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialization in seabirds. Mar Ecol Prog Ser 401:269-277

Kwok R, Comiso JC (2002) Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. J Clim 15:487-501

Loeb VA, Puglise KI, Outram DA (1997) AMLR program: salps and other macrozooplankton collected from January to March 1997. Ant J US 32:131-134

Lorenzen ED, Nogués-Bravo D, Orlando L, Weinstock J, Binladen J, Marske KA, Ugan A, Borregaard MK, Gilbert MT, Nielsen R, Ho SY (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. Nature 479:359-364

Lorrain A, Graham B, Ménard F, Popp B, Bouillon S, Van Breugel P, Cherel Y (2009) Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. Mar Ecol Prog Ser 391:293-306

Marinov I, Gnanadesikan A, Toggweiler JR, Sarmiento JL (2006) The southern ocean biogeochemical divide. Nature 441:964-967

McClelland JW, Montoya JP (2002) Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. Ecology 83:2173-2180

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697-714

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between δ^{15}N and animal age. Geochim Cosmochim Acta 48:1135-1140

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western western Antarctic Peninsula. Science 323:1470-1473

Parkinson CL (2002) Trends in the length of the Southern Ocean sea-ice season, 1979-99. Ann Glaciol 34:435-440

Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott MJ, López-Ibarra GA, Galván-Magaña F, Fry B (2007) Insight into the trophic ecology of the yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson T, Siegwolf R (eds) Stable Isotopes as Indicators of Ecological Change. Elsevier, New York, p 173-190

Schell DM, Barnett BA, Vinette KA (1998). Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. Mar Ecol Prog Ser 162:11-23

Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How do polar marine ecosystems respond to rapid climate change? Science 328:1520-1523

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: Projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425-435

Smith WO, Ainley DG, Cattaneo-Vietti R (2007) Trophic interactions within the Ross Sea continental shelf ecosystem. Philos Trans R Soc Lond B Biol Sci 362:95-111

Smith Jr WO, Ainley DG, Arrigo KR, Dinniman MS (2014) The oceanography and ecology of the Ross Sea. Ann Rev Mar Sci 6:469-487

Stammerjohn S, Massom R, Rind D, Martinson D (2012) Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophys Res Lett 39:L06501

Tortell PD, Payne CD, Li Y, Trimborn S, Rost B, Smith WO, Riesselman C, Dunbar RB, Sedwick P, DiTullio GR (2008) CO_2 sensitivity of Southern Ocean phytoplankton. Geophys Res Lett 35:L04605

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011) Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci USA 108:7625-7628

CARBON AND NITROGEN ISOSCAPES IN WEST ANTARCTICA REFLECT OCEANOGRAPHIC TRANSITIONS

ABSTRACT

Antarctic marine ecosystems are spatially and temporally dynamic. Regional climate change is significantly altering the patterns and magnitudes of this dynamism with cascading impacts on biogeochemistry, productivity, and food web architecture. Isoscapes, isotope landscapes, provide a valuable geospatial tool to characterize ecosystem processes and address questions about trophic dynamics, animal movement, and elemental cycling. However, application of stable isotope methods to Antarctic ecosystems is currently limited by a paucity of information on geospatial isotope characteristics within the Southern Ocean. In response, we have created the first empirically derived zooplankton isoscapes for West Antarctica based on analysis of bulk nitrogen (N) and carbon (C) isotope values ($\delta^{15}N$ and $\delta^{13}C$, respectively) in 94 zooplankton specimens from the Drake Passage, West Antarctic Peninsula (WAP), Amundsen Sea, and Ross Sea. $\delta^{15}N$ values increased by ~ 3 ‰ from north of the Polar Front (3.3 ± 0.6 ‰) to the Ross Sea (6.2 ± 0.8 ‰), reflecting a productivity gradient across this region. Abundant open water polynyas in the Amundsen and Ross Seas exhibit strong drawdown of nitrate, resulting in more ^{15}N-enriched phytoplankton and thus higher zooplankton $\delta^{15}N$ values relative to those from the

WAP and Drake Passage where productivity is generally lower. $\delta^{13}C$ values decreased by ~ 3 ‰ from north of the Polar Front (-24.2 ± 0.9 ‰) to the Ross Sea (-27.5 ± 1.6 ‰), likely driven by decreasing sea surface temperatures and increasing $[CO_2]_{aq}$ with increasing latitude. These isoscapes show significant spatial patterns for both $\delta^{15}N$ and $\delta^{13}C$ in West Antarctica, which are critical for addressing numerous ecosystem questions.

INTRODUCTION

The Southern Ocean is one of the largest, most dynamic ecosystems on Earth, playing a critical role in ocean primary productivity and fisheries production, biogeochemical cycling, and global climate (Falkowski et al. 1998, Gille 2002, Croxall and Nicol 2004, Marinov et al. 2006). This ocean consists of the waters south of the Subtropical Front, including the Antarctic Circumpolar Current (ACC) and high latitude waters surrounding the continent. West Antarctica, the Southern Ocean region between the Ross and Weddell Seas, is experiencing some of the most profound and rapid regional climate change on Earth (Meredith and King 2005, Ducklow et al. 2007, 2012, Stammerjohn et al. 2012). Warming is predicted to result in increased upper ocean stratification and to alter the phytoplankton assemblage with unknown long-term ecosystem consequences (Arrigo et al. 2000, Jacobs et al. 2002, Tortell et al. 2008). Climate change impacts on a range of taxa have been documented in the Southern Ocean over the past 50 years, including phytoplankton (Montes-Hugo

et al. 2009), Antarctic krill and other pelagic invertebrates at the base of the food web (Atkinson et al. 2004), and upper trophic level consumers, including sea birds, penguins, and marine mammals (Trathan et al. 2007, Nicol et al. 2008, Siniff et al. 2008, Forcada and Trathan 2009). Given the rapid physical, chemical, and biological changes occurring in West Antarctica, it is critical to understand the underlying biogeochemical cycling that supports the base of Antarctic food webs and ultimately controls the ecological response to climate change.

Stable isotope analysis is now a routine tool to characterize elemental cycling and trophic dynamics (Boecklen et al. 2011). Stable nitrogen (N) isotope values ($\delta^{15}N$) are typically used to determine the number of trophic transfers between a consumer and the base of the food web, while stable carbon (C) isotope values ($\delta^{13}C$) are often used to infer sources of primary production fueling food webs (Peterson and Fry 1987). Ecological application of stable isotope data, termed ecogeochemistry, requires careful consideration of the spatio-temporal dynamics of isotope values at the base of the food web (Graham et al. 2010, McMahon et al. 2013a).

Geospatial maps of isotopic values, termed isoscapes, of organisms at the base of the food web provide insight into regional biogeochemical processes (Bowen 2010, West et al. 2010, McMahon et al. 2013a). A number of factors can influence baseline stable nitrogen ($\delta^{15}N_{baseline}$) and carbon ($\delta^{13}C_{baseline}$) isotope values. For instance, phytoplankton $\delta^{15}N$ values are set by their nutrient source (i.e., nitrate, ammonium, or N_2), biological transformations (e.g., N_2-fixation and denitrification), isotopic fractionation during N assimilation, and nutrient pool size (or the extent of nitrogen

pool drawdown) (reviewed in McMahon et al. 2013a). For carbon, variability in the $\delta^{13}C$ of phytoplankton reflects dissolved inorganic carbon $\delta^{13}C$ values, $[CO_2]_{aq}$, temperature, cell size and geometry, internal biological parameters (e.g., growth rate), and CO_2 drawdown (reviewed in McMahon et al. 2013a). Spatial and temporal variations in these driving forces, e.g., seasonal or latitudinal gradients in temperature, will in turn create spatial and temporal variations in phytoplankton isotope values (e.g., Schell et al. 1998). Phytoplankton $\delta^{15}N$ and $\delta^{13}C$ values at the base of the food web are subsequently passed on, with modifications associated with trophic transfer, to upper trophic level consumers (e.g., Lorrain et al. 2009, Graham et al. 2010, Jaeger et al. 2010).

In recent years, researchers have established baseline isotope values for various regions (McMahon et al. 2013a, Vokhshoori et al. 2014, Vokhshoori and McCarthy 2014), but efforts in the Southern Ocean have been limited. Here, four major fronts separate the Southern Ocean into five distinct biogeographic zones. From north to south, these zones are: the Subtropical (STZ), Subantarctic (SAZ), Polar Front (PFZ), Antarctic (AZ), and Antarctic Continental (ACZ) Zones. Baseline isotope values have not yet been determined for all major frontal zones and seas, such as the Amundsen and Ross Seas in the Pacific Sector. Where available, however, isotopic baselines are proving useful in interpreting broad ecosystem dynamics.

Off East Antarctica (the portion of the continent largely within the Eastern Hemisphere), DiFiore et al. (2006) have determined summer and winter $\delta^{15}N_{NO3-}$ for the STZ, SAZ and PFZ. They described a seasonal increase of $\delta^{15}N_{NO3-}$ in surface

waters, which were greatest in the summer and associated with a decrease in NO_3^- concentration [NO_3^-]. The authors attributed the inverse relationship between $\delta^{15}N_{NO3-}$ and [NO_3^-] and the resulting seasonal pattern in $\delta^{15}N_{NO3-}$ to phytoplankton NO_3^- consumption, which increases the $\delta^{15}N$ of the NO_3^- pool. DiFiore et al. (2006) also reported decreasing surface $\delta^{15}N_{NO3-}$ with increasing latitude from ~ 13.5 ‰ at 42 °S to ~ 7.5 ‰ at 54 °S, which may have resulted from decreasing productivity between the STZ and PFZ. DiFiore et al. (2009) measured $\delta^{15}N_{NO3-}$ at three regions along the East Antarctic continental margin and in the Ross Sea polynya, all sites within the ACZ and at latitudes between about 65 °S and 80 °S. The authors found surface $\delta^{15}N_{NO3-}$ values ranging from about 5 ‰ to 8 ‰, with the highest values at productivity "hot spots," which have the greatest surface NO_3^- depletions. The surface $\delta^{15}N_{NO3-}$ values of hot spot locations were similar to those measured in the PFZ at ~ 54 °S, conflicting with prior work suggesting a consistent decrease in $\delta^{15}N_{NO3-}$ with increasing latitude (DiFiore et al. 2006). Somes et al. (2010) used a marine ecosystem model with N isotopes to construct a global map of $\delta^{15}N_{NO3-}$, which was compared to a global database of $\delta^{15}N_{NO3-}$. From their model, $\delta^{15}N_{NO3^-}$ decreased with increasing latitude in the Southern Ocean, likely due to increasing [NO_3^-] (Somes et al. 2010). Jaeger et al. (2010) defined the isotopic baseline in open waters of the southwest Indian Ocean by measuring isotopic values in the feathers of seabirds. They found decreases in both $\delta^{15}N$ (12.9 ‰ to 8.2 ‰) and $\delta^{13}C$ (-19.0 ‰ to -23.7 ‰) values of light-mantled sooty albatross (*Phoebetria palpebrata*) from the STZ towards the AZ. Similar isoscape studies are lacking in the West Antarctic. This is particularly

troubling given that this system is experiencing rapid warming and associated ecological and environmental changes.

In this study, we generated the first empirical isoscapes for the West Antarctic region by measuring $\delta^{15}N$ and $\delta^{13}C$ of multiple taxa of zooplankton and phytoplankton. These isoscapes cover an expansive area of the West Antarctic: from the tip of South America to the Antarctica Peninsula, and along the West Antarctic coast from the peninsula to the Ross Sea. In particular, this study focuses on isoscapes of West Antarctic continental margins, which are ecologically critical zones for fisheries, seabirds, and marine mammals, and have not been fully assessed in prior isoscapes. This work not only provides a framework for understanding baseline variability in Antarctic food webs, past and present, but also serves as a benchmark for evaluating future ecological and biogeochemical changes associated with rapid climate change.

MATERIALS AND METHODS

Sampling sites

Plankton samples were collected between 2007 and 2015 adjacent to shore over the continental shelves of the West Antarctic Peninsula (WAP), Amundsen Sea, and Ross Sea, and from open water off the continental shelf in the AZ, as well as from the PFZ and SAZ between the WAP and South America. Ninety-four discrete samples were collected at 34 stations over this area, comprising a variety of

zooplankton taxa (average of 4 taxa per station; Table 1.1), including 5 stations across the PFZ and SAZ waters, 5 stations within the AZ, 10 nearshore stations off the WAP in the ACZ, and at 7 stations each in the Amundsen and Ross Seas.

Within the Palmer Long-Term Ecological Research (PAL-LTER) study area along the WAP and on the continental shelf, phytoplankton and Antarctic krill were collected during austral summers between 2007 and 2011: phytoplankton, 2009/10 and 2010/11 and krill, 2007/08 and 2010/11. We incorporate $\delta^{15}N$ and $\delta^{13}C$ values of PAL-LTER krill samples reported in Brault (2012) into our isoscapes. Amundsen and Ross Sea zooplankton and phytoplankton were collected on the 2007/08 and 2010/11 *RV Oden* austral summer cruises. All Ross Sea samples were obtained on the continental shelf. For the Amundsen Sea samples, four samples were collected on the continental shelf and the other three samples were collected within the continental margin. Zooplankton samples were taken from the ACZ, AZ, PFZ and SAZ during the early austral fall 2015 cruise of the *SV Lawrence M. Gould*. Of these samples, only sampling within the ACZ was on the continental shelf. Mixed phytoplankton and zooplankton samples were obtained from the western Ross Sea during the 2011/2012 austral summer cruise of the *RV Nathaniel B. Palmer*, all samples were from sites on the continental shelf.

Sample collection

Phytoplankton samples from the PAL-LTER surveys were collected using an 80 μm ring net towed through the upper water column (≤ 50 m depth) for ~ 30 minutes. The phytoplankton sample was rinsed into a pre-cleaned plastic tub, re-

concentrated by sieving through a 25 µm mesh, and then frozen at -80 °C. A sub-sample of each tow was examined under a compound microscope to determine the dominant species (diatoms in all cases) and any microzooplankton were removed manually. Phytoplankton were collected during the *Oden* cruises of 2007/08 and 2010/11 via vertical tows from depths of ~ 20 m with a 30 µm ring net. Samples were similarly re-concentrated and frozen at -80 °C. The 2010/11 samples were dominated by the prymnesiophyte *Phaeocystis antarctica* according to onboard microscopy of tow sub-samples and any microzooplankton were discarded manually. The 2007/08 samples were not evaluated under a microscope to identify the dominant phytoplankton species.

Krill obtained during the PAL-LTER sampling, mixed zooplankton samples collected during the *Oden* cruise in 2010/11, and one sample of *Clione limacina* from a 2007/08 *Oden* cruise were derived from oblique tows (700 µm square-frame net) in 120 m and 400 m water depth for PAL-LTER and *Oden* cruises, respectively. Samples were transferred from the cod end into pre-cleaned buckets, re-concentrated by sieving through 700 µm mesh (retaining the retentate), and frozen at -80 °C. Samples were identified to the lowest taxonomic group possible prior to freezing. Zooplankton samples from the *L. M. Gould* cruise were obtained with open oblique hauls of a 505 µm mesh net from ~ 150 m to the surface using a 1.8 m Isaacs-Kidd midwater trawl. Samples were filtered through a 505 µm mesh sieve, sorted by species, and frozen at -20 °C. Mixed phytoplankton and zooplankton samples from the 2011/2012 cruise aboard the *RV Nathaniel B. Palmer* were collected with 200 µm

bongo net tows in the upper water column (0-200 m). The samples were stored in a 4 % formaldehyde-seawater mixture at 4 °C.

Taxonomic groups

All of the phytoplankton samples were treated together as "phytoplankton". Zooplankton taxonomic categories from the Ross and Amundsen Seas were copepods, gammarid and hyperiid amphipods, euphausiids (larval, juvenile, adult), *Salpa thompsoni*, and pteropods *Clione limacina* (naked) and *Limacina helicina* (shelled) (Table 1.1). The WAP and Drake Passage samples consisted of euphausiid species *E. superba, E. crystallorophias, E. frigida, E. triacantha* and *Thysanoessa macrura*, hyperiid amphipod species *Themisto gaudichaudii*, *Vibilia antarctica* and *Primno macropa, Salpa thompsoni* and pteropod *Spongiobranchia australis* (naked) (Table 1.1).

Sample preparation

All samples were kept frozen until laboratory preparation, except for the formaldehyde-preserved plankton samples. Phytoplankton collected on the *Oden* cruises, and phytoplankton and krill from the PAL-LTER cruises were freeze-dried at the Virginia Institute of Marine Science (VIMS, Gloucester Point, VA) with a Labconco Freezone Plus 6 at -80 ˚C for ~ 72 hours. The krill were homogenized with a Virtis "45" tissue homogenizer (Virtis Co., Inc.) before freeze-drying. Phytoplankton samples were manually homogenized after freeze-drying. Zooplankton, sorted by taxon at each station, from the *Oden* and *L. M. Gould* cruises were freeze-dried at the University of California, Santa Cruz (UCSC) using a

Labconco Freeze Dry System (Lyph Lock 4.5) at -40 ˚C for ~ 48 hours and then manually homogenized. All phytoplankton and zooplankton samples were stored in a dessicator after drying.

Sub-samples of all zooplankton samples were lipid-extracted, except for the Antarctic shelled-pteropods, to account for lipid ^{13}C-depletion relative to other biochemical classes. Carbonate shells of the pteropod *Limacina helicina* were acidified and decarbonated with a 10 % HCl solution. After HCl treatment, the samples were neutralized with Milli-Q water (Thermo Fisher Scientific, Inc.) and freeze-dried in the UCSC Labconco Freeze Dry System (Lyph Lock 4.5; -40 ˚C for ~ 48 hours). These samples were not lipid-extracted due to specimen limitations but are lipid-poor relative to other pteropod and zooplankton species (Kattner et al. 1998).

The PAL-LTER krill were lipid-extracted at the VIMS over 3 days using a chloroform:methanol (1:2; v:v) mixture via Soxhlet extraction (Bligh and Dyer 1959). After lipid extraction, samples were dried and frozen at -80 ˚C until stable isotope analysis. While non-lipid extracted material was not retained for $\delta^{15}N$ analysis, the $\delta^{15}N$ of the lipid-extracted krill from PAL-LTER were not significantly different from the $\delta^{15}N$ of *E. superba* material without lipid removal that was collected in the same area during the 2015 *L. M. Gould* cruise. A portion of each zooplankton sample from the *Oden* and *L. M. Gould* cruises was lipid-extracted via ASE extraction (1500 psi; 60 ˚C; 3 cycles) with petroleum ether, according to a lab-established protocol at the UCSC (Dobush et al. 1985, Kurle et al. 2002). For these zooplankton samples, $\delta^{13}C$

values were obtained from lipid-extracted material and $\delta^{15}N$ values were obtained from the non-extracted material.

To remove the formaldehyde-seawater solution from the Ross Sea mixed plankton samples, samples were transferred to 50 ml BD Falcon centrifuge tubes, centrifuged (15 min, 10,000 rpm), and decanted. The pellet was rinsed with Milli-Q and centrifuged (15 min, 10,000 rpm) three times, discarding the supernatant between rinses. Samples were then transferred to 10 ml borosilicate vials and dried at 60 ˚C. We acknowledge that prior research has shown that formalin-preservation may affect $\delta^{15}N$ and $\delta^{13}C$ values (Sarakinos et al. 2002, González-Bergonzoni et al. 2015). From analysis of fish tissues, González-Bergonzoni et al. (2015) suggest that the formalin preservation effect (4 % formalin solution) on $\delta^{15}N$ values is ecologically insignificant relative to the range of values in our system. Formalin-fixed $\delta^{13}C$ values were ~ 0.9 ‰ less than those of fresh material. Since formalin may affect isotope values, we produced separate nitrogen and carbon isoscapes for the formalin-preserved samples in this study (Table 1.S1).

Isotopic analysis

For $\delta^{15}N$ and $\delta^{13}C$ analyses, about 1 mg of sample was weighed into tin cups (Costech, 3×5 mm) for elemental analysis-isotope ratio mass spectrometry (EA-IRMS). The PAL-LTER krill were analyzed at VIMS on a Costech ECS 4010 CHNS-O EA (Costech Analytical Technologies, Inc.) coupled to a Delta V Advantage IRMS with a Conflo IV Interface (Thermo Electron North America, LLC). The $\delta^{15}N$ and $\delta^{13}C$ values are referenced to AIR and V-PDB standards, respectively. Blanks and

international standards (USGS 40 and USGS 41) were analyzed on the EA-IRMS after every ten samples (standard deviations were < 0.1 ‰ for both $\delta^{15}N$ and $\delta^{13}C$).

All other phytoplankton and zooplankton samples were analyzed at the Stable Isotope Lab at UCSC using a Carlo Erba EA 1108 EA coupled to a Thermo-Finnigan Delta^{Plus} XP IRMS referenced to AIR and V-PDB for N and C, respectively. We applied mass and drift corrections during each instrument session with analysis of gelatin standard replicates. Standard deviations for standards were < 0.1 ‰ for both $\delta^{15}N$ and $\delta^{13}C$ (7 standards analyzed at the start of each session, and a standard analyzed after every 8 samples during the session).

Data analyses

Analyses of spatial patterns in the $\delta^{15}N$ and $\delta^{13}C$ values of phytoplankton and zooplankton taxa were performed with Ocean Data View (ODV) version 4.7.4 (Schlitzer 2015) using Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010). DIVA gridding is highly optimized and relies on a finite-element resolution that takes into account the distance between analysis and data (observation constraint), the regularity of the analysis (smoothness constraint) and physical laws (behavior constraint). DIVA also takes into account coastlines, sub-basins, and advection. Color-shaded maps were produced to display $\delta^{15}N$ and $\delta^{13}C$ values using DIVA gridding for phytoplankton and zooplankton taxa. In cases where multiple phytoplankton tows or zooplankton taxa were collected at a given site, the mean isotope value was calculated for that location and used for the isoscapes of "all phytoplankton" or "all zooplankton." Since sampling of two major zooplankton

taxonomic groups – euphausiids and amphipods – spanned our entire study area, we generated taxon-specific isoscapes for them, using mean values for euphausiids or amphipods if multiple replicates were sampled at a given station.

Statistical comparisons in $\delta^{15}N$ and $\delta^{13}C$ values for phytoplankton, all zooplankton taxa, euphausiids, and amphipods of different regions and sampling periods were performed with separate two-way Analysis of Variance (ANOVA) with post-hoc pairwise comparisons. Samples were clustered into five geographic regions: Ross Sea, Amundsen Sea, WAP, AZ, and combined PFZ and SAZ (PFZ/SAZ). Prior to using an ANOVA, tests of normality and equal variance were conducted to assure that the statistical test assumptions were met. No assumptions were violated in all cases. All statistical tests were performed in R (R Core Team 2014).

RESULTS

$\delta^{15}N$ isoscapes

Zooplankton $\delta^{15}N$ values varied significantly across the West Antarctic ($p < 0.001$, ANOVA), and sampling period had no significant effect. Ross Sea and Amundsen Sea zooplankton had significantly higher $\delta^{15}N$ values (6.2 ± 0.8 ‰ and 6.2 ± 0.6 ‰, respectively; $n = 7$ for both regions; mean ± standard deviation) than those from the WAP (4.1 ± 0.7 ‰, $n = 10$), AZ (3.7 ± 0.6 ‰, $n = 5$), and PFZ/SAZ (3.3 ± 0.6 ‰, $n = 5$) (Fig. 1.1a, Table 1.1, $p < 0.001$ for all Bonferroni post-hoc pairwise comparisons). Interestingly, these isotope gradients were not reflected in the

phytoplankton $\delta^{15}N$ values across this region, which did not vary significantly across region but did vary significantly among sampling periods ($p = 0.004$, ANOVA, Fig. 1.S1a, Table 1.S2).

The $\delta^{15}N$ isoscapes for euphausiids and amphipods are similar to that of all zooplankton. The $\delta^{15}N$ value of euphausiids varied significantly between the regions ($p < 0.001$, ANOVA). Euphausiid $\delta^{15}N$ values were significantly higher in the Ross Sea (6.5 ± 0.4 ‰, $n = 6$) and Amundsen Sea (6.7 ± 0.9 ‰, $n = 6$) than in the WAP (4.1 ± 0.8 ‰, $n = 10$), AZ (4.8 ± 0.9 ‰, $n = 5$), and PFZ/SAZ (3.8 ± 1.0 ‰, $n = 5$) based on Bonferroni post-hoc tests ($p < 0.001$ in all cases, except $p = 0.02$ and 0.004 for the Ross Sea versus AZ and Amundsen Sea versus AZ, correspondingly, Fig. 1.2a). Although sample sizes were low, the $\delta^{15}N$ pattern of amphipods across the five regions (Fig. 1.3a) was similar to that of all zooplankton: the $\delta^{15}N$ values of amphipods in the Ross (6.9 ± 0.8 ‰, $n = 3$) and Amundsen (6.2 ± 1.2 ‰, $n = 3$) Seas were higher than those in the WAP (3.8 ± 2.7 ‰, $n = 2$), the AZ (3.4 ± 1.2 ‰, $n = 4$), and the PFZ/SAZ (3.4 ± 1.4 ‰, $n = 4$). Spatial coverage was poor for the other taxa, but the $\delta^{15}N$ patterns for pteropods, salps, copepods, and mixed plankton (0-200 μm, 4 % formaldehyde-seawater mixture) were consistent with the significant patterns of all zooplankton taxa and euphausiids (Figs. 1.S2a, 1.S3a, 1.S4a, and 1.S5a, Tables 1.1 and 1.S1).

$\delta^{13}C$ isoscapes

The $\delta^{13}C$ values for all zooplankton taxa varied significantly across the West Antarctic ($p < 0.001$, ANOVA); sampling period did not significantly affect these

isotopic values (Fig. 1.1b, Table 1.1). Zooplankton from the Ross Sea had significantly lower $\delta^{13}C$ values (-27.5 ± 1.6 ‰, n = 7) than those from the WAP (-25.1 ± 1.7 ‰, n = 10) and the PFZ/SAZ (-24.2 ± 0.9 ‰, n = 5) (Bonferroni post-hoc test p-values of 0.01 and 0.002, respectively). Additionally, all zooplankton $\delta^{13}C$ values from AZ waters (-27.1 ± 0.7 ‰, n = 5) were significantly lower than those of the PFZ/SAZ (p = 0.01 in Bonferroni post-hoc test). All zooplankton from the Amundsen Sea had $\delta^{13}C$ values (-26.1 ± 1.1 ‰, n = 7) similar to those from the Ross Sea. As was observed with the $\delta^{15}N$ patterns between phytoplankton and zooplankton, phytoplankton $\delta^{13}C$ values were not significantly different among these regions in contrast with the zooplankton $\delta^{13}C$ pattern (Fig. 1.S1b). Additionally, phytoplankton $\delta^{13}C$ values did not vary significantly between sampling time periods (Table 1.S2).

The $\delta^{13}C$ isoscapes for euphausiids and amphipods follow that of all zooplankton. Euphausiid $\delta^{13}C$ values were -26.9 ± 1.0 ‰ (n = 6) for the Ross Sea, -25.9 ± 1.3 ‰ (n = 6) for the Amundsen Sea, -25.3 ± 1.7 ‰ (n = 10) for the WAP, -26.9 ± 0.5‰ (n = 5) for the AZ, and -24.1 ± 0.8 ‰ (n = 5) for the PFZ/SAZ (Fig. 1.2b). Ross Sea and AZ euphausiids had significantly lower $\delta^{13}C$ values than those from the PFZ/SAZ (p = 0.01 and 0.02, respectively, in Bonferroni post-hoc tests). Amphipod $\delta^{13}C$ values were -26.5 ± 2.3 ‰ (n = 3), -26.0 ± 1.7 ‰ (n = 3), -25.7 ± 0.2 ‰ (n = 2), -27.2 ± 0.7 ‰ (n = 4), and -24.4 ± 1.5 ‰ (n = 4) for the Ross Sea, Amundsen Sea, WAP, AZ, and PFZ/SAZ, respectively, and there were no significant

differences among the five regions (Fig. 1.3b). Again, the smaller sample sizes of amphipods relative to those of all zooplankton and euphausiids may explain the lack of significant spatial variability. Consistent with the pattern observed for all zooplankton taxa, $\delta^{13}C$ values of both euphausiids and amphipods increased as follows: Ross Sea < Amundsen Sea < WAP < PFZ/SAZ, and $\delta^{13}C$ values for the AZ were lower than PFZ/SAZ. The $\delta^{13}C$ patterns of the other taxa – pteropods, salps, copepods, and mixed plankton (0-200 μm, 4 % formaldehyde-seawater mixture) – were similar to the significant patterns observed in all zooplankton taxa and euphausiids (Figs. 1.S2b, 1.S3b, 1.S4b, and 1.S5b, Table 1.1 and 1.S1).

DISCUSSION

Understanding spatial and temporal variations in isotopic baselines is critical to ecogeochemical approaches to questions of food web architecture, biogeochemical cycling, and animal movement in dynamic marine environments, like the Southern Ocean (Graham et al. 2010, McMahon et al. 2013a). Isotopic data from zooplankton (Fig. 1.1) show clear spatial patterns across the West Antarctic, while those of phytoplankton do not. The presence of patterns in isotopic data from zooplankton but not phytoplankton is not surprising when isotopic integration and turnover rate are considered. Phytoplankton measurements only capture a short window of time (days to weeks), while zooplankton measurements integrate geochemical signals of ecosystem dynamics over longer time scales (months). As such, time of collection

had a significant effect on phytoplankton $\delta^{15}N$ values, but not those of all zooplankton. Phytoplankton communities are highly dynamic, experiencing considerable variability in species composition, biomass, growth rate etc, over relatively short scales of time and space (Cloern and Jassby 2010, Zingone et al. 2010). Previous studies have shown that sampling zooplankton provides a more robust, integrative view of biogeochemical processes than sampling phytoplankton on ecological scales relevant to top consumer trophic dynamics (Mullin et al. 1984, Pinkerton et al. 2013). As such, we focus on zooplankton for the remainder of this discussion of West Antarctic isoscapes.

$\delta^{15}N$ isoscapes track productivity gradients

We observed a strong spatial gradient in zooplankton isotope values from low $\delta^{15}N$ in the WAP, AZ, and PFZ/SAZ to high $\delta^{15}N$ values in the Ross and Amundsen Seas. The $\delta^{15}N$ values of all zooplankton from the Ross and Amundsen Seas were about 2 ‰ and 3 ‰ higher than those from the WAP and PFZ/SAZ, respectively (Fig. 1.1a). These patterns in zooplankton $\delta^{15}N$ values are consistent with previously reported data for the region. Pinkerton et al. (2013) reported mean (± standard deviation) lipid-extracted zooplankton $\delta^{15}N$ values of 6.1 ± 2.3 ‰ across 14 zooplankton taxa from the Ross Sea (austral summer 2008), indistinguishable from the mean for our Ross Sea zooplankton samples (6.2 ± 0.8 ‰) collected in the austral summers of 2007/08 (n = 1) and 2010/11 (n = 6). Similarly, Schmidt et al. (2003) have reported mean (± standard deviation) $\delta^{15}N$ values for zooplankton (without lipid extraction) collected from the PFZ/SAZ and 65 °S (similar latitude to that of the

WAP) of 3.6 ± 1.1 ‰ (all 15 taxa) and 3.5 ± 1.1 ‰ (all 4 taxa), respectively, between 1996 and 2000 that are similar to our $\delta^{15}N$ values for all zooplankton from the PFZ/SAZ to the WAP (3.3 ± 0.6 ‰ and 4.1 ± 0.7 ‰, respectively). McMahon et al. (2013b) used meta-analyses of published $\delta^{15}N$ values to produce a global $\delta^{15}N$ isoscape. Although much of the West Antarctic was not included in the isoscape due to a paucity of data, their analysis suggested $\delta^{15}N$ values for the WAP of ~ 3 ‰, similar to our measurements, but higher values for the AZ, PFZ, and SAZ (e.g., of 4-6 ‰) than we observed. However, little data were available for these three regions and, thus their isotopic values were largely driven by data for the WAP and South American coast.

The observed patterns in $\delta^{15}N$ variation within the West Antarctic isoscape likely reflects variable NO_3^- drawdown associated with productivity (Wada et al. 1987, Altabet and Francois 1994). The Southern Ocean is the largest high nutrient, low chlorophyll (HNLC) region in the world, with the majority of NO_3^- in the surface waters remaining unused on an annual basis due to iron limitation, which results in relatively high surface [NO_3^-] (Fig. 1.4) and low phytoplankton and zooplankton $\delta^{15}N$ values (de Baar et al. 1990, Martin et al. 1990, Altabet and Francois 2001). However, localized regions of more complete NO_3^- utilization associated with high rates of primary productivity may result in increased $\delta^{15}N$ values of phytoplankton and, consequently, zooplankton (DiFiore et al. 2009).

Our $\delta^{15}N$ spatial pattern suggests lower nutrient utilization and productivity in the PFZ/SAZ and off the WAP than on the large continental margins of the

Amundsen and Ross Seas, which is consistent with the results of prior studies on West Antarctic productivity. The Ross Sea – where the large Ross Sea and Terra Nova Bay polynyas form each spring – has been shown to exhibit high productivity (~ 503 Tg C a^{-1}) on an annual basis compared to other Southern Ocean sectors (Arrigo et al. 1998, 2008, Smith and Comiso 2008). Smith and Cosimo (2008) found that productivity decreased from the southern Ross Sea (2.74 g C m^{-2} d^{-1}) to the central Ross Sea (2.26 g C m^{-2} d^{-1}) to the WAP (1.56 g C m^{-2} d^{-1}). More recently, the Amundsen Sea has been shown to experience high productivity due to iron inputs and stratification from melting glaciers, with water column productivity ranging from 1.56 (sea ice) to 4.18 (Pine Island polynya) g C m^{-2} d^{-1} (Alderkamp et al. 2012). This prior work points to the extensive coastal polynyas of the Ross and Amundsen Seas having higher productivity, NO_3^- drawdown, and, thus, $\delta^{15}N_{baselines}$ than the WAP and HNLC zones off the continental shelf since within them light is available, water column stratification is high, and glacial input relieves iron limitation (Gordon et al. 2000, Arrigo et al. 2015).

Our hypothesis for the cause of the strong isotopic gradient in zooplankton $\delta^{15}N$ values is also supported by work in other sectors of the Southern Ocean. DiFiore et al. (2009) measured the $\delta^{15}N$ value of suspended particulate organic nitrogen (PN) along the East Antarctic continental margin, including Dumont the D'Urville Sea, Davis Sea, and Prydz Bay. They discovered a shift in PN $\delta^{15}N$ values from < 1.5 ‰ for samples from more offshore, pelagic locations to values of ~ 5 ‰ in persistent coastal polynyas, productivity "hot spots" where NO_3^- drawdown is extensive

(DiFiore et al. 2009). Similarly, Schmidt et al. (2003) found $\delta^{15}N$ values of POM, *Euphausia superba* furcilia larvae, and copepods (*Metridia gerlachei* and *Calanoides acutus*) that were 4 to 5 ‰ higher in Marguerite Bay (67° 30' S, 70 °W) than in the Lazarev Sea (~ 69 °S, 5 °W), likely due to differing degrees of NO_3^- utilization by phytoplankton between these two sites. During their time of sample collection, phytoplankton abundance in the Lazarev Sea was low (~ 0.5 µg chlorophyll *a* L^{-1}) in contrast with Marguerite Bay, which was experiencing a several-month-long diatom bloom (7-10 µg chlorophyll *a* L^{-1}) (Schmidt et al. 2003).

In contrast to our observations, previous modeling work by Somes et al. (2010) predicted relatively consistent $\delta^{15}N_{baseline}$ values across the West Antarctic, and Jaeger et al. (2010) modeled a decrease in $\delta^{15}N_{baseline}$ from the STZ towards the AZ. Both the Somes et al. (2010) and Jaeger et al. (2010) isoscapes focus on open water systems where the NO_3^- pool remains large and underutilized due to apparent iron limitation. As such, productivity and associated NO_3^- drawdown, and thus $\delta^{15}N$ values of POM, decreased from the more productive STZ into the HNLC open ocean waters of the Southern Ocean. Our isoscapes include continental margins across the West Antarctic, regions likely to experience higher productivity than open water areas due to increased iron inputs and stratification from glacial melting. The WAP has a relatively narrow continental shelf, with reduced productivity compared to the wide shelves of the Ross and Amundsen Seas. Thus, our $\delta^{15}N_{baseline}$ increased from the HNLC open ocean waters to the continental margins, and this gradient is pronounced in the Amundsen and Ross Sea sectors since they have extensive continental shelves.

The productivity gradient within our systems offers the most parsimonious explanation for the observed $\delta^{15}N$ isoscape along the continental shelf of the West Antarctic. However, it is possible that either variability in the zooplankton taxa obtained from each region or spatially shifting trophic positions for sampled taxa, contributed to the observed $\delta^{15}N$ isoscape patterns. Changes in zooplankton sampling are an unlikely source of the observed pattern because even when analyzed at the level of individual taxa, zooplankton $\delta^{15}N$ values in the Amundsen and Ross Seas are ~ 2 ‰ higher than those in the WAP (Figs. 1.2a, 1.3a, 1.S2a, 1.S3a, 1.S4a, and 1.S5a). In contrast, a gradient in zooplankton trophic position for certain taxa cannot be ruled out, but we believe it is an unlikely explanation of the spatial pattern. For instance, the $\delta^{15}N$ gradient is present in the dominantly herbivorous *E. superba* (Siegel and Loeb 1995, Nicol 2006, Pinkerton et al. 2010). While we cannot rule out potential variations in zooplankton trophic position as a contributor to the $\delta^{15}N_{baseline}$ gradient, it is unlikely to be the dominant factor driving the patterns observed across all zooplankton in our study.

We note that temporal variation may be an important factor in the West Antarctic $\delta^{15}N$ isoscape. The $\delta^{15}N_{baseline}$ values in the Southern Ocean fluctuate with the extent of nutrient utilization and productivity, both of which experience seasonal and interannual variability (Smith et al. 1998, Arrigo and van Dijken 2004, Arrigo et al. 2008). Productivity slowly increases in the early austral spring (October) as a result of increased insolation and iron inputs from retreating sea ice (Arrigo and van Dijken 2003). Phytoplankton blooms peak in the austral summer, returning to pre-

bloom levels by March or April (Arrigo and van Dijken 2003). The temporal progression of phytoplankton blooms results in a seasonal pattern of nutrient drawdown and, consequently, $\delta^{15}N_{baseline}$ shift, whereby the surface layer [NO_3^-] is low and $\delta^{15}N_{baseline}$ is high at the bloom peak (DiFiore et al. 2006, DiFiore et al. 2009). The timing, duration, and size of the production can vary interannually in relation to sea ice cover, sea surface temperature, and other factors (Smith et al. 1998, Arrigo and van Dijken 2004, Arrigo et al. 2008). All of our phytoplankton samples and most of our zooplankton samples were collected during the austral summer, largely between mid-December and mid-January. Some of our zooplankton samples were obtained during the early austral fall. Sampling period did not significantly affect a region's $\delta^{15}N$ value for our all zooplankton, euphausiid, or amphipod isoscapes, but it did have a significant effect on the phytoplankton $\delta^{15}N$ isoscape. This finding was unsurprising given the greater time integration of zooplankton (months) than phytoplankton (days). Since our zooplankton sampling was predominately within the summer and did not occur over several years – sampling largely took place in 2010/11 – our isoscapes may not fully capture the seasonal and interannual variation in productivity and, consequently, $\delta^{15}N_{baseline}$ values.

$\delta^{13}C$ isoscapes track temperature gradients

Our $\delta^{13}C$ isoscape reveals an inverse relationship between $\delta^{13}C_{baseline}$ values and latitude. The Ross Sea (sampling stations at latitudes between 71 °S and 79 °S) had significantly lower $\delta^{13}C$ values than the WAP and PFZ/SAZ (sampling latitudes between 69 °S and 55 °S) by about 2 ‰ and 3 ‰, respectively (Fig. 1.1b). These

patterns in zooplankton $\delta^{13}C$ value are generally consistent with previously reported data for the region. Pinkerton et al. (2013) found Ross Sea zooplankton had a mean $\delta^{13}C$ value of -26.7 ± 2.0 ‰ (14 taxa), which was similar to that for all Ross Sea zooplankton (-27.5 ± 1.6 ‰). Schmidt et al. (2003) found a comparable pattern in decreasing zooplankton $\delta^{13}C$ values from the PFZ/SAZ (-25.6 ± 3.3 ‰; 15 taxa) to 65 °S (-30.0 ± 0.6 ‰; 4 taxa) as we did across a similar latitudinal gradient. Their $\delta^{13}C$ values for zooplankton are lower than ours for all zooplankton from the PFZ/SAZ (-24.2 ± 0.9 ‰) and WAP (-25.1 ± 1.7 ‰), which is at ~ 65 °S. Schmidt et al. (2003) reported zooplankton $\delta^{13}C$ values without lipid extraction, which might have led to lower $\delta^{13}C$ values than for lipid-extracted samples. Since higher latitude zooplankton typically have higher lipid stores than lower latitude zooplankton, lipid content likely has a larger effect on the $\delta^{13}C$ value of the former than the latter (Lee et al. 2006). Lastly, McMahon et al. (2013b) produced a global $\delta^{13}C$ isoscape from meta-analyses of published $\delta^{13}C$ values, which indicated a decrease in $\delta^{13}C_{baseline}$ values from -23 ‰ to -25 ‰ in the PFZ/SAZ to values between -25 ‰ and -30 ‰ in the AZ/WAP, similar to the gradient reported in this study. Their isoscape did not cover the Amundsen Sea and included part of the Ross Sea, reporting values from about -25 ‰ to -30 ‰ for the latter, a range encompassing our measurements.

The observed patterns in $\delta^{13}C$ variation within the West Antarctic isoscape are likely explained by the latitudinal gradient in sea surface temperature (SST). As mentioned above, the $\delta^{13}C$ value of primary production is greatly influenced by SST

as CO_2 solubility in the ocean increases with decreasing temperature (Goericke and Fry 1994, Graham et al. 2010). Previous studies have shown a latitudinal decrease in $\delta^{13}C$ value in the Southern Ocean associated with decreasing SST (Cherel and Hobson 2007, Quillfeldt et al. 2010, Quillfeldt et al. 2015). Using SST values for our sampling locations (Gouretski and Koltermann 2004, Fig. 1.5) within these regions (-1.5 °C, 1.0 °C, and 4 °C for the Ross Sea, WAP, and PFZ/SAZ, correspondingly) and equations derived by Rau et al. (1989) relating SST, CO_2 (aq), and phytoplankton $\delta^{13}C$, we predicted an offset between Ross Sea and WAP zooplankton $\delta^{13}C$ of 1.6 ‰ and an offset of 3.3 ‰ between the Ross Sea and PFZ/SAZ zooplankton. Thus, the SST gradient across the Drake Passage and along West Antarctica likely contributes greatly to our spatial pattern of zooplankton $\delta^{13}C$ values. As mentioned earlier, factors other than SST may affect baseline $\delta^{13}C$ values (e.g., phytoplankton size and geometry, growth and photosynthetic rates of phytoplankton, and transport of HCO_3^- versus CO_2). We note that $\delta^{13}C$ values are lower in the AZ for all zooplankton (-27.1 ± 0.7 ‰, $n = 5$) given its latitude. The nearby regions of the WAP and PFZ/SAZ have higher $\delta^{13}C_{baseline}$ values of -25.1 ± 1.7 ‰ and -24.2 ± 0.9 ‰, respectively. Factors besides SST must be driving the low $\delta^{13}C_{baseline}$ in the AZ.

Temporal variation may also be an important factor in the West Antarctic $\delta^{13}C$ isoscape. SSTs fluctuate seasonally with sea ice dynamics, as well as interannually with the Southern Annular Mode (SAM) (Arrigo et al. 2008). The SAM drives interannual variation in SST; positive SAM events associated with lower SSTs, but the strength of this relationship varies regionally in the West Antarctic (Arrigo et al.

2008). Despite potential seasonal and interannual dynamism, our $\delta^{13}C$ isoscapes for all zooplankton, euphausiids, amphipods, and phytoplankton were not significantly affected by sampling period. However, our sampling was limited primarily to the austral summer and did not cover several years. Thus, our $\delta^{13}C_{baseline}$ may not fully capture the seasonal and interannual patterns.

CONCLUSIONS

This study presents the first empirically derived zooplankton isoscapes for West Antarctica, reflecting dynamic biogeochemical change across the region. Our isoscapes reveal a ~ 3 ‰ increase in $\delta^{15}N$ values from the PFZ/SAZ to the Amundsen and Ross Seas, which we attribute to increasing productivity and nutrient utilization. Conversely, there is a ~ 3 ‰ decrease in $\delta^{13}C$ values from the PFZ/SAZ to the Ross Sea, which we attribute to decreasing SST. These isoscapes will provide essential data for ecological, paleoecological, and oceanographic studies of food web architecture, biogeochemical cycling, and animal migration in the Southern Ocean. Furthermore, these isoscapes will serve as an anchor for future studies of biogeochemical change in this highly dynamic system, which is experiencing rapid climate change. Limitations of our $\delta^{15}N$ and $\delta^{13}C$ isoscapes include variability in sampling season, year, location, and taxa. Ideally, similar quantities of multiple zooplankton taxa should be obtained in a temporally and geographically consistent manner. For this first attempt at generating empirical zooplankton isoscapes,

specimens had been acquired opportunistically. Future work should advance these isoscapes to completely capture temporal variation in baseline isotope values and increase spatial resolution. Our isoscapes are an important first step in characterizing Southern Ocean isotope patterns and assessing their underlying biogeochemical mechanisms. We also focus on the Antarctic coastal margins, ecologically critical zones for fisheries, seabirds, and marine mammals, which have not been fully covered in prior isoscapes.

ACKNOWLEDGEMENTS

We thank Valerie Loeb, Walker Smith Jr, Heidi Geisz, Deborah Steinberg, Kate Ruck, Heidi Geisz, and Rebecca Dickhut for providing us with an array of samples. We are grateful to Colin Carney and Dyke Andreasen for laboratory assistance. We also thank the crew and staff on the *RV Oden* (austral summers of 2007/08 and 2010/11), *RV Nathaniel B. Palmer* (austral summer 2011/12), and *SV Lawrence M. Gould* (early fall 2015), as well as the staff of the PAL-LTER (from 2007 through 2011). The National Science Foundation (NSF ANT-1142108 and OPP-1347911) provided funding to complete this project.

REFERENCES

Alderkamp AC, Mills MM, van Dijken GL, Laan P, Thuróczy CE, Gerringa LJA, de Baar HJW, Payne CD, Visser RJW, Buma AGJ, Arrigo KR (2012) Iron from

melting glaciers fuels phytoplankton blooms in the Amundsen Sea (Southern Ocean): Phytoplankton characteristics and productivity. Deep Sea Res II 71-76:32-48

Altabet MA, Francois R (1994) Sedimentary nitrogen isotopic ratio as a recorder for surface ocean nitrate utilization. Global Biogeochem Cycles 8:103-116

Altabet MA, Francois R (2001) Nitrogen isotope biogeochemistry of the Antarctic Polar Frontal Zone at 170 W. Deep Sea Res Part II 48:4247-4273

Arrigo KR, Weiss AM, Smith WO (1998) Physical forcing of phytoplankton dynamics in the southwestern Ross Sea. J Geophys Res, C, Oceans 103:1007-1021

Arrigo KR, DiTullio GR, Dunbar RB, Robinson DH, VanWoert M, Worthen DL, Lizotte MP (2000) Phytoplankton taxonomic variability in nutrient utilization and primary production in the Ross Sea. J Geophys Res, C, Oceans 105:8827-8846

Arrigo KR, van Dijken GL (2003) Phytoplankton dynamics within 37 Antarctic coastal polynya systems. J Geophys Res, C, Oceans 108:3271

Arrigo KR, van Dijken GL (2004) Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. Deep Sea Res II 51:117-138

Arrigo KR, van Dijken GL, Bushinsky S (2008) Primary production in the Southern Ocean, 1997–2006. J Geophys Res, C, Oceans 113:C08004

Arrigo KR, van Dijken GL, Strong AL (2015) Environmental controls of marine productivity hot spots around Antarctica. J Geophys Res, C, Oceans, 120:5545-5565

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the southern ocean. Nature 432:100-103

Barth A, Alvera A, Troupin C, Ouberdous M, Beckers JM (2010) A web interface for griding arbitrarily distributed in situ data based on Data-Interpolating Variational Analysis (DIVA). Adv Geosci 28:29-37

Bidigare RR, Fluegge A, Freeman KH, Hanson KL, Hayes JM, Hollander D, Jasper JP, King LL, Laws EA, Milder J, Millero FJ, Pancost R, Popp BN, Steinberg PA, Wakeham SG (1997) Consistent fractionation of ^{13}C in nature and in the laboratory: Growth-rate effects in some haptophyte algae. Global Biogeochem Cycles 11:279-292

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911-917

Boecklen, W.J., Yarnes, C.T., Cook, B.A. and James, A.C., 2011. On the use of stable isotopes in trophic ecology. Annu Rev Ecol Evol Syst 42:411-440

Bowen GJ (2010) Isoscapes: spatial pattern in isotopic biogeochemistry. Annu Rev Earth Planet Sci 38:161-187

Brault EK (2012) Evaluating Persistent Organic Pollutants (POPs) and Mercury in the West Antarctic Peninsula (WAP) Food Web, with a Focus on Antarctic Fur Seals (*Arctocephalus gazella*). MS thesis, Virginia Institute of Marine Sciences, Gloucester Point, VA.

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281-287

Cloern, JE, Jassby AD (2010) Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuar Coasts 33:230-241

Croxall JP, Nicol S (2004) Management of Southern Ocean fisheries: global forces and future sustainability. Antarct Sci 16:569-584

de Baar HJ, Buma AG, Nolting RF, Cadée GC, Jacques G, Tréguer PJ (1990) On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas. Mar Ecol Prog Ser 65:105-122

DiFiore PJ, Sigman DM, Trull TW, Lourey MJ, Karsh K, Cane G, Ho R (2006) Nitrogen isotope constraints on subantarctic biogeochemistry. J Geophys Res, C, Oceans 111:C08016

DiFiore PJ, Sigman DM, Dunbar RB (2009) Upper ocean nitrogen fluxes in the Polar Antarctic Zone: Constraints from the nitrogen and oxygen isotopes of nitrate. Geochem Geophys Geosyst 10:Q11016

Dobush GR, Ankney CD, Krementz DG (1985) The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. Can J Zool 63:1917-1920

Ducklow, HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC (2007) Marine pelagic ecosystems: The West Antarctic Peninsula. Philos Trans R Soc Lond B Biol Sci 362:67-94

Ducklow HW, Clarke A, Dickhut R, Doney SC, Geisz H, Huang K, Martinson DG, Meredith MP, Moeller HV, Montes-Hugo M, Schofield O, Stammerjohn SE, Steinberg D, Fraser W (2012) The marine system of the Western Antarctic Peninsula. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) Antarctic ecosystems: an extreme environment in a changing world, Blackwell Publishing LTD, Hoboken, New Jersey, USA, p 121-159

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281:200-206

Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. Glob Change Biol 15:1618-1630

Gille ST (2002) Warming of the Southern Ocean since the 1950s. Science 295:1275-1277

Goericke R, Fry B (1994) Variations in marine plankton $\delta^{13}C$ with latitude, temperature, and dissolved CO_2 in the world ocean. Global Biogeochem Cycles 8:85-90

González-Bergonzoni I, Vidal N, Wang B, Ning D, Liu Z, Jeppesen E, Meerhoff M (2015) General validation of formalin-preserved fish samples in food web studies using stable isotopes. Methods Ecol Evol 6:307-314

Gordon LI, Codispoti LA, Jennings JC, Millero FJ, Morrison JM, Sweeney C (2000) Seasonal evolution of hydrographic properties in the Ross Sea, Antarctica, 1996–1997. Deep Sea Res II 47:3095-3117

Gouretski VV, Koltermann KP (2004) WOCE global hydrographic climatology. Berichte des Bundesamtes für Seeschifffahrt und Hydrographie Tech Rep 35:1-52

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes. Springer, Netherlands, p 299-318

Jacobs SS, Giulivi CF, Mele PA (2002) Freshening of the Ross Sea during the late 20th century. Science 297:386-389

Jaeger A, Connan M, Richard P, Cherel Y (2010) Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialization in seabirds. Mar Ecol Prog Ser 401:269-277

Kattner G, Hagen W, Graeve M, Albers C (1998) Exceptional lipids and fatty acids in the pteropod Clione limacina (Gastropoda) from both polar oceans. Mar Chem 61:219-228

Kurle CM, Worthy GA (2002) Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal Callorhinus ursinus: implications for dietary and migratory reconstructions. Mar Ecol Prog Ser 236:289-300

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306

Lorrain A, Graham B, Ménard F, Popp B, Bouillon S, Van Breugel P, Cherel Y (2009) Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. Mar Ecol Prog Ser 391:293-306

Marinov I, Gnanadesikan A, Toggweiler JR, Sarmiento JL (2006) The southern ocean biogeochemical divide. Nature 441:964-967

Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. Nature 345:156-158

McMahon KW, Hamady LL, Thorrold SR (2013a) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697-714

McMahon KW, Hamady L, Thorrold SR (2013b) Ocean ecogeochemistry: a review. Oceanogr Mar Biol Annu Rev 51:327-374

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western western Antarctic Peninsula. Science 323:1470-1473

Mullin MM, Rau GH, Eppley RW (1984). Stable nitrogen isotopes in zooplankton: some geographic and temporal variations in the North Pacific. Limnol Oceanogr 29:1267-1273

Nicol S (2006) Krill, currents, and sea ice: Euphausia superba and its changing environment. Bioscience 56:111-120

Nicol S, Worby A, Leaper R (2008) Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. Mar Freshw Res 59:361-382

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293-320

Pinkerton MH, Bradford-Grieve JM, Hanchet SM (2010) A balanced model of the food web of the Ross Sea, Antarctica. CCAMLR Sci 17:1-31

Pinkerton MH, Forman J, Bury SJ, Brown J, Horn P, O'Driscoll RL (2013) Diet and trophic niche of Antarctic silverfish Pleuragramma antarcticum in the Ross Sea, Antarctica. J Fish Biol 82:141-164

Quillfeldt P, Masello JF, McGill RA, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? Front Zool 7:1-11

Quillfeldt P, Ekschmitt K, Brickle P, McGill RA, Wolters V, Dehnhard N, Masello JF (2015) Variability of higher trophic level stable isotope data in space and time–a case study in a marine ecosystem. Rapid Commun Mass Spectrom 7:667-674

R Core Team (2014). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria.

Rau GH, Takahashi T, Des Marais DJ (1989) Latitudinal variations in plankton $\delta^{13}C$: implications for CO_2 and productivity in past oceans. Nature 341:516-518

Sarakinos HC, Johnson ML, Zanden MJV (2002) A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. Can J Zool 80:381-387

Schell DM, Barnett BA, Vinette KA (1998). Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. Mar Ecol Prog Ser 162:11-23

Schlitzer R (2015) Ocean Data View (ODV) version (4.7.4). http://odv.awi.de

Schmidt K, Atkinson A, Stübing D, McClelland JW, Montoya J P, Voss M (2003) Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. Limnol Oceanogr 48:277-289

Siegel V, Loeb V (1995) Recruitment of Antarctic krill Euphausia superba and possible causes for its variability. Mar Ecol Prog Ser 123:45-56

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: Projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425-435

Smith RC, Baker KS, Vernet M (1998) Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula. J Mar Syst 17:229-243

Smith WO, Comiso JC (2008). Influence of sea ice on primary production in the Southern Ocean: A satellite perspective. J Geophys Res, C, Oceans 113:C05S93

Somes CJ, Schmittner A, Galbraith ED, Lehmann MF, Altabet MA, Montoya JP, Letelier RM, Mix AC, Bourbonnais A, Eby M (2010) Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem Cycles 24:GB4019

Stammerjohn S, Massom R, Rind D, Martinson D (2012) Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophys Res Lett 39:L06501

Sweeting CJ, Polunin NVC, Jennings S (2006) Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Commun Mass Spectrom 20:595-601

Tortell PD, Payne CD, Li Y, Trimborn S, Rost B, Smith WO, Riesselman C, Dunbar RB, Sedwick P, DiTullio GR (2008) CO_2 sensitivity of Southern Ocean phytoplankton. Geophys Res Lett 35:L04605

Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philos Trans R Soc Lond B Biol Sci 362:2351-2365

Vokhshoori NL, Larsen T, McCarthy MD (2014) Reconstructing $\delta^{13}C$ isoscapes of phytoplankton production in a coastal upwelling system with amino acid isotope values of littoral mussels. Mar Ecol Prog Ser 504:59-72

Vokhshoori NL, McCarthy MD (2014) Compound-specific $\delta^{15}N$ amino acid measurements in littoral mussels in the California upwelling ecosystem: a new approach to generating baseline $\delta^{15}N$ isoscapes for coastal ecosystems. PLOS ONE 9:e98087

Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) 15N and 13C abundances in the Antartic Ocean with emphasis on the biogeochemical structure of the food web. Deep Sea Res I 34:829-841

West JB, Bowen GJ, Dawson TE, Tu KP (2010) Isoscapes. Springer, Netherlands

Zingone A, Phlips EJ, Harrison PJ (2010) Multiscale variability of twenty-two coastal phytoplankton time series: a global scale comparison. Estuar Coasts 33:224-229

FIGURES

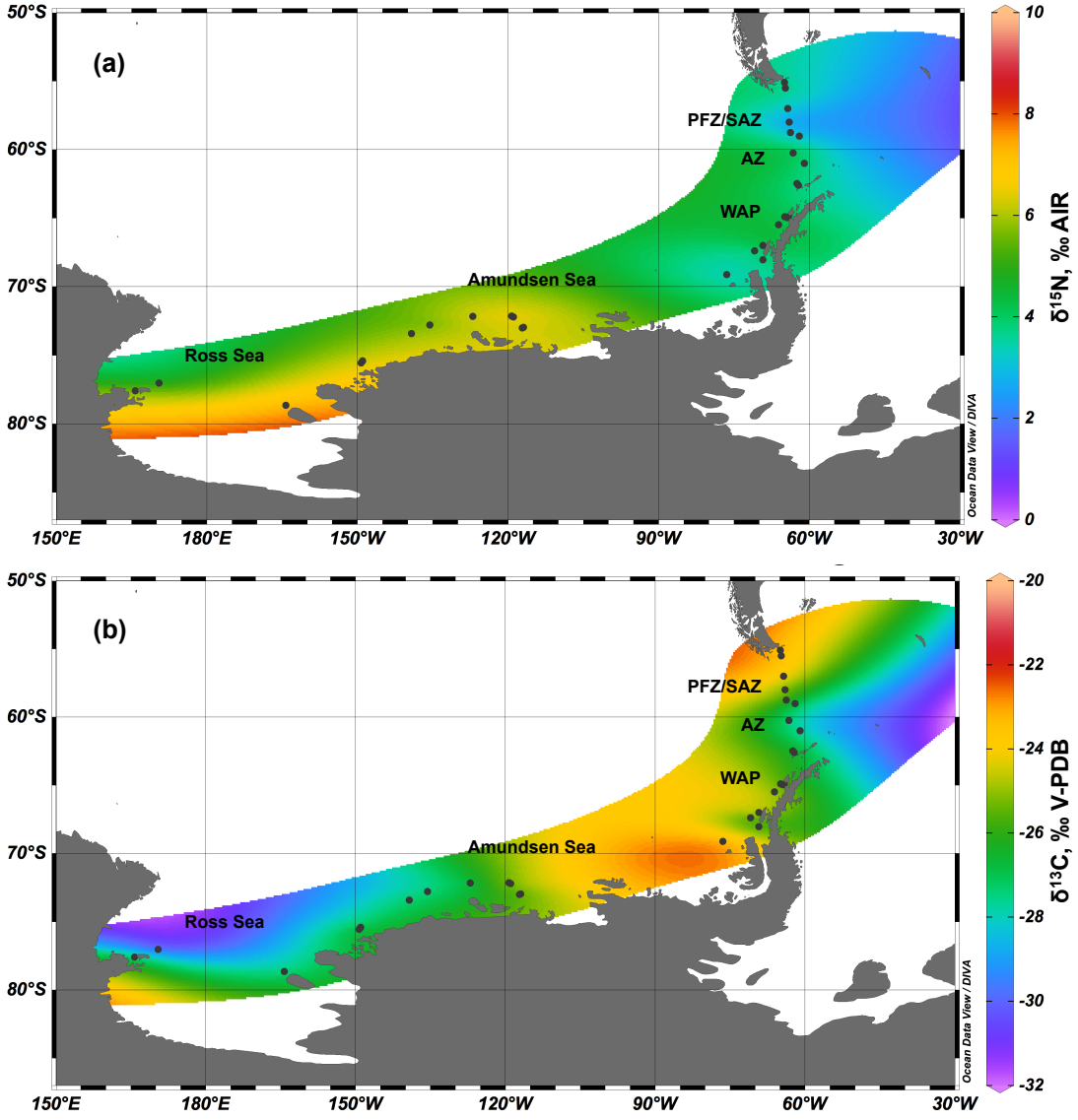

Figure 1.1. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of all zooplankton taxa from West Antarctica. $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data for all zooplankton from all sampling periods. PFZ/SAZ, AZ, and WAP abbreviate Polar Front Zone/Subantarctic Zone, Antarctic Zone, and West Antarctic Peninsula, respectively. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015) using Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010).

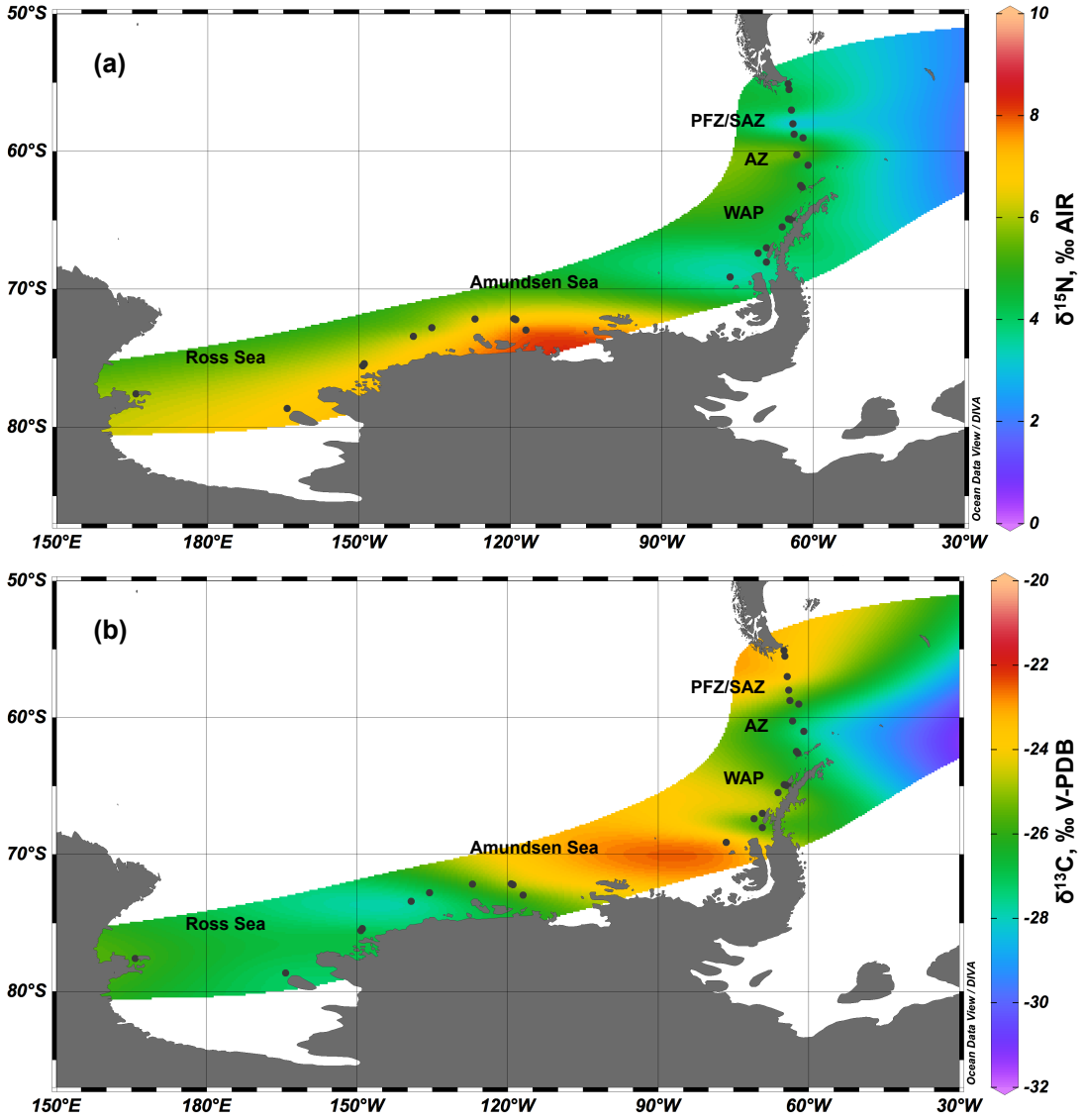

Figure 1.2. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of all euphausiids from West Antarctica. Euphausiid $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data from all sampling periods. PFZ/SAZ, AZ, and WAP abbreviate Polar Front Zone/Subantarctic Zone, Antarctic Zone, and West Antarctic Peninsula, respectively. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015) using Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010).

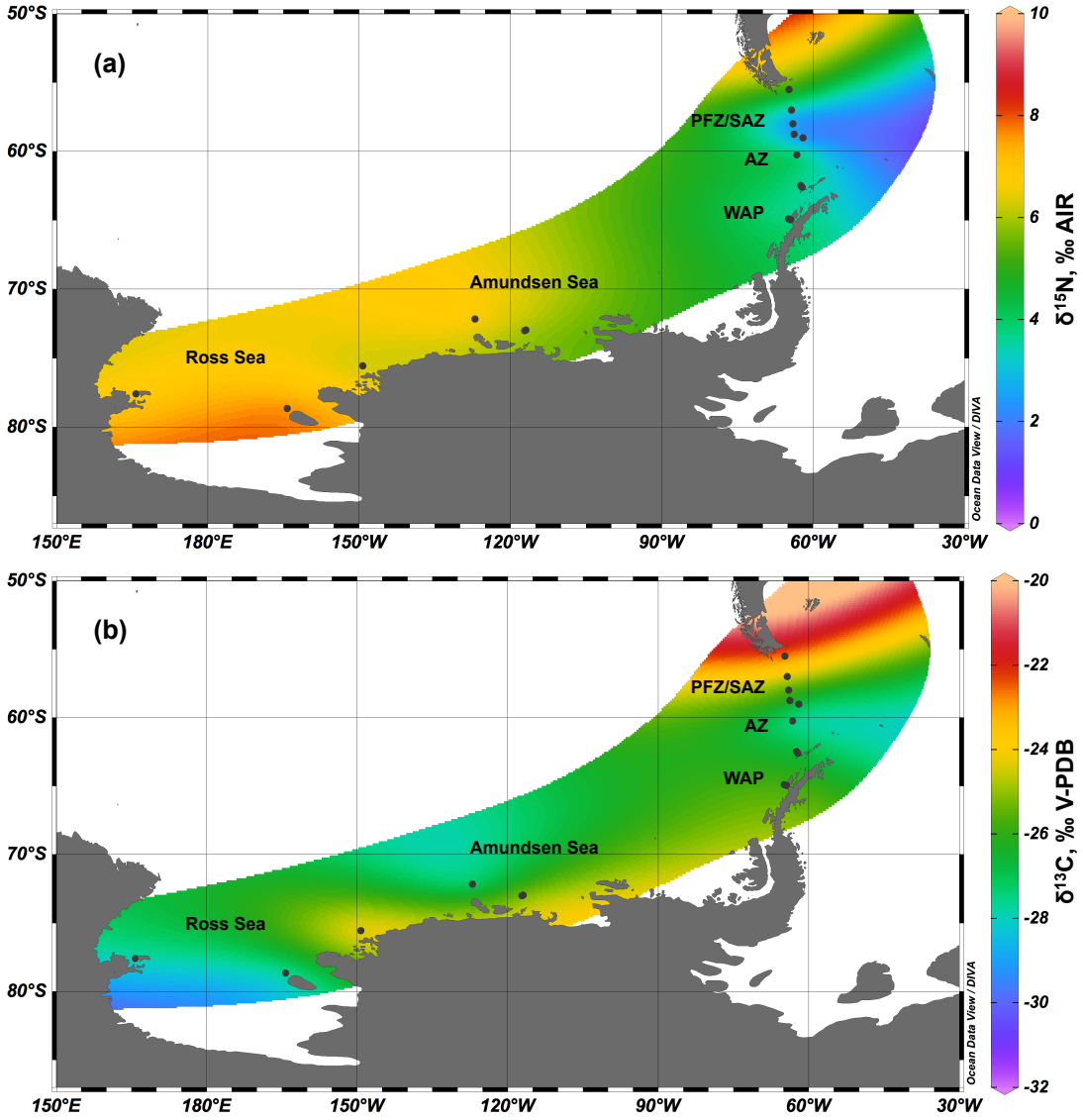

Figure 1.3. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of all amphipods from West Antarctica. Amphipod $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data from all sampling periods. PFZ/SAZ, AZ, and WAP abbreviate Polar Front Zone/Subantarctic Zone, Antarctic Zone, and West Antarctic Peninsula, respectively. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015) using Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010).

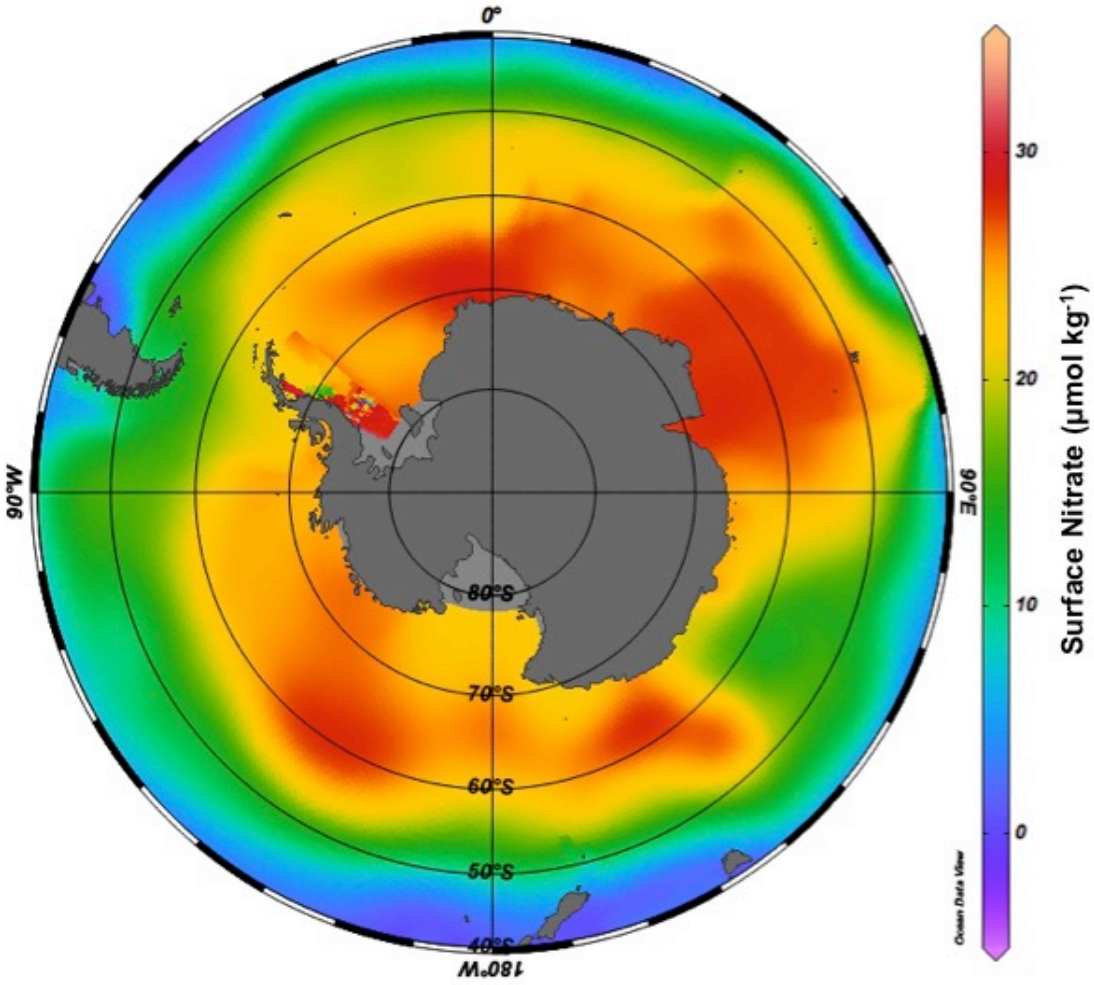

Figure 1.4. Surface nitrate (µmol kg^{-1}) in the Southern Ocean. Plot produced in Ocean Data View 4.7.4 using a dataset from Gouretski and Koltermann (2004).

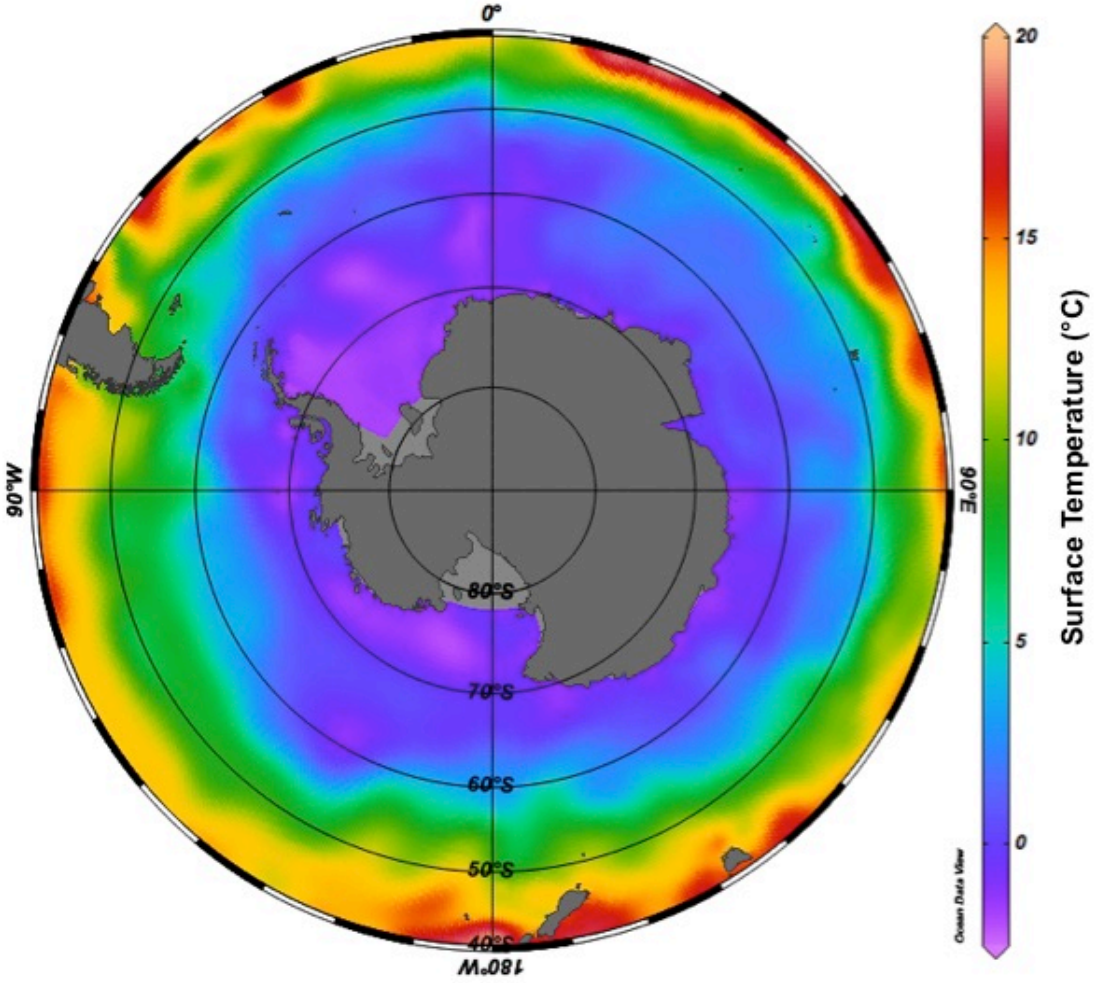

Figure 1.5. Surface temperature (°C) in the Southern Ocean. Plot produced in Ocean Data View 4.7.4 using a dataset from Gouretski and Koltermann (2004).

TABLES

Table 1.1. Isotopic data for all zooplankton. If multiple taxa were collected at a given site, then the mean ± standard deviation is reported for all zooplankton. Samples labeled OSO1011, OSO0708, LMG15, PAL-0708, and PAL-1011 were collected from the *RV Oden* summer 2010/11 cruise, *RV Oden* summer 2007/08 cruise, *SV L.M. Gould* April 2015 cruise, summer 2007/08 Palmer Station season, and summer 2010/11 Palmer Station season, respectively. *E*. is *Euphausia*. The C:N (atomic) ratios are reported for lipid-extracted material. The C:N ratios are atom:atom.

Sample ID	Latitude (DD)	Longitude (DD)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N	Taxa	Source
1 OSO1011	-72.99	-117.19	-25.8±2.5 -26.1 -23.1 -28.2	5.3±0.9 6.3 4.6 5.2	 4.1 7.0 5.7	All Zooplankton Copepod Gammarid amphipod Hyperiid amphipod	This Study
2 OSO1011	-72.96	-116.97	-25.2±1.6 -26.2 -22.8 -26.0 -25.6	7.2±1.9 6.9 4.7 9.2 8.3	 4.0 7.3 4.4 4.1	All Zooplankton Copepod Gammarid amphipod Hyperiid amphipod Euphausiid (larval)	This Study
3-1 OSO1011	-72.19	-118.96	-25.1±0.6 -25.6 -24.7	6.3±0.1 6.2 6.4	 3.9 4.3	All Zooplankton Copepod Euphausiid (larval)	This Study
3-2 OSO1011	-72.14	-119.32	-24.9±0.6 -25.4 -24.5	6.7±0.9 6.1 7.3	 3.8 4.2	All Zooplankton Copepod Euphausiid (larval)	This Study
4 OSO1011	-72.16	-127.08	-27.03±1.0 -27.4 -27.8 -25.9	6.3±0.8 5.4 6.9 6.6	 4.3 5.3 –	All Zooplankton Copepod Hyperiid amphipod Euphausiid (larval)	This Study
5 OSO1011	-72.78	-135.59	-27.5±2.0 -28.6 -28.6	5.5±0.2 5.4 5.8	 4.0 4.2	All Zooplankton Copepod Euphausiid (larval)	This Study

			-25.2	5.4	4.1	Euphausiid (adult)	
6 OSO1011	-73.40	-139.28	-27.2±1.5 -28.2 -27.9 -25.4	6.0±0.5 5.4 6.3 6.2	 4.3 4.8 3.8	All Zooplankton Copepod Euphausiid (larval) *Salpa thomsoni*	This Study
7 OSO1011	-75.40	-149.00	-27.4±0.6 -27.8 -26.9	6.1±0.0 6.1 6.1	 3.7 4.2	All Zooplankton Copepod Euphausiid (juvenile)	This Study
8 OSO1011	-75.42	-149.00	-27.1±0.3 -27.4 -26.9 -26.9	6.5±0.6 6.3 7.2 6	 4.4 4.2 4.3	All Zooplankton Copepod Euphausiid (larval) Euphausiid (juvenile)	This Study
9 OSO1011	-75.43	-149.01	-28.1±0.5 -27.8 -28.5	6.2±0.8 5.7 6.8	 4.1 4.6	All Zooplankton Copepod Euphausiid (larval)	This Study
RMD OSO0708	-77.02	170.46	-30.5	4.7	8.4	*Clione limacina*	This Study
10 OSO1011	-75.54	-149.30	-25.3±2.5 -26.8 -21.1 -26.5 -27.2 -24.7	6.5±1.3 6.7 4.8 7.6 5.7 7.8	 4.1 8.3 4.7 4.2 4.5	All Zooplankton Copepod Gammarid amphipod Hyperiid amphipod Euphausiid (juvenile) Euphausiid (adult)	This Study
12 OSO1011	-78.64	-164.3	-27.5±0.4 -27.7 -27.9 -27.9 -27.4 -27.0 -26.8	7.3±0.6 7.6 7.9 7.6 7.4 6.2 7.7	 4.3 5.6 4.5 4.2 4.1 4.8	All Zooplankton Copepod Gammarid amphipod Hyperiid amphipod Euphausiid (larval) Euphausiid (juvenile) *Clione limacina*	This Study

			-27.8	6.6	6.8	*Limacina helicina*	
13 OSO1011	-77.59	165.71	-26.6±1.1 -26.8 -28.1 -27.5 -26.1 -25.4 -25.3 -26.9	5.8±1.1 6.1 6.6 7.2 6.5 5.4 4.9 4.2	 4.0 8.5 6.3 4.1 4.1 4.3 6.3	All Zooplankton Copepod Gammarid amphipod Hyperiid amphipod Euphausiid (larval) Euphausiid (juvenile) *Clione limacina* *Limacina helicina*	This Study
7 LMG15	-61.00	-61.00	-27.8±0.2 -27.7 -27.9	3.7±0.2 3.8 3.6	 4.3 5.3	All Zooplankton *Euphausia superba* *Salpa thomsoni*	This Study
11 LMG15	-64.88	-64.90	-25.2±1.7 -26.1 -23.1 -27.2 -25.8 -23.7	4.4±1.7 4.0 5.6 6.4 1.9 4.2	 4.2 4.1 4.7 4.5 4.4	All Zooplankton *E. superba* *E. crystallorophias* *Thysanoessa macrura* *Themisto gaudichaudii* *Spongiobrachia australis*	This Study
12 LMG15	-64.95	-64.43	-25.3±1.5 -26.7 -25.7 -25.6 -23.1	5.1±1.0 4.0 6.0 5.7 4.5	 4.3 4.3 4.4 5.2	All Zooplankton *E. superba* *Thysanoessa macrura* *Themisto gaudichaudii* *Salpa thomsoni*	This Study
13 LMG15	-62.60	-62.02	-26.6±0.6 -26.6 -27.1 -26.6 -27.2 -25.7	3.7±0.9 3.5 5.1 3.4 3.8 2.5	 3.9 4.6 4.6 4.7 4.9	All Zooplankton *E. superba* *Thysanoessa macrura* *Vibilia antarctica* *Themisto gaudichaudii* *Salpa thomsoni*	This Study

14 LMG15	-62.47	-62.47	-26.1±0.8 -26.0 -27.1 -26.3 -26.4 -25.0	4.0±1.2 5.0 5.3 3.6 3.6 2.5	 4.1 4.5 4.7 4.4 4.8	All Zooplankton *E. frigida* *Thysanoessa macrura* *Vibilia antarctica* *Themisto gaudichaudii* *Salpa thomsoni*	This Study
15 LMG15	-60.23	-63.27	-27.5±0.8 -26.8 -28.5 -27.1 -27.5	4.5±2.2 6.2 2.5 6.6 2.7	 4.2 4.6 4.5 5.4	All Zooplankton *Thysanoessa macrura* *Vibilia antarctica* *Themisto gaudichaudii* *Salpa thomsoni*	This Study
16 LMG15	-59.00	-62.00	-27.7±1.5 -26.5 -26.6 -28.3 -27.1 -29.9	2.8±1.7 4.0 5.1 2.6 0.9 1.6	 4.1 4.1 5.1 4.5 5.7	All Zooplankton *E. frigida* *E. triacantha* *Vibilia antarctica* *Themisto gaudichaudii* *Salpa thomsoni*	This Study
17 LMG15	-58.75	-63.78	-24.8±0.2 -24.5 -25.0 -24.7	3.3±0.8 4.0 3.4 2.5	 3.9 4.8 4.3	All Zooplankton *E. triacantha* *Vibilia antarctica* *Themisto gaudichaudii*	This Study
18 LMG15	-58.00	-64.00	-25.4±2.0 -25.2 -28.8 -24.4 -25.0 -23.6	2.3±0.7 2.1 1.8 1.6 2.9 3.2	 4 5.3 4.4 4.4 4.5	All Zooplankton *E. triacantha* *Vibilia antarctica* *Primno macropa* *Themisto gaudichaudii* *Spongiobrachia australis*	This Study
19 LMG15	-57.00	-64.33	-23.9±0.4 -23.4 -24.4	3.3±1.1 4.6 2.4	 4.1 4.4	All Zooplankton *E. triacantha* *Primno macropa*	This Study

			-24.0 -23.8	3.9 2.4	4.5 4.4	*Themisto gaudichaudii* *Spongiobrachia australis*	
20 LMG15	-64.00	-64.80	-23.2±0.7 -23.7 -22.5 -23.5	4.0±1.6 4.4 5.4 2.3	 4.1 4.3 4.3	All Zooplankton *E. triacantha* *Themisto gaudichaudii* *Spongiobrachia australis*	This Study
21 LMG15	-55.1	-64.95	-23.5±0.0 -23.5 -23.5	3.3±0.8 3.9 2.8	 4.1 4.2	All Zooplankton *E. triacantha* *Spongiobrachia australis*	This Study
281.043 PAL-0708	-66.99	-69.28	-23.6±1.2 -22.6 -22.8 -23.9 -25.2	4.8±0.5 5.0 5.1 5.1 4.0	 3.9 4.0 4.1 4.0	All Zooplankton *E. superba* (gravid) *E. superba* (mature females) *E. superba* (adults) *E. superba* (juveniles)	Brault (2012)
610.035 PAL-0708	-64.9	-64.18	-26.9	3.5	4.2	*E. superba* (adults)	Brault (2012)
200-040 PAL-0708	-68.03	-69.28	-26.0	4.1	4.0	*E. superba* (adults)	Brault (2012)
605.035 PAL-0708	-64.93	-64.25	-27.4±0.2 -27.3 -27.6	3.5±0.0 3.5 3.5	 4.2 3.9	All Zooplankton *E. superba* (adults) *E. superba* (juveniles)	Brault (2012)
-100.06 PAL-1011	-69.10	-76.45	-22.7	3.3	4.2	*E. superba* (gravid)	Brault (2012)
600.04 PAL-1011	-64.93	-64.40	-22.7	4.4	4.2	*E. superba* (juveniles)	Brault (2012)
500.06 PAL-1011	-65.48	-66.15	-24.9	4.3	4.0	*E. superba* (adults)	Brault (2012)
200.06 PAL-0708	-67.38	-70.91	-26.5	3.2	4.2	*E. superba* (adults)	Brault (2012)

SUPPLEMENTAL MATERIAL

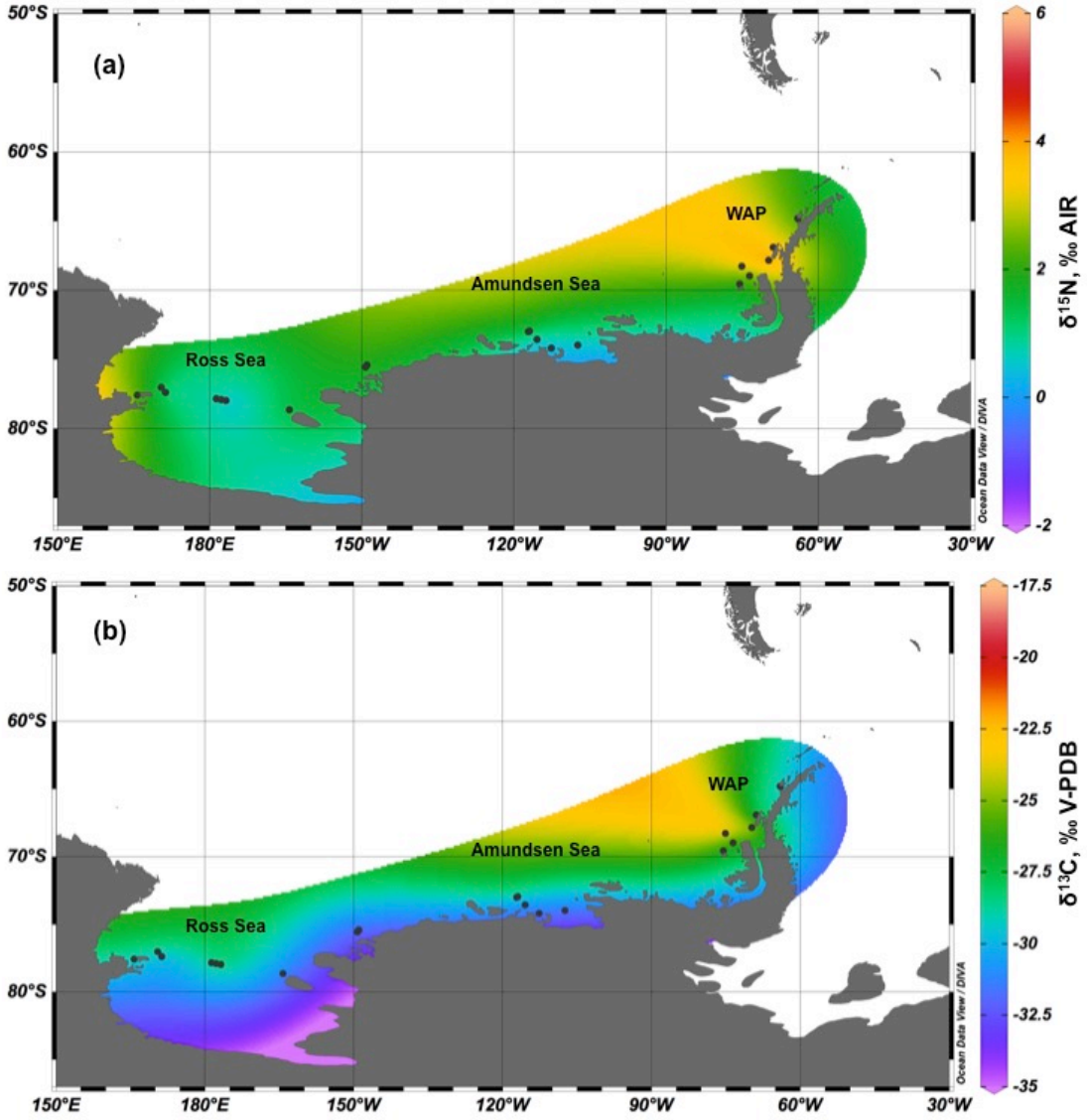

Figure 1.S1. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of phytoplankton from West Antarctica. Phytoplankton $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data from all sampling periods. WAP abbreviates West Antarctic Peninsula. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015) using Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010).

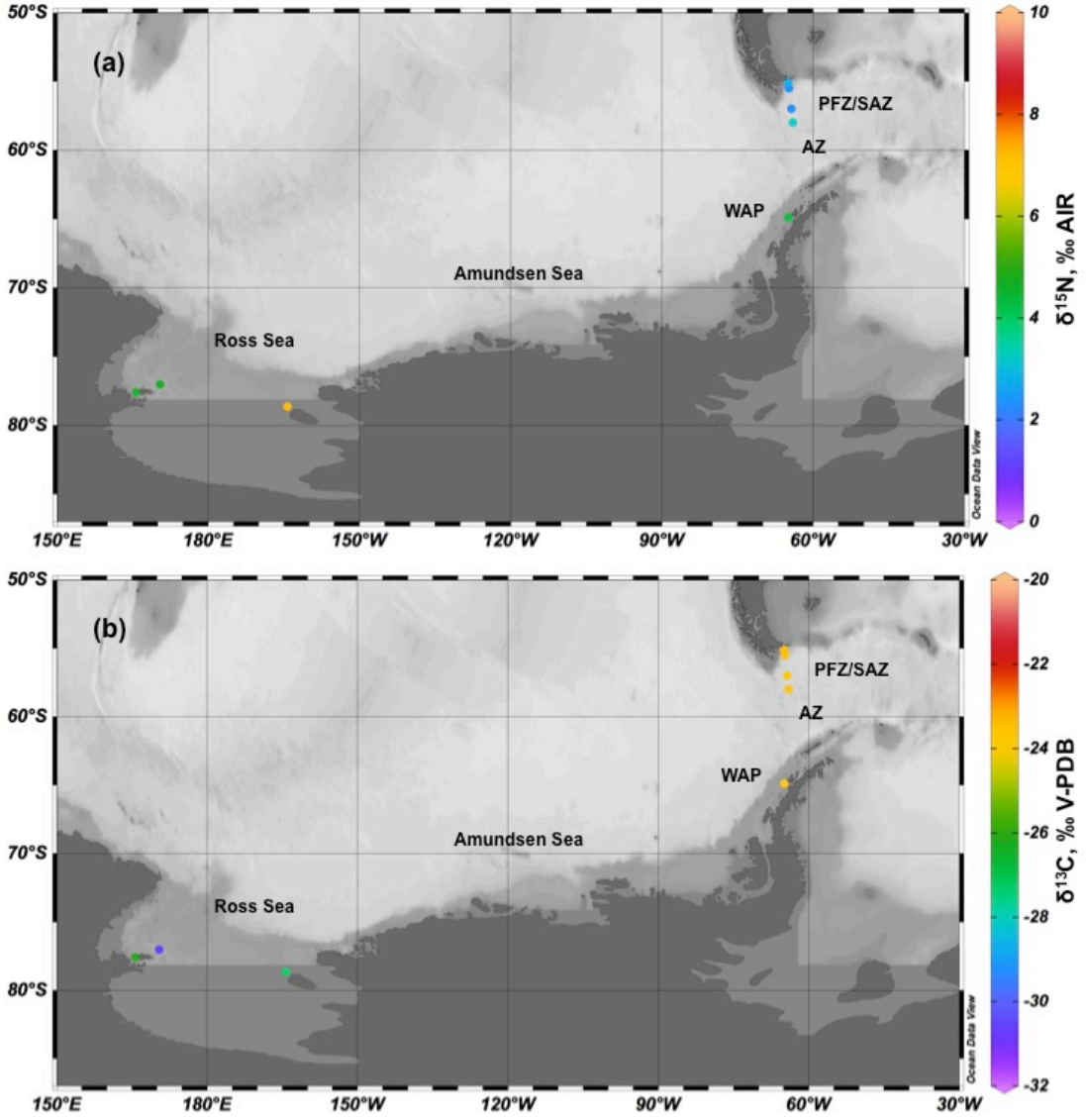

Figure 1.S2. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of pteropods from West Antarctica. Pteropod $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data from all sampling periods. PFZ/SAZ, AZ, and WAP abbreviate Polar Front Zone/Subantarctic Zone, Antarctic Zone, and West Antarctic Peninsula, respectively. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015).

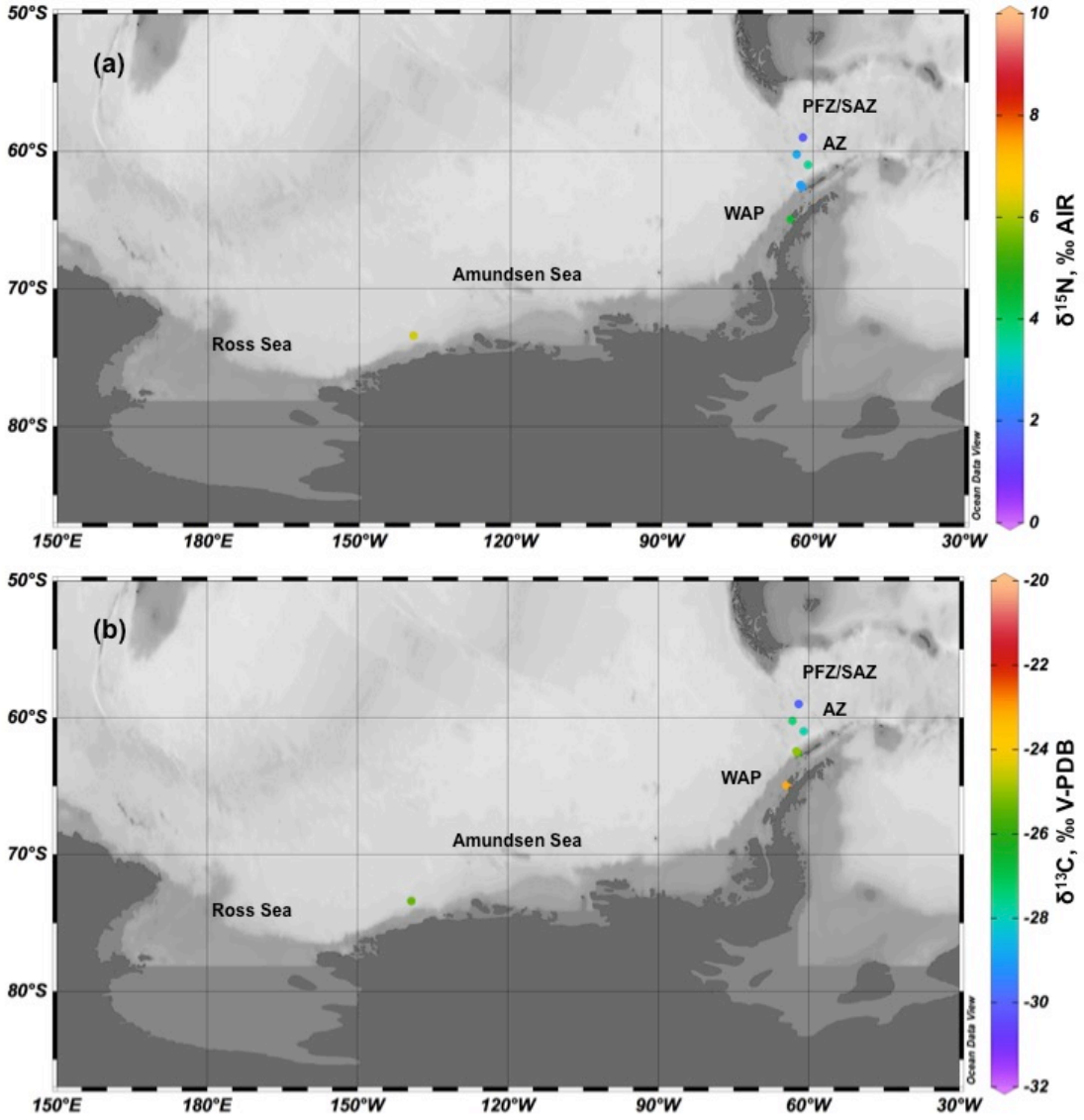

Figure 1.S3. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of salps from West Antarctica. Salp $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data from all sampling periods. PFZ/SAZ, AZ, and WAP abbreviate Polar Front Zone/Subantarctic Zone, Antarctic Zone, and West Antarctic Peninsula, respectively. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015).

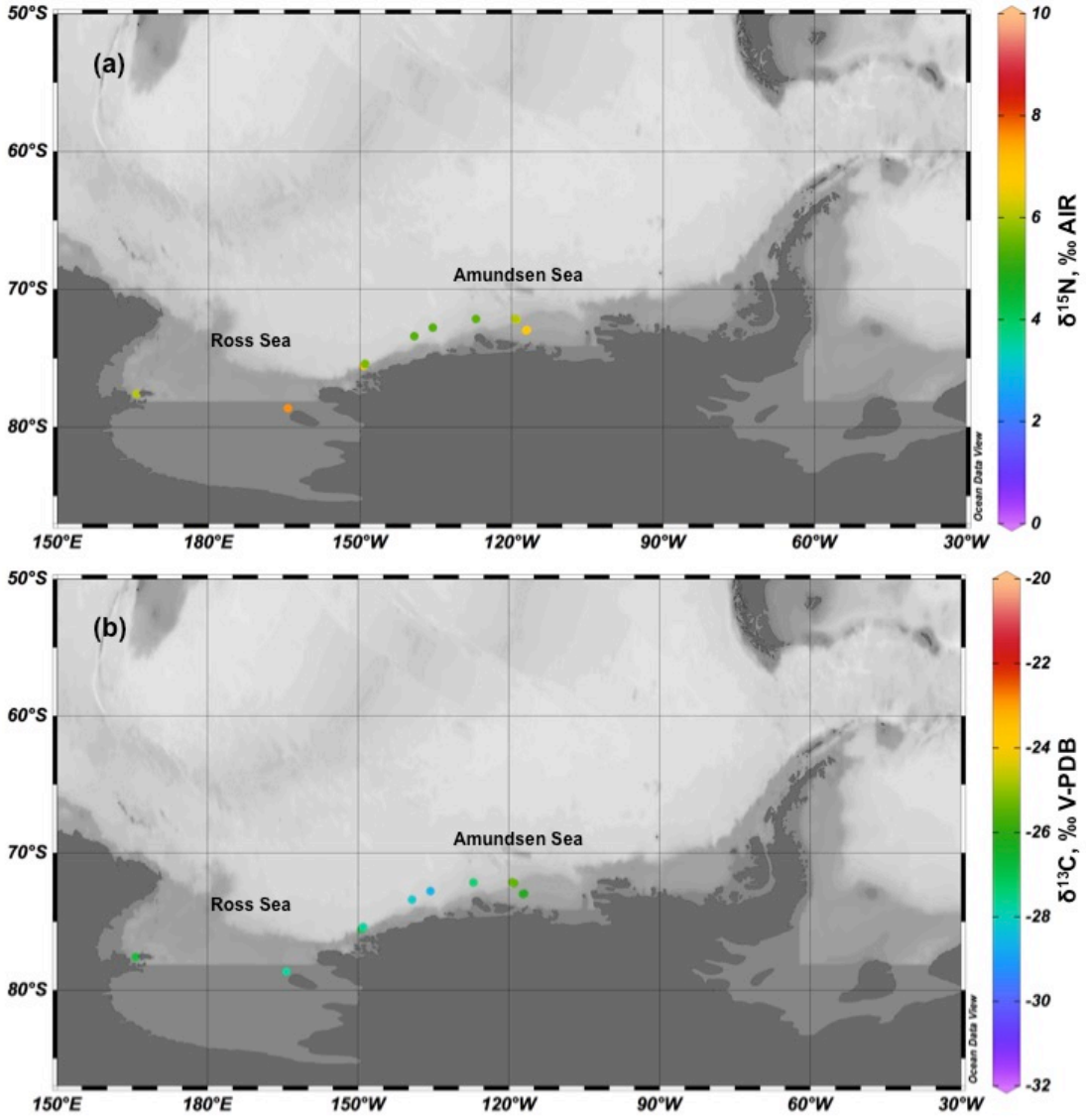

Figure 1.S4. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of copepods from West Antarctica. Copepod $\delta^{15}N$ and $\delta^{13}C$ isoscapes include data from all sampling periods. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015).

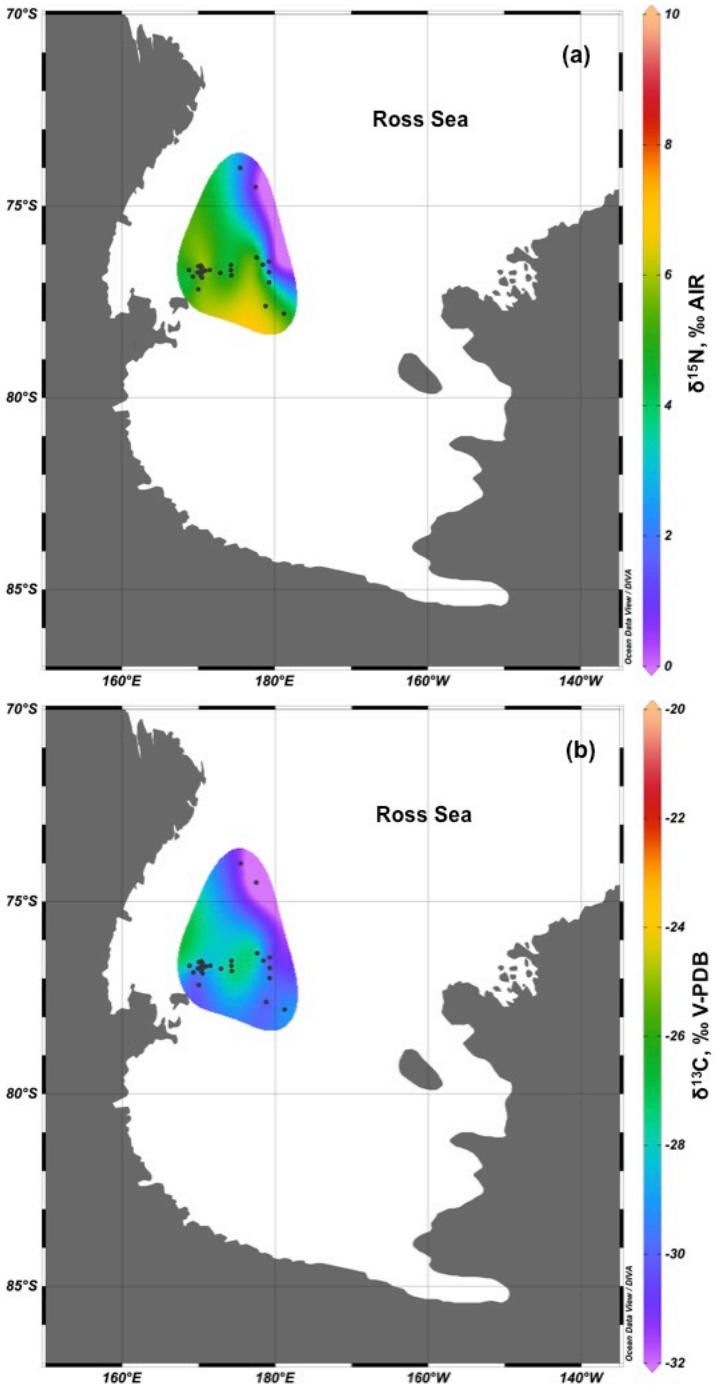

Figure 1.S5. $\delta^{15}N$ (a) and $\delta^{13}C$ (b) values of Ross Sea mixed, formalin-exposed plankton (0-200 µm). Mean ± standard deviation (sample size) for $\delta^{15}N$ and $\delta^{13}C$ are 4.7 ± 1.8 (27) and -29.0 ± 1.6 (27), respectively. Isoscapes were produced in ODV 4.7.4 (Schlitzer 2015) using Data Interpolating Variational Analysis (DIVA) gridding software (Barth et al. 2010).

Table 1.S1. Isotopic values of formalin-exposed plankton (0-200 µm) from the Ross Sea. $\delta^{13}C$ and $\delta^{15}N$ values of all plankton measured.

Sample ID	Latitude (DD)	Longitude (DD)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C:N (Atomic)
Phyt_38	-76.72	179.26	-30.8	0.5	6.6
Phyt_92	-74.50	177.50	-33.2	0.2	7.1
Phyt_19	-76.74	172.88	-28.1	4.6	6.2
Phyt_26	-76.80	174.30	-27.0	4.9	5.9
Phyt_105	-76.57	170.00	-27.8	5.3	6.6
Phyt_42	-76.34	177.62	-27.1	5.6	4.9
Phyt_10	-76.73	170.48	-28.0	5.5	7.6
Phyt_110	-77.17	170.00	-29.9	6.2	6.4
Phyt_113	-76.84	169.30	-30.8	2.8	6.7
Phyt_12	-76.73	169.89	-29.9	6.0	6.6
Phyt_14	-76.73	170.06	-28.1	6.2	6.1
Phyt_15	-76.86	170.47	-28.2	4.4	6.3
Phyt_18	-76.60	170.48	-28.4	5.9	6.9
Phyt_22	-76.53	174.25	-28.4	4.2	5.7
Phyt_27	-76.81	170.33	-31.0	6.3	7.6
Phyt_29	-76.68	170.33	-27.0	5.6	6.0
Phyt_31	-76.55	170.33	-29.5	6.3	6.6
Phyt_35	-76.68	170.91	-29.3	6.3	7.9
Phyt_40	-76.53	178.43	-29.2	5.4	6.2
Phyt_44	-76.45	179.25	-30.3	0.8	7.8
Phyt_48	-76.98	179.25	-29.0	5.2	6.0
Phyt_56	-77.80	-178.80	-29.0	5.2	5.8
Phyt_65	-77.61	178.80	-30.3	5.8	6.7
Phyt_7	-76.67	168.78	-26.9	5.3	5.7
Phyt_8	-76.67	171.50	-28.2	5.5	5.9
Phyt_89	-74.00	175.49	-31.4	2.5	6.6
Phyt_9	-76.67	174.25	-27.6	4.4	5.6

Table 1.S2. Isotopic values of phytoplankton. $\delta^{13}C$ and $\delta^{15}N$ values of all phytoplankton sampled during various field seasons for three Antarctic regions (WAP, Amundsen Sea, and Ross Sea). Isotopic data are reported as mean ± standard deviation (sample size).

Region	$\delta^{13}C$ (‰)			$\delta^{15}N$ (‰)		
	2007/08	**2009/10**	**2010/11**	**2007/08**	**2009/10**	**2010/11**
WAP	–	-30.2 ± 3.3 (3)	-25.0 ± 5.7 (5)	–	1.8 ± 0.8 (3)	3.4 ± 1.8 (5)
Amundsen Sea	-31.5 ± 0.9 (4)	–	-28.2 ± 0.8 (2)	0.3 ± 0.6 (4)	–	1.9 ± 0.1 (2)
Ross Sea	-28.8 ± 3.3 (7)	–	-31.1 ± 1.8 (5)	0.9 ± 1.4 (7)	–	2.0 ± 0.6 (5)

COMPOUND-SPECIFIC ISOTOPE ANALYSIS REVEALS NEW INSIGHTS ON THE TROPHIC POSITION AND FORAGING ECOLOGY OF ROSS, WEDDELL, AND CRABEATER SEALS

ABSTRACT

Ross seals (*Ommatophoca rossii*) are one of the least studied marine mammals. Research to date using stable isotopes places this species at a trophic position, which provides insights on this animal's foraging ecology and role within their food web, less than that of the Weddell seal (*Leptonychotes weddellii*) and higher than that of the crabeater seal (*Lobodon carcinophaga*). The effects of baseline isotope variation have not been considered in devising the Ross seal trophic position, however, and at present, no study has used compound (amino acid) – specific isotope analysis (CSIA) to better understand the foraging of Ross, Weddell, and crabeater seals. Using this approach, we find that these seals use different habitats; Ross seals forage in a pelagic food web distinct from that of crabeater and Weddell seals. Crabeater and Weddell seals are foraging within similar food webs closer to shore, but crabeater seals are likely following sea ice, while Weddell seals target productive areas of the continental shelves within the western Antarctic. Our CSIA reveals a higher trophic position for Ross seals, equivalent to that of Weddell seals and in contrast to prior isotopic results on bulk tissues. Crabeater seals are at a trophic position lower than that of Ross and Weddell seals. Our results redefine the view of

the Ross seal trophic position based on stable isotopes and highlight the importance and power of understanding baseline isotope variations in foraging studies.

INTRODUCTION

The Ross seal (*Ommatophoca rossii*) is one of the least studied marine mammals. The total population estimate for this species is around 200,000, considerably less than the estimates for other true Antarctic seals, which are 10 to 15 million individuals for crabeater seals (*Lobodon carcinophaga*) and approximately one million individuals for Weddell seals (*Leptonychotes weddellii*) (Laws 1977, Reeves et al. 2008, Bengtson et al. 2011). With animals likely spending most of their time at sea and in habitats that are hard to access by researchers, the Ross seal is not commonly observed. Several keys aspects of their biology remain poorly understood, including their preferred prey and foraging habitat and behavior. In contrast, many studies have been conducted on crabeater and Weddell seals and, thus, more information is available on their ecologies.

Conventional techniques for studying an animal's diet, such as scat and stomach content analysis, have had limitations. Firstly, these methods capture only a snapshot of a predator's diet, perhaps one to two days (Dellinger and Trillmich 1988, Burns et al. 1998). Secondly, since soft tissues are more completely digested than hard tissues, traditional techniques tend to be biased towards prey with indigestible hard parts (Burns et al. 1998, Staniland 2002, Arim and Naya 2003, Yonezaki et al.

2003). Given the drawbacks of conventional methods, recent research on Antarctic seal ecology has used bulk isotope values.

Measurements of carbon isotopes ($\delta^{13}C$) and nitrogen isotopes ($\delta^{15}N$) in bulk material from animal tissues have been shown to indicate a predator's foraging region and trophic position. Isotopic measurements also integrate an animal's diet over a longer time (weeks to years depending on the tissue) than the traditional procedures. Carbon isotope values show little ^{13}C-enrichment with trophic level, which is unlike $\delta^{15}N$, discussed below. Yet, $\delta^{13}C$ data are useful in studying the foraging areas of a predator since $\delta^{13}C$ values of the base of marine food webs, phytoplankton, differ across regions as a result of several factors and this variation is incorporated in consumer tissues. Spatial changes in the $\delta^{13}C$ of phytoplankton reflect variations in dissolved inorganic carbon $\delta^{13}C$ values, dissolved CO_2 concentrations, temperature, cell size and geometry, internal biological parameters (e.g., growth rate), and CO_2 drawdown (reviewed in McMahon et al. 2013). Provided the primary processes driving fluctuations in $\delta^{13}C$ are known, bulk $\delta^{13}C$ values of an animal give valuable information on its foraging habitat.

The baseline values of $\delta^{13}C$ ($\delta^{13}C_{baseline}$) are understood to vary with space in the Southern Ocean. Several studies have observed decreasing $\delta^{13}C$ values with increasing latitude, a pattern that has been considered to result from variations in sea surface temperature (Rau et al. 1982, Graham et al. 2010, Quillfeldt et al. 2010, Chapter 1). The relationship between $\delta^{13}C$ values and sea surface temperatures exists because CO_2 is in higher concentrations in colder waters than warmer, more stratified

waters, resulting in a greater carbon fractionation during photosynthesis (Rau et al. 1982, Graham et al. 2010, Chapter 1). Therefore, $\delta^{13}C_{baseline}$ values generally decrease with increasing latitude with offsets between about 55 °S and 79 °S of approximately 3 ‰ (Rau et al. 1982, Graham et al. 2010, Chapter 1).

In constrast to $\delta^{13}C$, trophic transfers considerably affect an animal's $\delta^{15}N$ values. Since a consumer's tissues become enriched in ^{15}N by ~ 3-5 ‰ with each trophic step (primary producers to herbivores to carnivores) due to the preferential loss of ^{14}N during amino acid metabolism (Minagawa and Wada, 1984) its $\delta^{15}N$ value is indicative of the animal's trophic position. However, like phytoplankton $\delta^{13}C$ values, several variables affect the $\delta^{15}N$ values of phytoplankton, which are passed on, with the modifications from trophic transfers, to upper trophic level predators. Their nutrient source (i.e., nitrate, ammonium, or N_2), the biological transformations (e.g., N_2-fixation and denitrification) and nutrient pool size (or the extent of nitrogen pool drawdown) occurring in their environment, and isotopic fractionation during their assimilation of nitrogen all affect phytoplankton $\delta^{15}N$ values (reviewed in McMahon et al. 2013). If variations in these driving forces are understood, then the bulk $\delta^{15}N$ values of a consumer provide insights into its foraging region and trophic position (McMahon et al. 2013).

In the Southern Ocean, recent work has shown spatial variation in baseline $\delta^{15}N$ values ($\delta^{15}N_{baseline}$). Low $\delta^{15}N_{baseline}$ have been found for much of the Southern Ocean, except in areas near the continent where high $\delta^{15}N_{baseline}$ have been measured (DiFiore et al. 2006, DiFiore et al. 2009, Somes et al. 2010, Jaeger et al. 2010,

Chapter 1). This spatial pattern likely follows changes in the extent of nutrient drawdown from primary productivity, which is the main process influencing $\delta^{15}N_{baseline}$ in the Southern Ocean as it is a high nutrient-low chlorophyll (HNLC) region (DiFiore et al. 2006, DiFiore et al. 2009, Graham et al. 2010). This area is an extensive HNLC site since its low iron concentrations and light availability limit primary productivity, resulting in a large residual pool of NO_3^- (de Baar et al. 1990, Martin et al. 1990, Altabet and Francois 2001). With a substantial NO_3^- reservoir, uptake of NO_3^- in the Southern Ocean is typically incomplete, resulting in phytoplankton – which selectively assimilate the lighter isotope (^{14}N) – having low $\delta^{15}N$ values (Graham et al. 2010, McMahon et al. 2013, Chapter 1). Yet, in areas of more complete NO_3^- drawdown, like polynyas along the Antarctic coasts, the $\delta^{15}N_{baseline}$ will increase, eventually approaching that of the source ^{15}N-enriched NO_3^- pool (Graham et al. 2010, McMahon et al. 2013). Thus, spatial variation in the extent of nitrogen drawdown has created a pelagic-to-coastal gradient in Antarctic waters with a higher $\delta^{15}N_{baseline}$ in coastal than pelagic waters by up to ~ 3 ‰ (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1).

Isotopic measurements, as well as the results of traditional methods, have indicated that Weddell seals forage near the top of the Antarctic food web, consuming diverse diets of fish, cephalopods, and invertebrates (Laws 1977, Clarke and MacLeod 1982, Plötz 1991, Casaux et al. 1997, Burns et al. 1998, Plötz 2001, Lake et al. 2003, Lake et al. 2006, Zhao et al. 2004, Casaux et al. 2006, Casaux et al. 2009, Aubail et al. 2011). Researchers have debated the contribution of the upper trophic

level prey species, Antarctic toothfish (*Dissotichus mawsoni*), to the Weddell seal diet with some studies suggesting a substantial contribution of *D. mawsoni* (Fuiman et al. 2002, Burns et al. 1998, Davis et al. 1999, Ponganis and Stockard 2007, Ainley and Siniff 2009, Kim et al. 2011, Goetz et al. 2017). Hard parts of *D. mawsoni* are not consumed and, thus, not detected via scat and stomach content analyses, which have been used for much of the prior research on Weddell seals. Recently, Goetz et al. (2017) have assessed Weddell seal foraging ecology with bulk $\delta^{13}C$ and $\delta^{15}N$ measurements of vibrissae and red blood cells from Ross Sea specimens. They report considerable individual variability in diet and that Antarctic silverfish (*Pleuragamma antarcticum*) and cod icefishes (*Trematomus* species) have been the primary prey consumed by Weddell seals. Overall, *D. mawsoni* contribute less than 2 % to the Weddell seal diet although this prey may be increasingly important with age and at certain times in the life cycle, such as during reproduction and molting, since this fish has a high fat content and energy density (Goetz et al. 2017). Additionally, Goetz et al. (2017) note temporal diet shifts – likely in response to sea ice dynamics affecting prey abundances.

Crabeater seals occur at a much lower trophic level than Weddell seals, with diets dominated by Antarctic krill (*Euphausiia superba*), as evidenced by the results of both conventional techniques (e.g., scat and stomach content analysis) and isotopic analyses (Laws 1977, Rau et al. 1992, Burns et al. 2004, Zhao et al. 2004, Burns et al. 2008, Aubail et al. 2011). Recent work by Hückstädt et al. (2012a) has revealed temporal variability in crabeater seal diet composition via bulk $\delta^{13}C$ and $\delta^{15}N$

measurements of vibrissae, with the *E. superba* contribution ranging from 81.2 % to 94.8 %, likely in response to climate conditions affecting krill abundances. The authors also report significant variation in $\delta^{13}C$ values with body mass (increasing $\delta^{13}C$ values with increasing body mass) and season (highest $\delta^{13}C$ values in the austral winter), which they suggest might result from changes in baseline $\delta^{13}C$ values associated with temporal and/or spatial shifts between a predominately pelagic or sea ice phytoplankton community (Hückstädt et al. 2012a).

A relatively small number of studies have provided information on Ross seal foraging ecology. Dive records suggest that these animals undergo dives – typically 100 to 300 m, but with a maximum depth of 792 m recorded – in search of mesopelagic squid and fish (Bengtson and Stewart 1997, Blix and Nordøy 2007). Analysis of Ross seal stomach contents has found Antarctic silverfish (*Pleurogramma antarcticum*) and glacial squid (*Psychroteuthis glacialis*) in varying proportions (Skinner and Klages, 1994). Arcalís-Planas et al. (2015) show little use of sea ice by Ross seals via telemetry and remote sensing data; these seals have remained in pelagic regions except for haul outs on ice to molt (from December to January) and breed (from late October to mid-November). During their expansive pelagic period (February to mid October), Ross seals have been on average 838 km (a range of 587 to 1,282 km) seaward from the ice edge (Arcalís-Planas et al. 2015). Bulk $\delta^{13}C$ and $\delta^{15}N$ isotope measurements place the Ross seal at a lower trophic position than the Weddell seal and higher position than the crabeater seals (Rau et al. 1992, Zhao et al. 2004, Aubail et al. 2011). Thus, the present bulk isotope results suggest that Ross

seals consume mostly squid and fish, but also lower trophic level prey, like *E. superba*, to a smaller extent (Rau et al. 1992, Zhao et al. 2004, Aubail et al. 2011).

However, the results of past research on the trophic positions and foraging regions of Antarctic seals using bulk $\delta^{13}C$ and $\delta^{15}N$ values must be further considered since research has only recently established $\delta^{13}C_{baseline}$ and $\delta^{15}N_{baseline}$ for the Southern Ocean (DiFiore et al. 2006, DiFiore et al. 2006, Jaeger et al. 2010, Somes et al. 2010, Chapter 1). Given the observed spatial gradients in both $\delta^{13}C_{baseline}$ and $\delta^{15}N_{baseline}$ in the Antarctic, interpretations of patterns in the bulk isotope values of seals may be inaccurate if the isotopic baselines are wrongly assumed to be constant throughout the study site (Graham et al. 2010, McMahon et al. 2013). As mentioned above, Ross seals may spend more time in pelagic regions than other true Antarctic seals (Arcalís-Planas et al. 2015). Since these areas appear to have lower $\delta^{15}N_{baseline}$ than nearshore places in summer (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1), the bulk $\delta^{15}N$ values of Ross seals may be lower than those of pinnipeds moving predominately within Antarctic continental waters at least partly due to a baseline isotope shift. If this scenario were the case, then a lack of accounting for spatial variation in $\delta^{15}N_{baseline}$ would result in an interpretation of Ross seals being at a lower trophic position, which indicates an animal's foraging ecology and role in a food web, than the species mostly moving near the continent. Thus, consideration of baseline isotope variability is critical for studies of the ecologies of Antarctic predators.

Compound-specific isotopic analysis (CSIA) with amino acids allows discrimination of baseline versus trophic position effects on the isotopic composition

of consumers. Since only certain amino acids become enriched in ^{15}N with increasing trophic level ("trophic" amino acids), while others ("source" amino acids) do not, variations in baseline isotope values and trophic position on consumer $\delta^{15}N$ values can be disentangled (Popp et al. 2007, Chikaraishi et al. 2009, Sherwood et al. 2011). Glutamic acid/glutamine (Glu) and phenylalanine (Phe) have been considered the most representative trophic and source amino acids, respectively (McClelland and Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). Proline (Pro) has also been shown to be a reliable trophic amino acid and may provide more accurate trophic position calculations for upper trophic level organisms (McMahon et al., data unpublished) since the ^{15}N-enrichment factors for the trophic steps are less variable than those for Glu.

We perform the first CSIA of modern Ross, Weddell, and crabeater seals to provide a clearer view of the trophic positions of these species than what has been done with only bulk isotope measurements, as well as to gain information on their foraging regions. Using CSIA to account for potential baseline isotope differences is critical in light of recent research suggesting considerable variability in baseline isotope values in Antarctic waters (DiFiore et al. 2009, Chapter 1). Comparison of amino acid isotope data across these three Antarctic seals will also further our understanding of present Antarctic food web structures, which is especially valuable given ongoing climate change (Atkinson et al. 2004, Ducklow et al. 2007, 2012, Montes-Hugo et al. 2009).

MATERIALS AND METHODS

Sample collection

Tissue samples from Ross, Weddell, and crabeater seals were collected along western Antarctica from the West Antarctic Peninsula (WAP) to the Ross Sea during multiple field seasons and, in most cases, body mass, age class (juvenile, subadult, and adult), gender, and location were recorded for each sampled seal (Tables 2.S1). Ross (n = 15), Weddell (n = 38), and crabeater (n = 41) seals were sampled during the austral summers of 2008/09 and 2010/11 on *RV Oden* cruises along the western Antarctic coast. Mostly whole blood samples were obtained. In some cases, clot (blood with serum removed), red blood cells (RBCs, whole blood exposed to an anticoagulant, heparin, before having plasma removed), and hair samples were also taken. The sampling protocol is described in Aubail et al. (2011); all animal captures were conducted in accordance with the regulations of the Swedish Polar Research Secretariat (Registration No. 2010-112).

All other samples were obtained from animal captures conducted under National Marine Fisheries Service permit No. 87-1851-00. Additionally, the Institutional Animal Care and Use Committee (IACUC) at the University of Santa Cruz (UC Santa Cruz) approved all protocols for the following samples. Whiskers were taken from crabeater seals during multiple cruises on the *RV Lawrence M. Gould* along the WAP. Sample sizes for whisker collections in fall 2001, winter 2001, fall 2002, winter 2002, and fall 2007 were 7, 7, 15, 14, and 9, respectively. Plasma

was also obtained from a few of the fall 2007 individuals (G105, G110, and G112). In addition, serum or plasma was obtained from two Weddell seals during the fall 2007 sampling in this region, and whiskers were taken from two WAP Weddell seals in the austral summer of 2009/10. Hückstädt et al. (2012a) describe the procedure for sampling the whiskers, and Goetz et al. (2017) describe the protocol used for collecting the seal serum and plasma.

Several blood samples were obtained from Weddell seals in the McMurdo Sound region, Ross Sea, Antarctica over multiple field seasons. Twelve whole blood samples were taken from juvenile Weddell seals near Inexpressible Island (74.9 °S, 163.7 °E) during the austral summer of 2010/11. Whole blood samples were taken from Weddell seals in the austral summer of 2010/11 (n=5) and austral spring of 2012 (n=5). RBCs were sampled in the austral summer of 2009/10 (n=5), austral summer of 2011/12 (n=5), and austral spring of 2012 (n=5). Whole blood, plasma, and serum were obtained from 5 Weddell seals sampled in the austral spring of 2015, and whole blood from an additional 7 Weddell seals was also acquired during this time. Goetz et al. (2017) describe the sampling protocol for these Weddell seals.

Lastly, a few samples were obtained from crabeater seals in McMurdo Sound. Hair samples were taken from three recently deceased juvenile crabeater seals that were found on the seasonal pack ice around Cape Royds in the austral summer of 2009/10. Whole blood was sampled, using the protocol of Goetz et al. (2017), from a male adult crabeater seal found in Erebus Bay during the austral summer of 2010/11.

Sample preparation

After sample collection, all samples were kept frozen at -20 °C. Blood samples were freeze-dried with a Labconco Freeze Dry System (Lyph Lock 4.5) and homogenized manually prior to instrument analysis. Lipid extraction was not performed on the blood samples. Lipid extraction is typically performed on samples with high fat content since lipids tend to be depleted in ^{13}C relative other biochemical classes. Blood has a relatively low lipid content, however, and a test set of blood samples with and without lipid extraction revealed no significant effect of lipid extraction on the $\delta^{13}C$ blood values (Table 2.S2). Indeed, lipid extraction actually has a greater effect on the $\delta^{15}N$ values, which is almost certainly an artifact (Table 2.S2).

Hair samples are known to have high enough lipid contents to affect $\delta^{13}C$ values so these samples were lipid extracted. Hair samples were washed with Milli-Q water (Thermo Fisher Scientific, Inc.) and then rinsed 3 times in an ultrasonic bath with petroleum ether for 15 minutes. Hückstädt et al. (2012a) used a similar protocol to lipid-extract the crabeater seal whisker samples.

Bulk stable isotope analysis

For all blood and hair samples, ~ 1 mg was weighed into tin cups (Costech, 3x5 mm) for elemental analysis-isotope ratio mass spectrometry (EA-IRMS). After the follicle was removed, the entire hair sample was chopped up before being added to the tin cups. The follicle was removed since prior work has shown it to have a different biochemical and isotopic composition than the rest of the hair (Hückstädt et al. 2012b). This analysis was performed at the Stable Isotope Lab (SIL) of UC Santa Cruz on a Carlo Erba EA 1108 elemental analyzer coupled to a Thermo-Finnigan

Delta^{Plus} XP isotope ratio mass spectrometer. The $\delta^{13}C$ values were referenced to the V-PDB standard, and $\delta^{15}N$ values were referenced to AIR. Gelatin standard replicates were analyzed in each instrument session in order to correct for variations in mass across samples and instrument drift. Comparisons of standards resulted in standard deviations that were ≤ 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values (7 standards analyzed at the start of each session, and a standard analyzed after every 8 samples). Hückstädt et al. (2012a) describe the bulk isotope analysis of the crabeater whisker samples, which was also performed at the UC Santa Cruz SIL.

Compound-specific isotope analysis

CSIA was performed at UC Santa Cruz via gas chromatography-isotope ratio mass spectrometry (GC-IRMS). All samples were prepared for GC-IRMS analysis using the method described in McCarthy et al. (2007) and McCarthy et al. (2013). In brief, samples were hydrolyzed (6 N HCl for 20 hr at 110 °C) and converted to trifluoroacetic anhydride (TFAA) derivatives. Samples were stored in a -20 °C freezer in a 1:3 TFAA:DCM (methylene chloride) mixture until the day of instrumental analysis. Immediately before the analysis, the TFAA:DCM mixture was evaporated under N_2 and samples were diluted in ethyl acetate.

Amino acid $\delta^{15}N$ values was measured on a Thermo Trace GC coupled to a Thermo-Finnigan Delta^{Plus} XP isotope-ratio-monitoring mass spectrometer (oxidation furnace at 980 ºC and reduction furnace at 650 ºC). The column for the nitrogen isotope analysis was a SGE Analytical Science BPX5 column 60 m by 0.32 mm with a 1 μm film thickness. The injector temperature was 250 ºC with a split He flow of 2

mL/min. The GC temperature program for $\delta^{15}N$ analysis was: initial temp = 70 ºC hold for 1 min; ramp 1 = 10 ºC /min to 185 ºC, hold for 2 min; ramp 2 = 2 ºC/min to 200 ºC, hold for 10 min; ramp 3 = 30 ºC/min to 300 ºC, hold for 6 min. Directly measured amino acid $\delta^{15}N$ values were corrected based on bracketing external standards, as described in McCarthy et al. (2013).

The $\delta^{15}N$ values of 11 amino acids could be quantified. These were alanine (Ala), glycine (Gly), threonine (Thr), serine (Ser), valine (Val), leucine (Leu), Pro, aspartic acid + asparagine (Asp), Glu, Phe, and lysine (Lys). In all samples, isoleucine (Ile) was either not detectable or had low peak areas (< 70) and, thus, Ile $\delta^{15}N$ values should be considered with caution. Lysine was not detected in one sample (R101) and not in all injections of a few samples (R114, W006, and W013), but peak areas were sufficient (>70) when it was detectable.

Data analysis

Most samples were whole blood. Since bulk isotope values can vary across different tissues, a correction must be applied, accounting for isotopic offsets between differing sample types. Species-specific corrections for the bulk isotope values were determined and are presented in the supplementary material (Tables 2.S3-2.S6). These corrections were applied to all bulk isotope data from tissues other than whole blood that had significant isotopic offsets from whole blood. An isotopic offset > 0.2 ‰ is considered significant since the instrument error is ≤ 0.2 ‰. The isotopic offsets applied to non-whole blood tissues transformed them such that they represented whole blood isotope values.

All data analyses were done in R statistical software (R Core Team, 2014). Prior to all statistical analyses test of normality and equal variance were conducted to assure test assumptions were met. In a few cases, an assumption was violated and, thus, a data transformation was applied. This is noted in the text. Bulk isotopic values of the three different seal species were compared with a one-way analysis of variance (ANOVA). Data were Box-Cox transformed (Box and Cox, 1964). A four-way ANOVA was used to test for any significant effects of gender, sampling period, age class, and region (WAP, Amundsen Sea, and Ross Sea) on the bulk isotopic values of Ross, Weddell, and crabeater seals. Both Weddell and crabeater seal data were Box-Cox transformed. A linear regression analysis was used to test for significant relationships between bulk $\delta^{13}C$ and $\delta^{15}N$ values and body mass for each species.

A one-way ANOVA way used to test for significant differences in the $\delta^{15}N$ values of each amino acid among all three seal species. For both Weddell and crabeater seals, a two-tailed student's *t*-test was used to compare the $\delta^{15}N$ values of Pro, Glu and Phe for the WAP to those of a combined Amundsen/Ross Sea region. Amino acid $\delta^{15}N$ values for the Amundsen and Ross Seas (referred to as the "Amundsen/Ross Sea" in the subsequent text) were combined by species (crabeater or Weddell) since both species had bulk $\delta^{15}N$ values that were similar between these two regions, as discussed further below. This analysis was not done for Ross seals since this species was almost exclusively sampled in the Amundsen Sea. A two-tailed student's *t*-test was used to compare the Phe $\delta^{15}N$ values of Weddell seals to those of crabeater seals for the WAP, and a one-way ANOVA was conducted to assess

variation between the Phe $\delta^{15}N$ values of Ross, Weddell, and crabeater seals from the Amundsen/Ross Sea region.

Trophic positions were calculated based on prior work (Chikaraishi et al. 2009), but substituting Pro for Glu as the trophic amino acid as suggested by McMahon et al. (data unpublished). Trophic positions were calculated as follows:

$$TP = (\delta^{15}N_{Pro} - \delta^{15}N_{Phe} - \beta_{Pro/Phe})/TDF_{Pro} + 1$$

Here, TP, $\beta_{Pro/Phe}$, and TDF_{Pro} are the trophic position, isotopic difference between Pro and Phe in primary producers (3.1 ‰), and trophic discrimination factor (4.5 ‰), respectively. Note, that this TP calculation may be an underestimate, due to TDF_{Pro} values varying across species and tissue types, and a shortage of published TDF_{Pro} values (McMahon and McCarthy 2016). Here, we use a mean TDF_{Pro} value for published analyses of marine mammal blood samples (McMahon and McCarthy 2016). Differences in the trophic positions between the three seal species were determined with a one-way ANOVA using data for individuals only from the Ross and Amundsen Seas to reduce the effect of space on the findings. Differences in trophic positions between the two regions (WAP versus Amundsen and Ross Seas) were determined with a two-tailed students *t*-test for Weddell and crabeater seals. For all statistical analyses, a result was considered significant if $p < 0.05$.

Lastly, maps were produced in Ocean Data View (ODV) version (4.7.4) (Schlitzer 2015) to show spatial patterns in bulk $\delta^{13}C$ and $\delta^{15}N$ values and Phe and Pro $\delta^{15}N$ values.

RESULTS

Bulk $\delta^{13}C$ and $\delta^{15}N$ values of Ross, Weddell, and crabeater seals

Bulk $\delta^{13}C$ and $\delta^{15}N$ vary significantly between the three species (Fig. 2.1, Table 2.S7). Ross seals have significantly higher $\delta^{13}C$ values (-23.8 ± 0.3 ‰, n = 15) than both Weddell seals (-25.1 ± 0.7 ‰, n = 86) and crabeater seals (-25.0 ± 1.4 ‰, n = 97) ($p < 0.001$ for post hoc Bonferroni pairwise comparisons). All seals have $\delta^{15}N$ values significantly different from each other ($p < 0.001$ for all Bonferroni post-hoc comparisons). The $\delta^{15}N$ values increase as follows: crabeater seal (7.2 ± 0.8 ‰, n = 97) < Ross seal (9.1 ± 0.4 ‰, n = 15) < Weddell seal (12.2 ± 0.6 ‰, n = 86).

We have examined the effects of sampling period, gender, age class, and body mass on the bulk isotopic values of each seal species. We report a few significant effects, but they are inconsistent across the three species. We discuss these results in the supplementary material.

Spatial patterns in bulk $\delta^{13}C$ and $\delta^{15}N$ values for Antarctic seals

Spatial variation in bulk $\delta^{13}C$ and $\delta^{15}N$ values of Ross Seals across West Antarctica could not be examined because all but one of the individuals were from the Amundsen Sea (Fig. 2.S1). However, both Weddell and crabeater seals show significant spatial variation in their $\delta^{13}C$ values. For Weddell seals, all three regions have significantly different $\delta^{13}C$ values ($p < 0.001$ in all cases from Bonferroni post-hoc comparisons), which increase as follows: Ross Sea (-25.3 ± 0.4 ‰, n = 61) < Amundsen Sea (-24.7 ± 0.4 ‰, n = 21) < WAP (-22.9 ± 0.9 ‰, n = 4) (Fig. 2.2). The

$\delta^{13}C$ values of crabeater seals along the WAP are significantly higher (-24.0 ± 1.1 ‰, n = 52) than those in the Amundsen Sea (-26.1 ± 0.4 ‰, n = 35) and Ross Sea (-26.1 ± 0.5 ‰, n = 10) ($p < 0.001$ in both cases for Bonferroni post-hoc comparisons, Fig. 2.3).

Unlike their bulk $\delta^{13}C$ results, Weddell seals show no significant differences in bulk $\delta^{15}N$ values across the three regions (Fig. 2.2). In contrast, crabeater seals from the WAP have significantly lower $\delta^{15}N$ values (6.8 ± 0.6 ‰, n = 52) than those from the Amundsen Sea (7.6 ± 0.6 ‰, n = 35) and Ross Sea (8.0 ± 1.4 ‰, n = 10) ($p < 0.001$ in both cases from Bonferroni post-hoc comparisons, Fig. 2.3).

Comparison of compound-specific $\delta^{15}N$ values of Ross, Weddell, and crabeater seals

Nitrogen isotope values are significantly different between at least two of the three seal species for all amino acids, except Gly (Figs. 2.4 and 2.S2, Tables 2.S8 and 2.S9). For most trophic amino acids (Glu, Ala, Ile, Leu, Pro, and Val), $\delta^{15}N$ values differ significantly among all three species (Table 2.S9). For these five trophic amino acids, $\delta^{15}N$ values decrease significantly as follows: Weddell > Ross > crabeater. For another trophic amino acid, Asp, crabeater seals have significantly lower $\delta^{15}N$ values (10.1 ± 0.6 ‰, n = 6) than Weddell (16.2 ± 2.2 ‰, n = 6) and Ross seals (14.1 ± 1.0 ‰, n = 6) ($p < 0.001$ in both cases from Bonferroni post-hoc comparisons).

With the exception of Gly, $\delta^{15}N$ values were significantly different between at least two seal species for all source amino acids (Ser, Lys, and Phe). For Ser, $\delta^{15}N$ values of Weddell seals (8.8 ± 1.4 ‰, n = 6) were significantly higher than those of

both crabeater (4.2 ± 1.9 ‰, n = 6) and Ross seals (5.3 ± 0.6 ‰, n = 6) (p-values of < 0.001 and 0.002, respectively, from Bonferroni post-hoc comparisons). With Lys, Ross seals had significantly lower $\delta^{15}N$ values (2.8 ± 0.7 ‰, n = 6) than Weddell (5.2 ± 1.5 ‰, n = 6) and crabeater (5.0 ± 0.4 ‰, n = 6) seals (p-values of 0.005 and 0.009, correspondingly, from Bonferroni post-hoc comparisons). Likewise, for Phe, Ross seals had significantly lower $\delta^{15}N$ values (2.7 ± 0.7 ‰, n = 6) than Weddell (5.7 ± 0.5 ‰, n = 6) and crabeater seals (5.2 ± 1.0 ‰, n = 6) ($p < 0.001$ in both cases from Bonferroni post-hoc comparisons).

Spatial pattern of Phe, Pro, and Glu $\delta^{15}N$ values for Antarctic seals

As with bulk values, spatial variation in $\delta^{15}N$ values of source amino acids for Ross Seals could not be examined since all but one individual were from the Amundsen Sea (Fig. 2.S3). For Weddell seals, Phe, Pro, and Glu values do not differ significantly between the Amundsen/Ross Sea and the WAP (Fig. 2.S4). In contrast, crabeater seals have Phe $\delta^{15}N$ values that are significantly lower in the WAP (4.3 ± 0.4 ‰, n = 3) than the Amundsen/Ross Sea region (6.0 ± 0.7 ‰, n = 3) (p = 0.04, two-tailed student's t-test) (Figs. 2.5 and 2.6). Crabeater Pro and Glu $\delta^{15}N$ values are not significantly different between the WAP (15.9 ± 0.5 ‰ and 15.0 ± 0.2 ‰, respectively, n=3 for both) and the Amundsen/Ross Sea region (15.4 ± 0.6 ‰ and 14.8 ± 0.4 ‰, correspondingly, n = 3 for both).

Comparison of Phe $\delta^{15}N$ values of seal species by region

Both crabeater and Weddell seals have similar Phe $\delta^{15}N$ values for the Amundsen/Ross Sea region, 6.0 ± 0.7 ‰ (n = 3) and 5.7 ± 0.7‰ (n = 3), respectively,

that are significantly higher than the Phe $\delta^{15}N$ value for Ross seals (2.7 ± 0.7 ‰, n = 6) with p-values less than 0.001 in all cases from Bonferroni post-hoc comparisons. However, crabeater seals have significantly lower Phe $\delta^{15}N$ values (4.3 ± 0.4 ‰, n = 3) than Weddell seals (5.7 ± 0.4 ‰, n = 3) for the WAP (p = 0.01 from a two-tailed student's t-test).

Trophic positions of Ross, Weddell, and crabeater seals

Among individuals from the Amundsen or Ross Seas, both Ross seals (3.5 ± 0.2, n = 6) and Weddell seals (3.7 ± 0.1, n = 3) are at a significantly higher trophic position (TP) than crabeater seals (2.4 ± 0.2, n = 3) ($p < 0.001$ from Bonferroni post-hoc comparisons in both cases) (Fig. 2.7). Weddell seals have similar TPs for the WAP (3.3 ± 0.4, n = 3) and Amundsen/Ross Sea region. However, crabeater seals have significantly higher TPs in the WAP (2.9 ± 0.1, n = 3) than the Amundsen/Ross Sea region (p = 0.03 from a two-tailed student's t-test). For crabeater seals, one subadult and five adults are used in the CSIA. Although some significant variation in bulk $\delta^{15}N$ values is observed across different age classes for this species, see supplemental material, the TP of the subadult from the Amundsen/Ross sea region (2.3) is indistinguishable from that of the adults from this area (2.4 ± 0.2, n = 2). To note, some significant differences in the bulk $\delta^{15}N$ values of Weddell seal age classes also occurrs, which has been discussed in the supplemental material, but only adults are used in the CSIA.

DISCUSSION

Our Ross, Weddell, and crabeater seal bulk isotope values are very similar to those reported in earlier work on these species for our study region (Burns et al. 1998, Zhao et al. 2004, Aubail et al. 2011, Goetz et al. 2017) when isotopic offsets for different tissue types are applied, see Table 2.S10. Our bulk isotope results are especially valuable for Ross seals as little information on their ecology is presently available. Our results show spatial patterns in Weddell and crabeater seal bulk isotope values. Additionally, our bulk $\delta^{15}N$ values, like those of prior studies (Rau et al. 1992, Burns et al. 1998, Zhao et al. 2004, Aubail et al. 2011, Cipro et al. 2012, and Hückstädt et al. 2012a), all point to Ross seals being at an intermediate trophic position between those of Weddell and crabeater seals, such that the trophic position of these species increases as follows: crabeater < Ross < Weddell. In the proceeding discussion, we explore the implications of our bulk isotope data, complemented by additional information from our CSIA, in regards to the trophic positions, diets, and foraging habitats of these three seal species.

Spatial patterns in seal bulk and amino acid isotope values

Both Weddell and crabeater seals show spatial patterns in their bulk $\delta^{13}C$ values. Weddell seals have significantly decreasing $\delta^{13}C$ values across the western Antarctic (i.e., WAP > Amundsen Sea > Ross Sea), while crabeater seals have significantly higher $\delta^{13}C$ values in the WAP than the Amundsen and Ross Seas. As this $\delta^{13}C$ gradient occurs in consumers at different trophic levels, it is likely driven by changes in baseline $\delta^{13}C$ values. Prior research has shown that $\delta^{13}C$ values decrease

with increasing latitude in the West Antarctic as a result of increasing CO_2 solubility with decreasing sea surface temperatures (Cherel and Hobson 2007, Quillfeldt et al. 2010, Chapter 1). Thus, the spatial variation in the bulk $\delta^{13}C$ values of these two species likely reflects sea surface temperature differences in the West Antarctic, with colder temperatures in the higher latitude Amundsen and Ross Sea than the lower latitude WAP. An offset between the sea surface temperatures of the WAP and those of the Ross Sea (Ducklow et al. 2007, Ducklow et al. 2012, Smith et al. 2014) has been shown to contribute to about a 2 ‰ difference in the $\delta^{13}C_{baseline}$ between these regions, a magnitude similar to the variation between the WAP and Ross Sea bulk $\delta^{13}C$ values that we observe for Weddell and crabeater seals (2.4 ‰ and 2.1‰, respectively).

Weddell and crabeater seals have shown different spatial patterns in their bulk $\delta^{15}N$ values in West Antarctica. Crabeater seals have significantly lower bulk $\delta^{15}N$ values in the WAP than the Amundsen and Ross Seas, whereas bulk $\delta^{15}N$ values do not differ among these regions for Weddell seals. As described earlier, spatial patterns in the bulk $\delta^{15}N$ values can be related to shifts in diet, baseline $\delta^{15}N$ values, or both. CSIA reveals the contribution of diet versus $\delta^{15}N_{baseline}$ variation to a consumer's bulk $\delta^{15}N$ trend.

A spatial gradient in $\delta^{15}N_{baseline}$ in the Southern Ocean has been indicated by previous research, likely reflecting oceanographic changes. A lower $\delta^{15}N_{baseline}$ in the WAP than the Amundsen and Ross Seas has been shown in earlier work and the offset appears to be ~ 2 ‰ (Chapter 1), which is similar to the offset between WAP

and Amundsen/Ross Sea crabeater seal Phe $\delta^{15}N$ values (1.7 ‰). This transition in $\delta^{15}N_{baseline}$ appears to follow the role of oceanic versus coastal production across the West Antarctic (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1). Baseline $\delta^{15}N$ values likely increase from oceanic to coastal areas due to increasing productivity and nutrient drawdown towards the continent in the summer (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1). The WAP, with a narrow shelf, likely has a greater influence from the oceanic regions, beyond the continental margin, on its $\delta^{15}N_{baseline}$, whereas the Amundsen Sea and, particularly, the Ross Sea have wide, productive shelf systems and, thus, higher $\delta^{15}N_{baseline}$ (Arrigo et al. 1998, 2008, DiFiore et al. 2006, Smith & Comiso 2008, DiFiore et al. 2009, Alderkamp et al. 2012, Chapter 1). Continental shelves are especially productive areas since both light and iron become sufficiently available for phytoplankton growth during periods of the year due to coastal polynya formation and increased iron inputs from various sources (e.g., melting glaciers), respectively (Gordon et al. 2000, Alderkamp et al. 2012, Arrigo et al. 2015). Although annual production in the Amundsen and Ross Seas excceds that of the WAP (Arrigo et al. 1998, 2008, Smith and Comiso 2008, Alderkamp et al. 2012) the WAP likely experiences high primary productivity rates, comparable to those within the Amundsen and Ross Seas, in localized regions, which has been suggested by prior work. Schmidt et al. (2003) found that Marguerite Bay in the WAP can be a “hot spot” of productivity as revealed by high phytoplankton and zooplankton $\delta^{15}N$ measurements. To date, examinations of $\delta^{15}N_{baseline}$ variation in West Antarctica have suggested that it increases from oceanic to coastal waters,

tracking a gradient in productivity and nutrient drawdown (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1).

The spatial change in $\delta^{15}N_{baseline}$ in West Antarctica is useful for deducing the uses of various habitats by Weddell and crabeater seals. Weddell seals from the WAP to the Ross Sea consistently have high Phe $\delta^{15}N$ values (5.7 ± 0.4 ‰ for the WAP and 5.7 ± 0.7 ‰ for the Amundsen/Ross Sea region, $n = 3$ in both cases) given the range for all Antarctic seal Phe $\delta^{15}N$ values (1.90 ‰ to 6.81 ‰). This result suggests that Weddell seals throughout West Antarctica have similar foraging behavior in which they habitually target the most productive environments within an area, likely coastal regions given our understanding of the West Antarctic $\delta^{15}N_{baseline}$ gradient, to forage. In support of this hypothesis, Costa et al. (2010) discovered from satellite tracking data that in the WAP, Weddell seals, unlike southern elephant (*Mirounga leonina*) and crabeater seals, moved minimally, foraging almost exclusively in coastal fjords, which are likely highly productive places (Schmidt et al. 2003, Difiore et al. 2006, 2009). In contrast to Weddell seals, crabeater Phe $\delta^{15}N$ values vary across West Antarctica, being higher in the Amundsen and Ross Seas than the WAP, which has indicated that crabeater seals have more habitat flexibility than Weddell seals. Weddell and crabeater seals also have significantly different $\delta^{15}N_{baseline}$ for the WAP, which is not observed for the Amundsen/Ross Sea region, pointing to environmental heterogeneity in the WAP. Our current knowledge of crabeater seals indicates that this seal heavily consumes *E. superba* (Laws 1977, Rau et al. 1992, Burns et al. 2004, Zhao et al. 2004, Burns et al. 2008, Aubail et al. 2011, Hückstädt et al. 2012a), a

species with a distribution linked to that of sea ice and which moves on and off the continental shelf depending on its life cycle stage and the season (Nicol 2006). Thus, in capturing krill, crabeater seals likely move across the heterogeneous environments of the WAP, experiencing the lower, off-shelf $\delta^{15}N_{baseline}$, unlike Weddell seals. This behavior would explain the lower Phe $\delta^{15}N$ values of crabeater seals than those of Weddell seals within the WAP. Since crabeater seals in the Amundsen/Ross Sea region have Phe $\delta^{15}N$ values similar to those of Weddell seals in this area, crabeater seals are largely moving within the productive continental shelves of the Amundsen and Ross Seas, which are wider than that of the WAP. Overall, our results indicate that Weddell seals have a strong preference for a particular habitat type, productive coastal sites, whereas crabeater seals utilize diverse habitats in West Antarctica.

Interestingly, Ross seals, sampled in the Amundsen/Ross Seas, had significantly lower Phe $\delta^{15}N$ values than those of both Weddell and crabeater seals from this region. This result suggests that Ross seals are foraging in a very different region than the other two species. Given their low $\delta^{15}N_{baseline}$ and our current understanding of the West Antarctic $\delta^{15}N_{baseline}$ gradient (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1), we conclude that Ross seals are largely feeding further offshore, in the oceanic region of the Southern Ocean, which experiences low nutrient drawdown and production relative to coastal areas (DiFiore et al. 2006, DiFiore et al. 2009, Jaeger et al. 2010, Somnes et al. 2010).

Prior research supports the idea that Ross seals are largely oceanic feeders. Blix and Nordøy (2007) have examined the foraging behavior of Ross seals via

satellite-linked dive recorders. The tags tracked the movements of 10 adult Ross seals captured off Queen Maud Land (East Antarctica) just after their molt in February 2001. The animals migrated 2,000 km north to pelagic waters south of the Antarctic Polar Front. These Ross seals stayed in that area until October when they traveled south into the pack ice (Blix and Nordøy 2007). As mentioned earlier, Arcalís-Planas et al. (2015) reveal that these animals minimally use sea ice, hauling out for short periods each year to molt and breed. These authors report that Ross seals are moving from 587 to 1,282 km off the ice edge (Arcalís-Planas et al. 2015). Their low $\delta^{15}N_{baseline}$ in our study confirms that Ross seals are spending the majority of each year in less productive, oceanic waters and not foraging in the same food web as crabeater and Weddell seals.

Spatially varying trophic positions of crabeater seals

Unlike the situation for Weddell seals, we find a significant spatial change in the trophic position of crabeater seals. The TP of crabeater seals decreases by approximately 0.5 from the WAP to the Amundsen/Ross Sea region, suggesting slightly higher fish consumption in the former than the latter region. A role of age class in the spatial variation in crabeater TP seems unlikely, recall one individual from the Amundsen/Ross Sea area is a subadult and all other crabeater seals from both regions are adults, since the TP of the subadult was equivalent to that of adults from the Amundsen and Ross Seas. The WAP has been experiencing increased krill fishing pressure and dramatic warming, both of which have negative effects on *E. superba* abundance, perhaps decreasing the availability of this prey type to crabeater

seals in this area (Ducklow et al. 2007, Trivelpiece et al. 2011, Ducklow et al. 2012, Nicol et al. 2012). Alternatively, the TP of the euphasuiid species consumed by crabeater seals may have varied spatially, having had a slightly higher TP in the WAP than in the Amundsen and Ross Seas to have generated the observed spatial pattern in crabeater seal trophic position. Prior research has shown omnivorous behaviors by *E. superba* in the WAP and Drake Passage regions, possibly contributing to a higher euphausiid TP in this region than other areas of the Antarctic (Schmidt et al. 2006). Yet, euphausiid omnivory in the Ross Sea has also been suggested (Hopkins 1987, Pinkerton et al. 2010). If the degree of omnivory by euphausiids had been consistent across West Antarctica for the time periods integrated in our crabeater seal tissues, which may not have been the case since use of omnivorous feeding by this taxa has varied with time and space (Schmidt et al. 2006), then the spatial variation in TP observed for crabeater seals has likely been driven by regional differences in their diet. Overall, the roles of diet versus krill omnivory in our spatial gradient of crabeater seal TP are unclear.

Redefined trophic position of Ross seals

The difference between the $\delta^{15}N_{baseline}$ experienced by Ross seals and that of crabeater and Weddell seals (~ 3 ‰) leads to a redefinition of the TP for Ross seals. After accounting for $\delta^{15}N_{baseline}$ variation across these three seal species via the TP equation with amino acid $\delta^{15}N$ values, Ross seals have TPs similar to those of Weddell seals, while crabeater seals have significantly lower TPs than both Ross and Weddell seals. This result differs from those based on bulk $\delta^{15}N$ measurements for

these pinniped species, which have suggested that Ross seals are at an intermediate trophic position between crabeater and Weddell seals (Rau et al. 1992, Zhao et al. 2004, Aubail et al. 2011). Our results suggest that, like Weddell seals, Ross seals are eating high trophic level prey, such as mid-to-deep water fish and squid, and not consuming much low trophic level prey, such as *E. superba*. This conclusion is supported from dive records, which have indicated that Ross seals have been foraging at depths associated with capturing mesopelagic squid and fish (Bengtson and Stewart 1997, Blix and Nordøy 2007), and stomach content analysis that has reported Antarctic silverfish and glacial squid composing their diets in varying proportions (Skinner and Klages, 1994).

CONCLUSIONS

Our work using bulk and amino acid isotope analyses revealed variability in the habitats used by three Antarctic seal species. Ross seals are foraging in a pelagic-based food web separate from that of crabeater and Weddell seals. Crabeater and Weddell seals are foraging within similar food webs closer to shore, but crabeater seals are likely following sea ice to capture *E. superba*, while Weddell seals target the most productive areas within the western Antarctic to take prey.

Furthermore, our CSIA reveals a higher trophic position for Ross seals, equivalent to that of Weddell seals, in contrast to the bulk isotope results to date. Prior bulk isotope research did not capture the varying baseline isotope values of the

environments inhabited by these species. This study highlights the importance of understanding the baseline isotope values of a given predator's habitat prior to applying bulk isotope analysis for studies of foraging ecology on that species.

ACKNOWLEDGEMENTS

Dyke Andreasen, Colin Carney, Elizabeth Gier, Stephanie Christensen, Jonathan Nye, and Aaron Rosenfield provided considerable assistance with method development and laboratory analyses entailed in this study. Dr. Kimberly Goetz assisted with the interpretations of our data. The crew of *RV Oden* was extremely accommodating and helpful in completing our sampling protocols. The support staffs of McMurdo and Palmer Stations, similarly, gave us considerable assistance in performing our sample collections. The National Science Foundation (NSF) granted our funding for this study (NSF ANT-1142108). Drs. Elizabeth Canuel, Rebecca Dickhut, and Andrew Wozniak helped with the importation of samples (Permit No. 17178 from the National Marine Fisheries Service). Drs. Daniel Costa, Luis Hückstädt, Kimberly Goetz, Michael Goebel, Olle Karlsson, Jonas Teilmann, Tero Harkonen, and Karin Harding generously provided seal tissue samples for analysis in this research, along with help in data interpretation.

REFERENCES

Ainley DG, Siniff DB (2009) The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. Antarct Sci 21:317-327

Alderkamp AC, Mills MM, van Dijken GL, Laan P, Thuróczy CE, Gerringa LJA, de Baar HJW, Payne CD, Visser RJW, Buma AGJ, Arrigo KR (2012) Iron from melting glaciers fuels phytoplankton blooms in the Amundsen Sea (Southern Ocean): Phytoplankton characteristics and productivity. Deep-Sea Res Part II Top Stud Oceanogr 71-76:32-48

Altabet MA, Francois R (2001) Nitrogen isotope biogeochemistry of the Antarctic Polar Frontal Zone at 170 W. Deep Sea Res Part II 48:4247-4273

Arcalís-Planas A, Sveegaard S, Karlsson O, Harding KC, Wåhlin A, Harkonen T, Teilmann J (2015) Limited use of sea ice by the Ross seal (*Ommatophoca rossii*), in Amundsen Sea, Antarctica, using telemetry and remote sensing data. Polar Biol 38:445-461

Arim M, Naya DE (2003) Pinniped diets inferred from scats: analysis of biases in prey occurrence. Can J Zool 81:67-73

Arrigo KR, Weiss AM, Smith WO (1998) Physical forcing of phytoplankton dynamics in the southwestern Ross Sea. J Geophys Res Oceans 103:1007-1021

Arrigo KR, van Dijken GL (2003) Phytoplankton dynamics within 37 Antarctic coastal polynyas systems. J Geophys Res 108:3271

Arrigo KR, van Dijken GL, Bushinsky S (2008) Primary production in the Southern Ocean, 1997–2006. J Geophys Res Oceans 113:C08004

Arrigo KR, van Dijken GL, Strong AL (2015) Environmental controls of marine productivity hot spots around Antarctica. J Geophys Res, C, Oceans, 120:5545-5565

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the southern ocean. Nature 432: 100-103

Aubail A, Teilmann J, Dietz R, Rigét F, Harkonen T, Karlsson O, Rosing-Asvid A, Caurant F (2011) Investigation of mercury concentrations in fur of phocid seals using stable isotopes as tracers of trophic levels and geographic regions. Polar Biol 34:1411-1420

Bengtson JL, Stewart BS (1997) Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic Peninsula. Polar Biol 18:214-218

Bengtson JL, Laake JL, Boveng PL, Cameron MF, Hanson MB, Stewart BS (2011) Distribution, density, and abundance of pack-ice seals in the Amundsen and Ross Seas, Antarctica. Deep Sea Res Pt II 58:1261-1276

Blix AS, Nordøy ES (2007) Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. Polar Biol 30:1449-1458

Box GE, Cox DR (1964) An analysis of transformations. J R Stat Soc Series B Stat Methodol 26:211-252

Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biol 19:272-282

Burns JM, Costa DP, Fedak MA, Hindell MA, Bradshaw CJ, Gales NJ, McDonald B, Trumble SJ, Crocker DE (2004) Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. Deep Sea Res Pt II 51:2279-2303

Burns JM, Hindell MA, Bradshaw CJA, Costa DP (2008) Fine-scale habitat selection of crabeater seals as determined by diving behavior. Deep Sea Res Pt II 55:500-514

Casaux R, Baroni A, Carlini A (1997) The diet of the Weddell seal Leptonychotes weddelli at Harmony Point, South Shetland Islands. Polar Biol 18: 371-375

Casaux R, Baroni A, Ramón A (2006) The diet of the Weddell Seal *Leptonychotes weddellii* at the Danco Coast, Antarctic Peninsula. Polar Biol 29:257-262

Casaux R, Carlini A, Corbalán A, Bertolin L, DiPrinzio CY (2009) The diet of the Weddell seal *Leptonychotes weddellii* at Laurie Island, South Orkney Islands. Polar Biol 32:833-838

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281-287

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y, Suga H, Tomitani A, Miyashita H, Kitazato H, Ohkouchi N (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol Oceanogr: Methods 7:740-750

Cipro CV, Bustamante P, Taniguchi S, Montone RC (2012) Persistent organic pollutants and stable isotopes in pinnipeds from King George Island, Antarctica. Mar Pollut Bull 64:2650-2655

Clarke MR, Macleod N (1982) Cephalopod remains in the stomachs of eight Weddell seals. Br Antarct Surv Bull 57:33-40

Costa DP, Hückstädt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA (2010) Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. Integr Comp Biol 50: 1018-1030

Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. Science 283:993-996

de Baar HJ, Buma AG, Nolting RF, Cadée GC, Jacques G, Tréguer PJ (1990) On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas. Mar Ecol Prog Ser 65:105-122

Dellinger T, Trillmich F (1988) Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable? Can J Zool 66:1865-1870

DiFiore PJ, Sigman DM, Trull TW, Lourey MJ, Karsh K, Cane G, Ho R (2006) Nitrogen isotope constraints on subantarctic biogeochemistry. J Geophys Res Oceans 111:C08016

DiFiore PJ, Sigman DM, Dunbar RB (2009) Upper ocean nitrogen fluxes in the Polar Antarctic Zone: Constraints from the nitrogen and oxygen isotopes of nitrate. Geochem Geophys Geosyst 10:Q11016

Ducklow, HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC (2007) Marine pelagic ecosystems: The west WAP. Philos Trans R Soc B Biol Sci 362:67-94

Ducklow HW, Clarke A, Dickhut R, Doney SC, Geisz H, Huang K, Martinson DG, Meredith MP, Moeller HV, Montes-Hugo M, Schofield O, Stammerjohn SE, Steinberg D, Fraser W (2012) The marine system of the western WAP. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) Antarctic ecosystems: an extreme environment in a changing world, Blackwell Publishing LTD, Hoboken, New Jersey, USA, p 121-159

Fuiman L, Davis R, Williams T (2002) Behavior of midwater fishes under the Antarctic ice: observations by a predator. Mar Biol 140:815-822

Germain LR, Koch PL, Harvey J, McCarthy MD (2013) Nitrogen isotope fractionation in amino acids from harbor seals: implications for compound-specific trophic position calcuations. Mar Ecol Prog Ser 482:265-277

Goetz KT, Burns JM, Hückstädt LA, Shero MR, Costa DP (2017) Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. Deep Sea Res II 140:36-44

Gordon LI, Codispoti LA, Jennings JC, Millero FJ, Morrison JM, Sweeney C (2000) Seasonal evolution of hydrographic properties in the Ross Sea, Antarctica, 1996–1997. Deep Sea Res II 47:3095-3117

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes. Springer, Netherlands, p 299-318

Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Mar Biol 96:93-106

Hückstädt LA, Burns JM, Koch PL, McDonald BI, Crocker DE, Costa DP (2012a) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287-301

Hückstädt LA, Koch PL, McDonald BI, Goebel ME, Crocker DE, Costa DP (2012b) Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. Oecologia 169:395-406

Jaeger A, Connan M, Richard P, Cherel Y (2010) Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialization in seabirds. Mar Ecol Prog Ser 401:269-277

Kim SZ, Ainley DG, Pennycook J, Eastman JT (2011) Short Note: Antarctic toothfish heads found along tide cracks of the McMurdo Ice Shelf. Antarct Sci 23:469-470

Lake S, Burton H, van den Hoff J (2003) Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. Mar Ecol Prog Ser 254:293-305

Lake S, Burton H, Wotherspoon S (2006) Movements of adult female Weddell seals during the winter months. Polar Biol 29:270-279

Laws RM (1977) Seals and whales of the Southern Ocean. Phil Trans R Soc Lond B 279: 81-96

McCarthy MD, Benner R, Lee C, Fogel ML (2007) Amino acid nitrogen isotopic fractionation patterns as indicators of heterotrophy in plankton, particulate, and dissolved organic matter. Geochim Cosmochim Ac 71:4727-4744

McCarthy MD, Lehman J, Kudela R (2013) Compound-specific amino acid $\delta^{15}N$ patterns in marine algae: Tracer potential for cyanobacterial vs. eukaryotic organic nitrogen sources in the ocean. Geochim Cosmochim Ac 103:104-120

McClelland JW, Montoya JP (2002) Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. Ecology 83:2173-2180

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697-714

McMahon, KW, McCarthy MD (2016) Embracing variability in amino acid $\delta^{15}N$ fractionation: mechanisms, implications, and applications for trophic ecology. Ecosphere 7:e01511

Minagawa M, Wada E (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between $\delta^{15}N$ and animal age. Geochim Cosmochim Ac 48:1135-1140

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western WAP. Science 323:1470-1473

Nicol S (2006) Krill, currents, and sea ice: Euphausia superba and its changing environment. Bioscience 56:111-120

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

Pinkerton MH, Bradford-Grieve JM, Hanchet SM (2010) A balanced model of the food web of the Ross Sea, Antarctica. CCAMLR Sci 17:1-31

Plötz J, Ekau W, Reijnders PJ (1991). Diet of Weddell seals *Leptonychotes weddellii* at Vestkapp, eastern Weddell Sea (Antarctica), in relation to local food supply. Mar Mam Sci 7:136-144

Plötz J, Bornemann H, Bornemann H, Knust R, Schröder A, Bester M (2001) foraging behaviour of weddell seals and its ecological implications. Polar Biol 24:901-909

Ponganis PJ, Stockard TK (2007) Short Note: The Antarctic toothfish: how common a prey for Weddell seals? Antarct Sci 19:441-442

Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott MJ, López-Ibarra GA, Galván-Magaña F, Fry B (2007) Insight into the trophic ecology of the yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson T, Siegwolf R (eds) Stable Isotopes as Indicators of Ecological Change. Elsevier, New York, p 173-190

Quillfeldt P, Masello JF, McGill RAR, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? Front Zool 7:15

R Core Team (2014). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria

Rau GH, Sweeney RE, Kaplan IR (1982) Plankton 13C: 12C ratio changes with latitude: differences between northern and southern oceans. Deep Sea Res Pt I 29:1035-1039

Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar Ecol Prog Ser 84:1-8

Reeves RR (2008) Guide to marine mammals of the world. Knopf Doubleday Publishing Group, New York

Schlitzer R (2015) Ocean Data View (ODV) version (4.7.4). http://odv.awi.de

Schmidt K, Atkinson A, Stübing D, McClelland JW, Montoya J P, Voss M (2003) Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. Limnol Oceanogr 48:277-289

Schmidt K, Atkinson A, Petzke KJ, Voss M, Pond DW (2006) Protozoans as a food source for Antarctic krill, Euphausia superba: Complementary insights from stomach content, fatty acids, and stable isotopes. Limnol Oceanogr 51:2409-2427

Sherwood OA, Lehmann MF, Schubert CJ, Scott DB, McCarthy MD (2011) Nutrient regime shift in the western North Atlantic indicated by compound-specific $\delta^{15}N$ of deep-sea gorgonian corals. P Natl Acad Sci USA 108:1011-1015

Skinner JD, Klages NTW (1994) On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. Polar Biol 14:467-472

Smith WO, Comiso JC (2008). Influence of sea ice on primary production in the Southern Ocean: A satellite perspective. J Geophys Res Oceans 113:C05S93

Smith Jr WO, Ainley DG, Arrigo KR, Dinniman MS (2014) The Oceanography and Ecology of the Ross Sea. Annu Rev Mar Sci 6:469-487

Somes CJ, Schmittner A, Galbraith ED, Lehmann MF, Altabet MA, Montoya JP, Letelier RM, Mix AC, Bourbonnais A, Eby M (2010) Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem Cycles 24:16

Staniland IJ (2002) Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Mar Mamm Sci 18:223-243

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011)Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci USA 108:7625-7628

Yonezaki S, Kiyota M, Baba N, Koido T, Takemura A (2003) Size distribution of the hard remains of prey in the digestive tract of northern fur seal (*Callorhinus ursinus*) and related biases in diet estimation by scat analyses. Mamm Study 28:97-102

Zhao L, Castellini MA, Mau TL, Trumble SJ (2004) Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biol 27:368-373

FIGURES

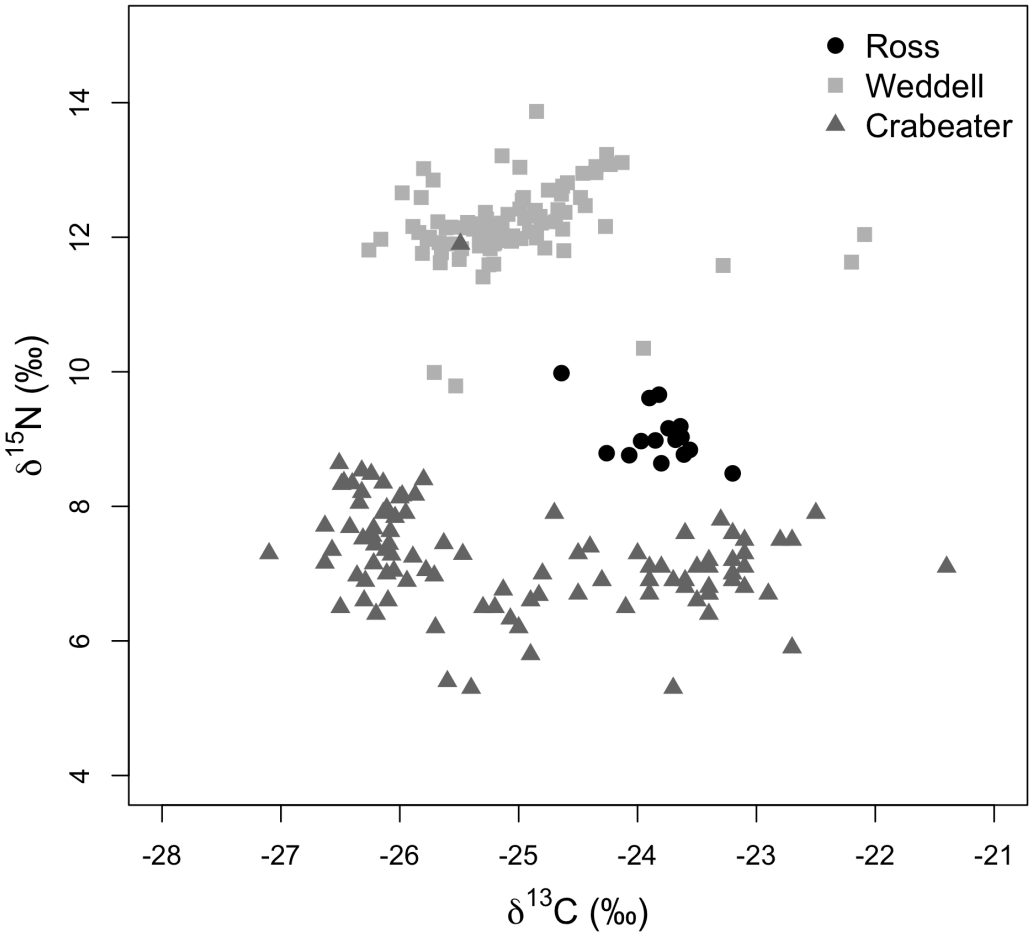

Figure 2.1. Bulk $\delta^{15}N$ values versus $\delta^{13}C$ values for crabeater, Weddell, and Ross seals. Species are indicated with colors and symbols: light grey squares for Weddell seals, medium grey triangles for crabeater seals, and black circles for Ross seals.

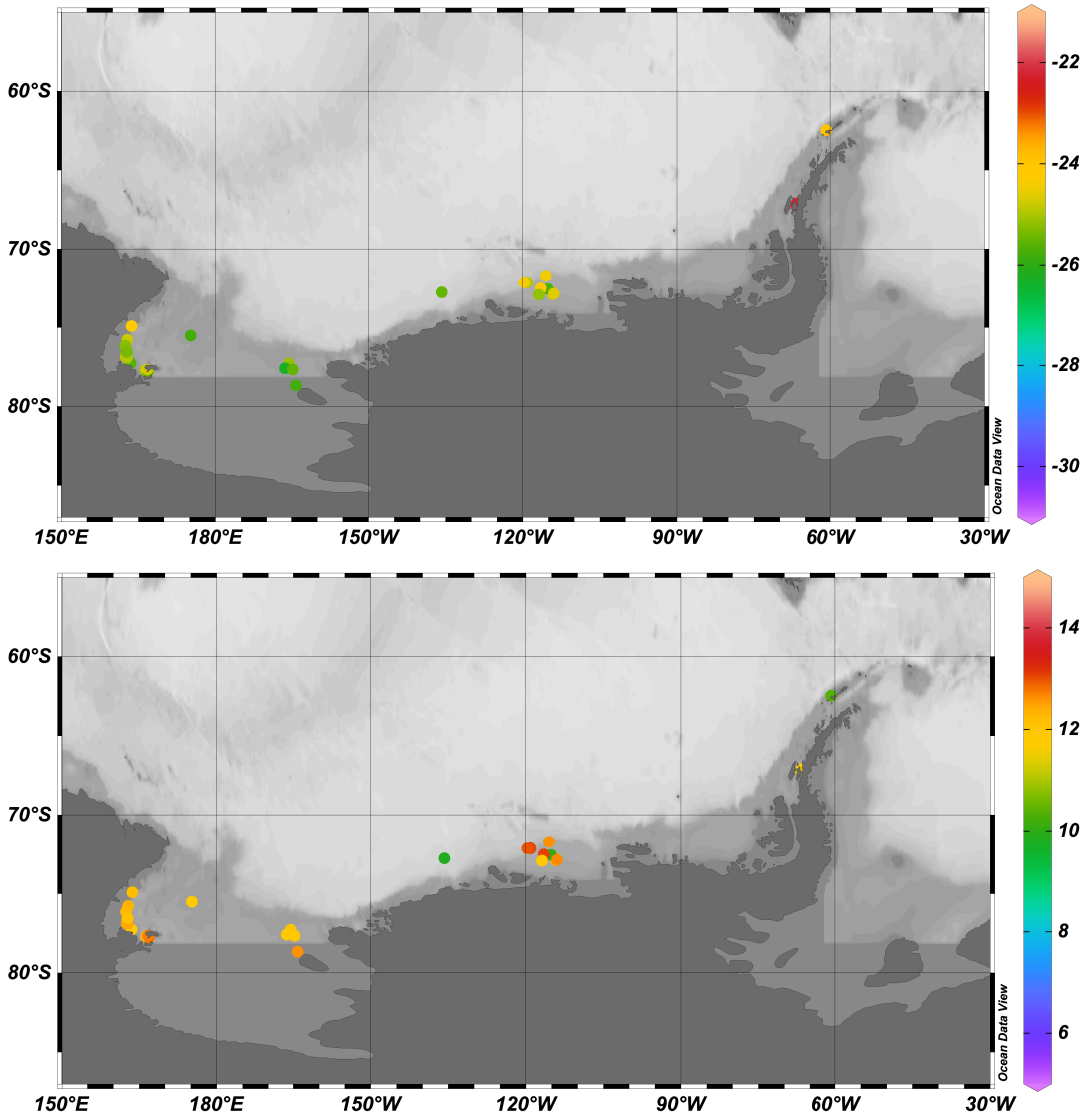

Figure 2.2. Spatial variation in $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values of Weddell seals. Figures were produced in Ocean Data View 4.7.4 (Schlitzer 2015).

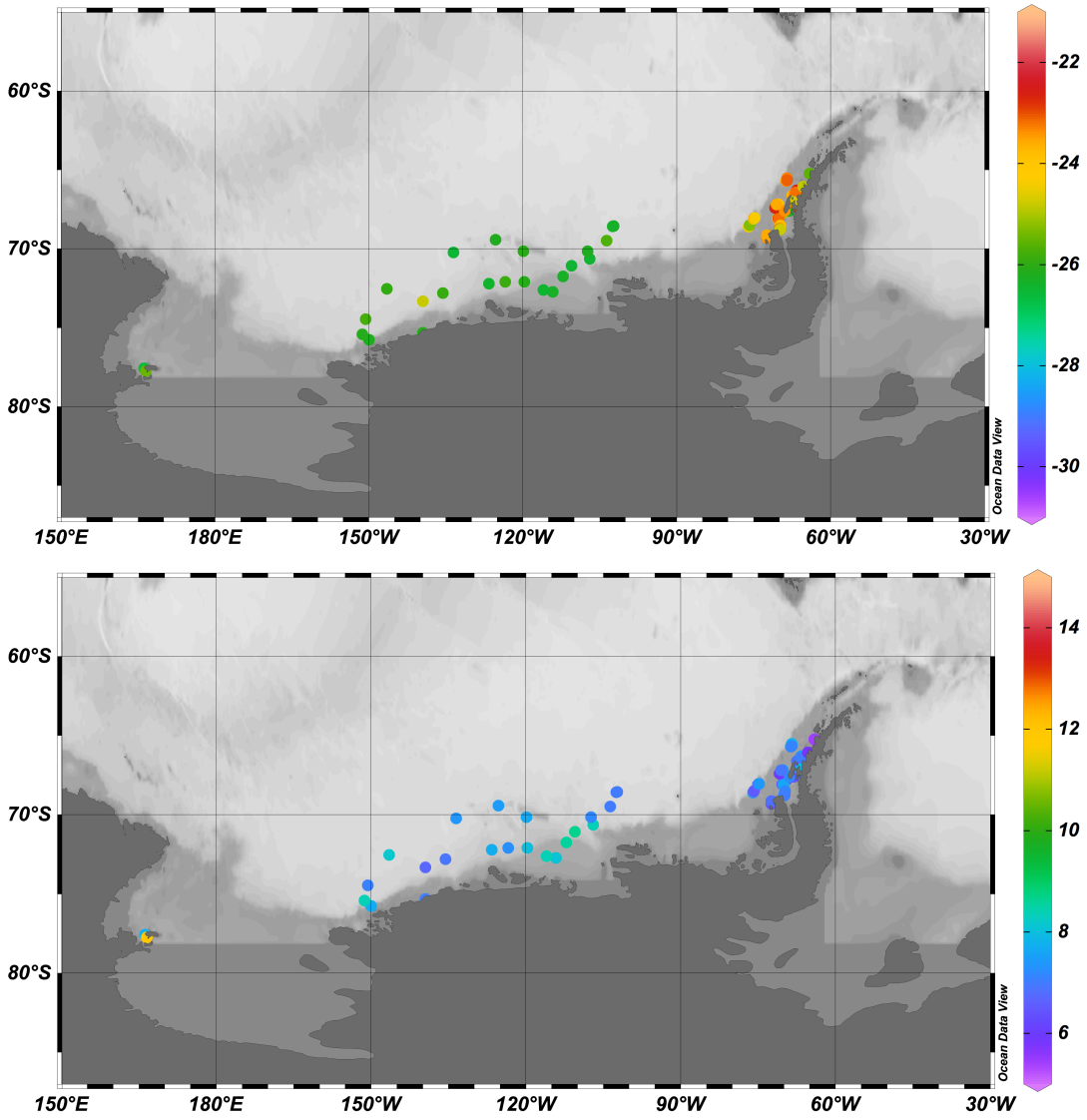

Figure 2.3. Spatial variation in $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values of crabeater seals. Figures were produced in Ocean Data View 4.7.4 (Schlitzer 2015).

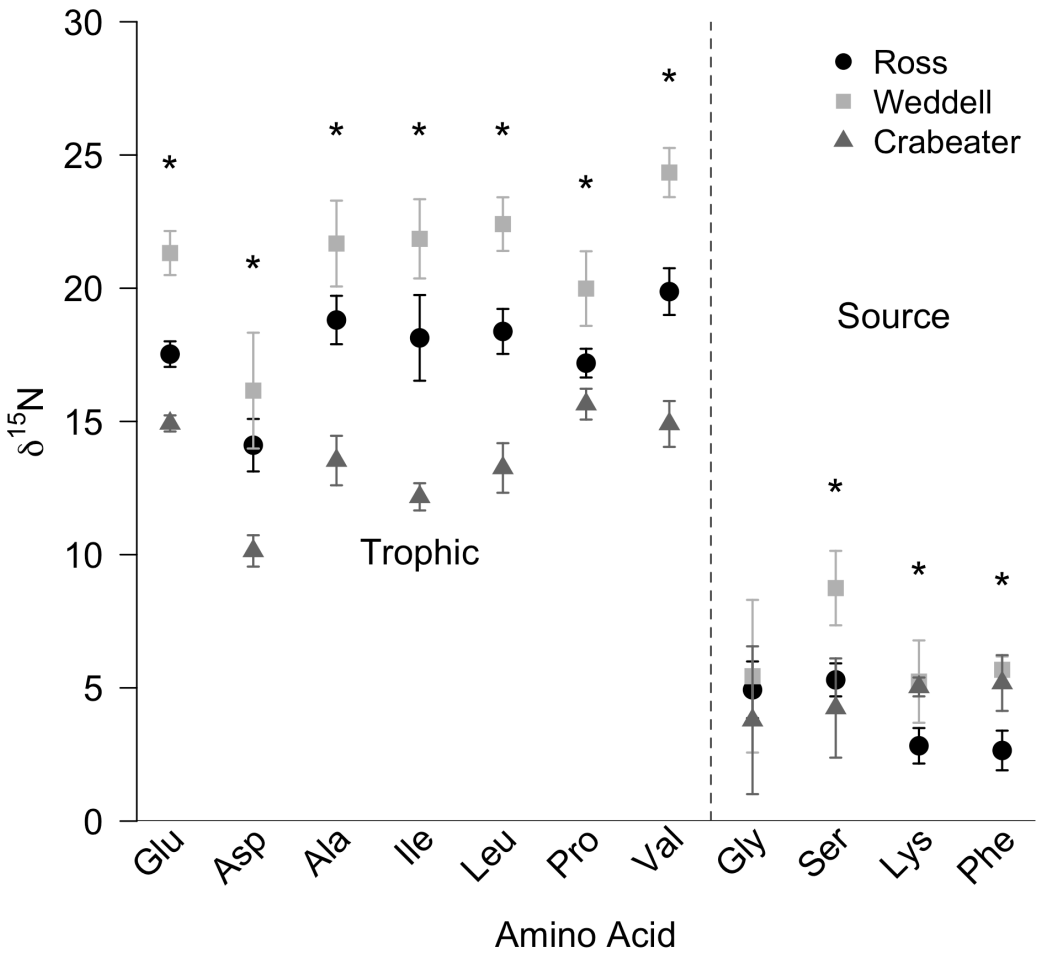

Figure 2.4. $\delta^{15}N$ values of amino acids for Ross, Weddell, and crabeater seals. Significant differences ($p < 0.05$) are indicated with asterisks. Species are shown with colors: light grey squares for Weddell seals, medium grey triangles for crabeater seals, and black circles for Ross seals.

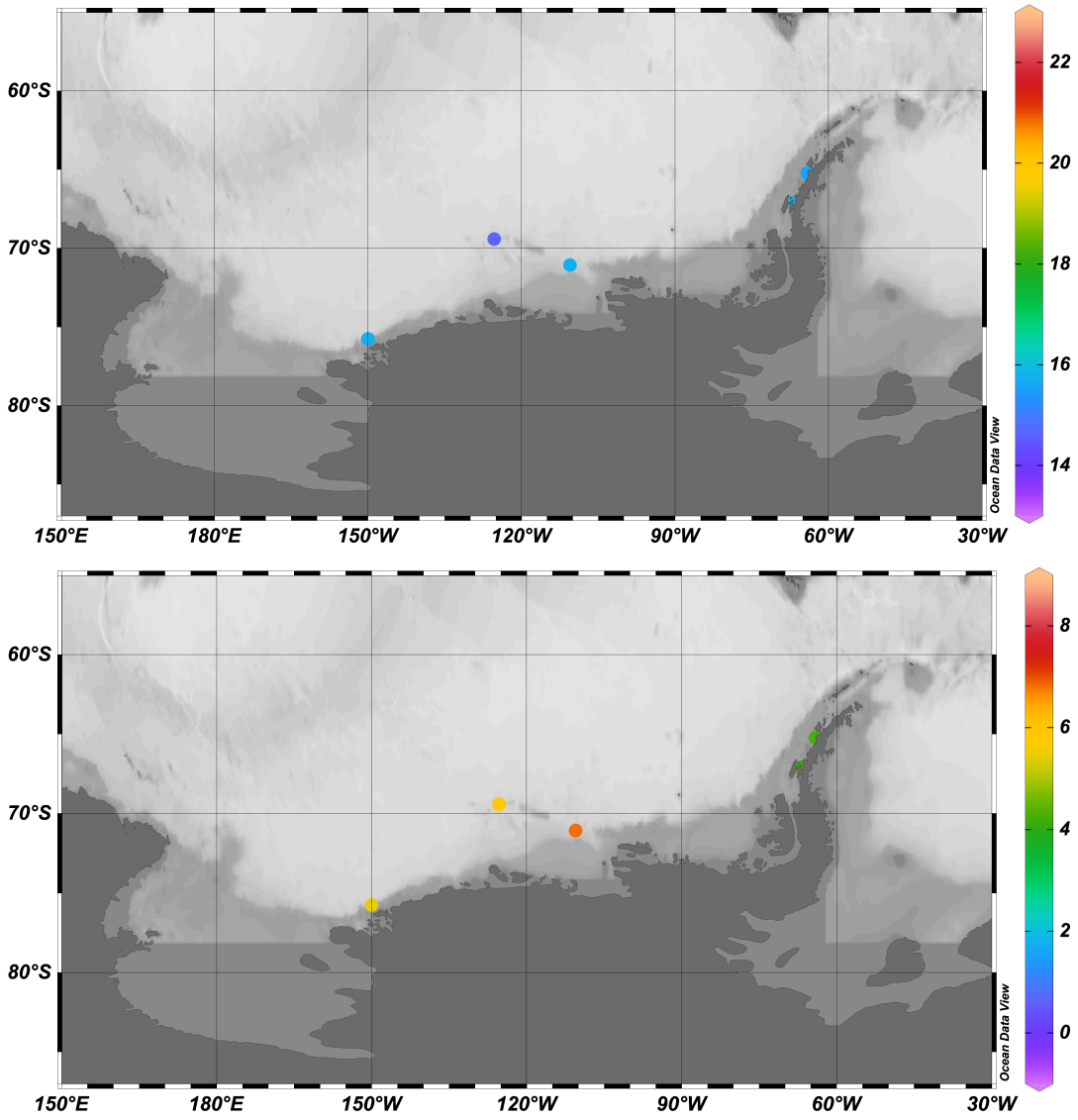

Figure 2.5. Spatial variation in $\delta^{15}N$ values of Pro (top) and Phe (bottom) values for crabeater seals. Figures were produced in Ocean Data View 4.7.4 (Schlitzer 2015).

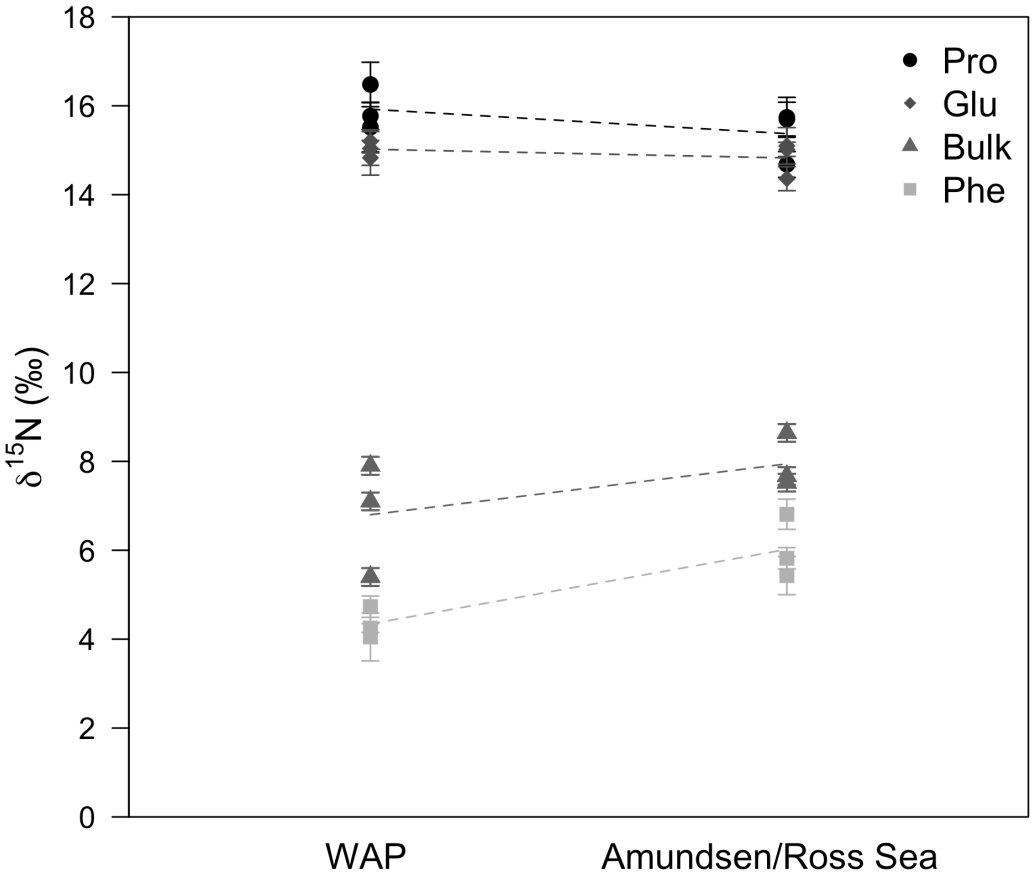

Figure 2.6. Comparison of $\delta^{15}N$ values of Pro, Glu, bulk material, and Phe for crabeater seals. Black circles, dark grey diamonds, medium grey triangles, and light grey squares represent Pro, Glu, bulk, and Phe $\delta^{15}N$ values, respectively. Bulk $\delta^{15}N$ values represent whole blood, with corrections applied if the given sample type analyzed was not whole blood.

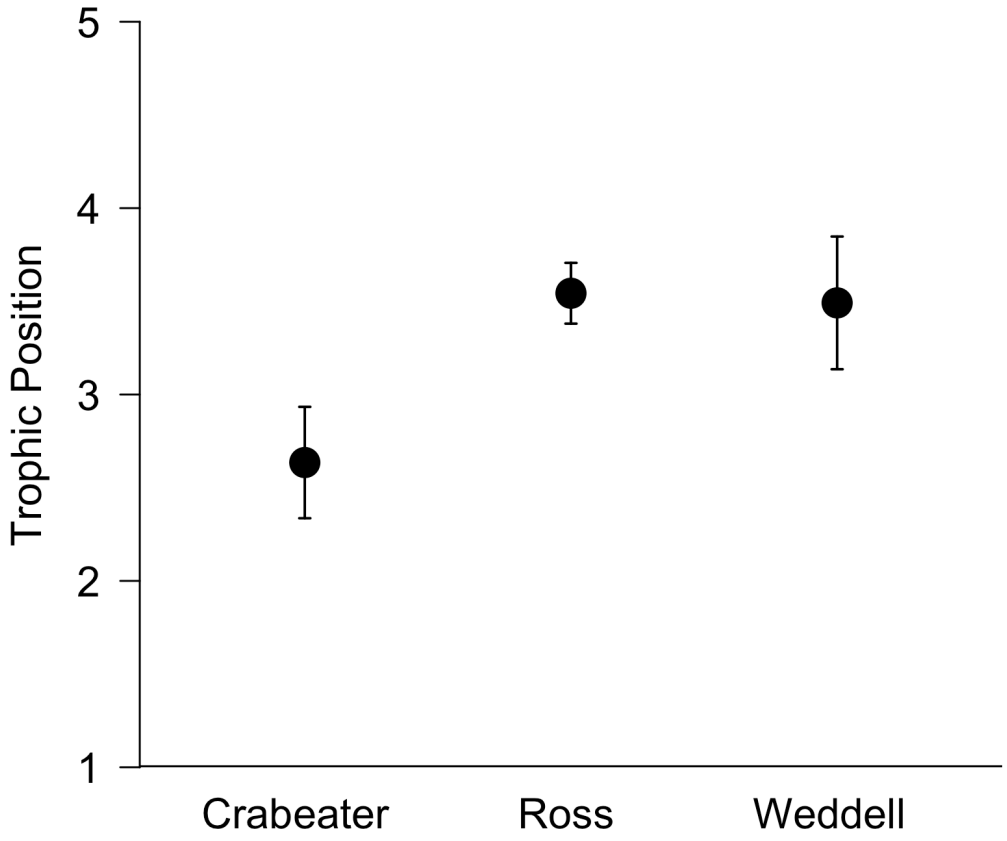

Figure 2.7. Trophic position estimates for crabeater, Ross, and Weddell seals from the Amundsen and Ross Seas. Trophic positions were calculated based on Pro and Phe $\delta^{15}N$ values.

SUPPLEMENTAL MATERIAL

Relationships of bulk $\delta^{13}C$ and $\delta^{15}N$ values with gender, sampling period, age class, and body mass of the Antarctic seals

Sampling period, gender, and age class have no significant effects on the bulk $\delta^{13}C$ values of Ross Seals (Figs. 2.S5 and 2.S6). However, there is a significant, but weak negative relationship between body mass and $\delta^{13}C$ values (R^2 value of 0.3 from a linear regression analysis, Fig. 2.S6). Sampling period, gender, age class, and body mass all have no significant effects on the bulk $\delta^{15}N$ values of Ross seals (Figs. 2.S5-2.S6).

For Weddell seals, sampling period, gender, age class, and body mass have no significant effects on bulk $\delta^{13}C$ values (Figs. 2.S7 and 2.S8). Sampling period, gender, and body mass have no significant effects on bulk $\delta^{15}N$ values (Figs. 2.S7, and 2.S8). However, Weddell bulk $\delta^{15}N$ values are significantly higher in juveniles (12.6 ± 0.6‰, *n*=17) than subadults (11.9 ± 0.7‰, *n*=15) and adults (12.1± 0.5‰, *n*=54) (*p*-values of 0.006 and 0.02, correspondingly, from Bonferroni post-hoc comparisons) (Fig. 2.S7).

Crabeater seal $\delta^{13}C$ values are not affected significantly by sampling period or gender (Fig. 2.S9). Adult crabeater seals have significantly higher $\delta^{13}C$ values (-24.6 ± 1.3 ‰, *n*=76) than subadults (-26.3 ± 0.2 ‰, *n*=10) and juveniles (-26.2 ± 0.4 ‰, *n*=11) from Bonferroni post-hoc comparisons ($p<0.001$ in both cases) (Fig. 2.S9). Additionally, crabeater seal $\delta^{13}C$ values increase significantly with increasing body

mass (R^2 value of 0.4 from a linear regression analysis) (Fig. 2.S10). For $\delta^{15}N$ values of crabeater seals do not vary significantly with gender (Fig. 2.S9). One significant difference occurs across sampling periods: Amundsen Sea $\delta^{15}N$ values are significantly higher for the austral summer 2007/08 sampling (8.1 ± 0.4 ‰, n = 14) than the austral summer 2010/11 sampling (7.3 ± 0.6 ‰, n = 21) (p<0.001 from Bonferroni post-hoc comparisons). Adult crabeater seals have significantly lower $\delta^{15}N$ values (7.0 ± 0.8 ‰, n = 76) than subadult animals (8.3 ± 0.4 ‰, n = 10, p<0.0001 for the Bonferroni post-hoc comparison) and juvenile seals (7.8 ± 0.3 ‰, n = 11, p = 0.01 for the Bonferroni post-hoc comparison) (Fig. 2.S9). The $\delta^{15}N$ values significantly increase with decreasing body mass (Fig. 2.S10, R^2 value of 0.4 from a linear regression analysis).

Discussion of relationships of bulk isotope values with gender, sampling period, age class, and body mass of the Antarctic seals

Our Ross seal bulk $\delta^{13}C$ and $\delta^{15}N$ results suggest a similar diet and foraging region across different genders and age classes. In contrast, the significant relationship between body mass and $\delta^{13}C$ (increasing $\delta^{13}C$ values with decreasing body mass) suggests that Ross seals of different sizes are foraging in slightly different areas. However, no significant relationship exists between body mass and phenylalanine (Phe) $\delta^{15}N$ value, which varies across different environments as described in the main text, for Ross seals. Zhao et al. (2004) found no significant effects of age or sex on Ross seal $\delta^{13}C$ and $\delta^{15}N$ values.

Our Weddell and crabeater seal results indicate no significant effects of gender on $\delta^{13}C$ and $\delta^{15}N$ values, indicating that foraging area and diet do not differ across genders for these species. This finding is consistent with the results of Zhao et al. (2004) and Burns et al. (1998) for crabeater and Weddell seals, respectively. However, Zhao et al. (2004) reported that male Weddell seals have significantly higher $\delta^{13}C$ and $\delta^{15}N$ values than females.

Weddell seal bulk $\delta^{13}C$ values do not vary significantly across age classes, suggesting that these animals do not change their foraging region with age. Zhao et al. (2004) and Aubail et al. (2011) also found no significant variation in bulk $\delta^{13}C$ values across Weddell seal age classes. However, Goetz et al. (2017) found increasing $\delta^{13}C$ values with age for Weddell seals from red blood cell (RBC) sample analysis. Our results point to adult crabeater seals foraging in a different area than subadults and juveniles, perhaps further offshore given their higher $\delta^{13}C$ values, as well as the positive relationship between body mass and $\delta^{13}C$ value for this species. Likewise, Aubail et al. (2011) found significantly higher $\delta^{13}C$ values in crabeater adults than juveniles, and Hückstädt et al. (2012) found $\delta^{13}C$ values significantly increasing with increasing crabeater seal body mass. In contrast, Zhao et al. (2004) found no significant variability in $\delta^{13}C$ values across age groups.

In this study, both Weddell and crabeater seals have significant variability in $\delta^{15}N$ values across age classes. For crabeater seals, our finding of significantly lower $\delta^{15}N$ values in adults than juveniles is supported by the results of Aubail et al. (2011). The observed bulk isotope variation for Weddell and crabeater seals in this study

could have resulted from differences in foraging regions, diet, or both between the various age classes. We did not attempt to explore the drivers of $\delta^{15}N$ variations across age classes of Weddell and crabeater seals further in our compound-specific isotope analysis (CSIA) since limitations entailed in this analysis (i.e., expense and extensive laboratory processing) did not allow for aminio acid $\delta^{15}N$ measurements from a sufficient number of samples for such an investigation. For Weddell seals, we only conducted CSIA on tissues from adults. We performed CSIA on one subadult and five adults for crabeater seals. The subadult had a higher Phe $\delta^{15}N$ value (6.8 ‰) relative to that of the adults (5.6 ± 0.3 ‰) for the Amundsen/Ross sea region. The nitrogen isotope values of Pro and Glu for the subadult (15.7 ‰ and 15.1 ‰, respecitvely) were slightly higher than Pro and Glu $\delta^{15}N$ values of adults (15.2 ± 0.8 ‰ and 14.7 ± 0.5 ‰) for the Amundsen and Ross Seas. This result indicates the higher bulk $\delta^{15}N$ values of subadult than adult crabeater seals may be driven by the former using a habitat with moderately higher baseline $\delta^{15}N$ values and, perhaps, nitrogen drawdown than the latter. However, CSIA must be conducted on considerably more crabeater seal samples before $\delta^{15}N$ variation across age classes can be clearly established and the possible causes can be identified.

The results of other studies measuring bulk $\delta^{15}N$ values of Weddell and crabeater seals differed from our findings. Goetz et al. (2017) found increasing $\delta^{15}N$ values with increasing Weddell seal age. Zhao et al. (2004) compared $\delta^{15}N$ values of Weddell seal pups, juveniles, subadults, and adults, and found only one significant result: adults have higher $\delta^{15}N$ values than subadults. Aubail et al. (2011) reported no

significant difference across Weddell seal age groups, which included juveniles and adults. For crabeater seals, Zhao et al. (2004) found no significant variability in $\delta^{15}N$ values of pups, juveniles, subadults, and adults. Overall, the effects of age, as well as gender, on the isotopic values of crabeater and Weddell seals vary across the research to date. Furthermore, isotope baseline variability may contribute to the differences in bulk isotope values across age groups or genders, as mentioned above and discussed in detail in the main text.

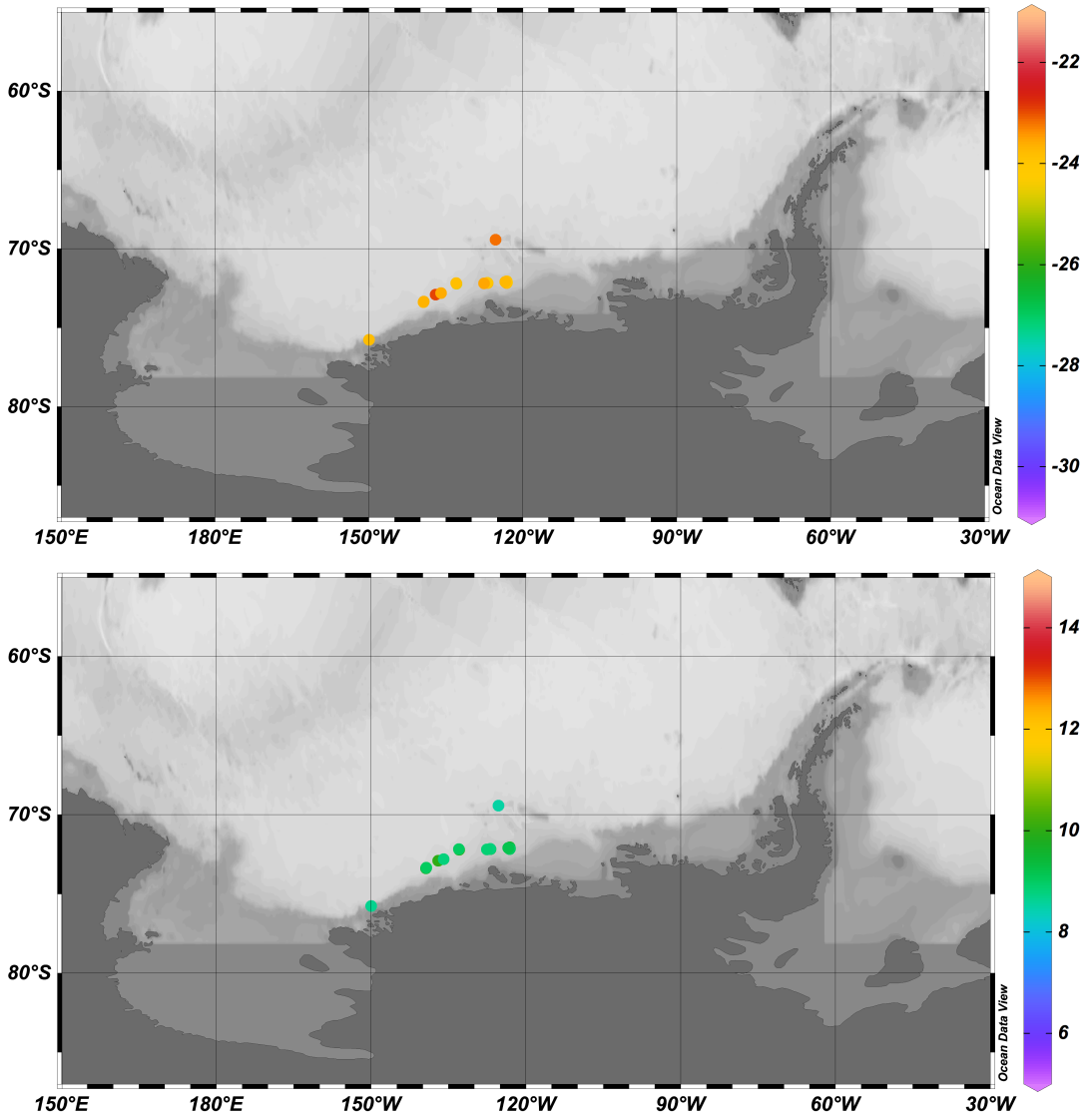

Figure 2.S1. Spatial variation in bulk $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values of Ross seals. Figures were produced in Ocean Data View 4.7.4 (Schlitzer 2015).

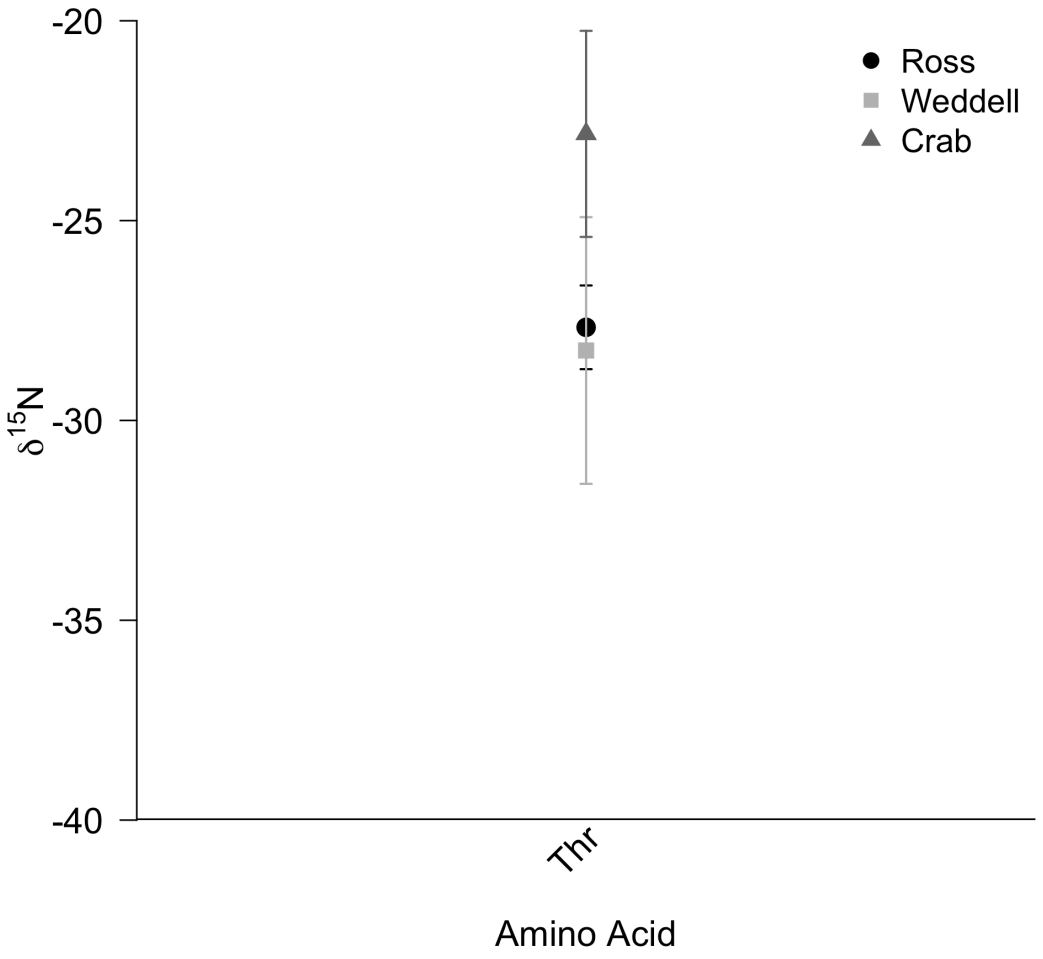

Figure 2.S2. $\delta^{15}N$ values of threonine for Ross, Weddell, and crabeater seals. Species are shown with colors: light grey squares for Weddell seals, medium grey triangles for crabeater seals, and black circles for Ross seals

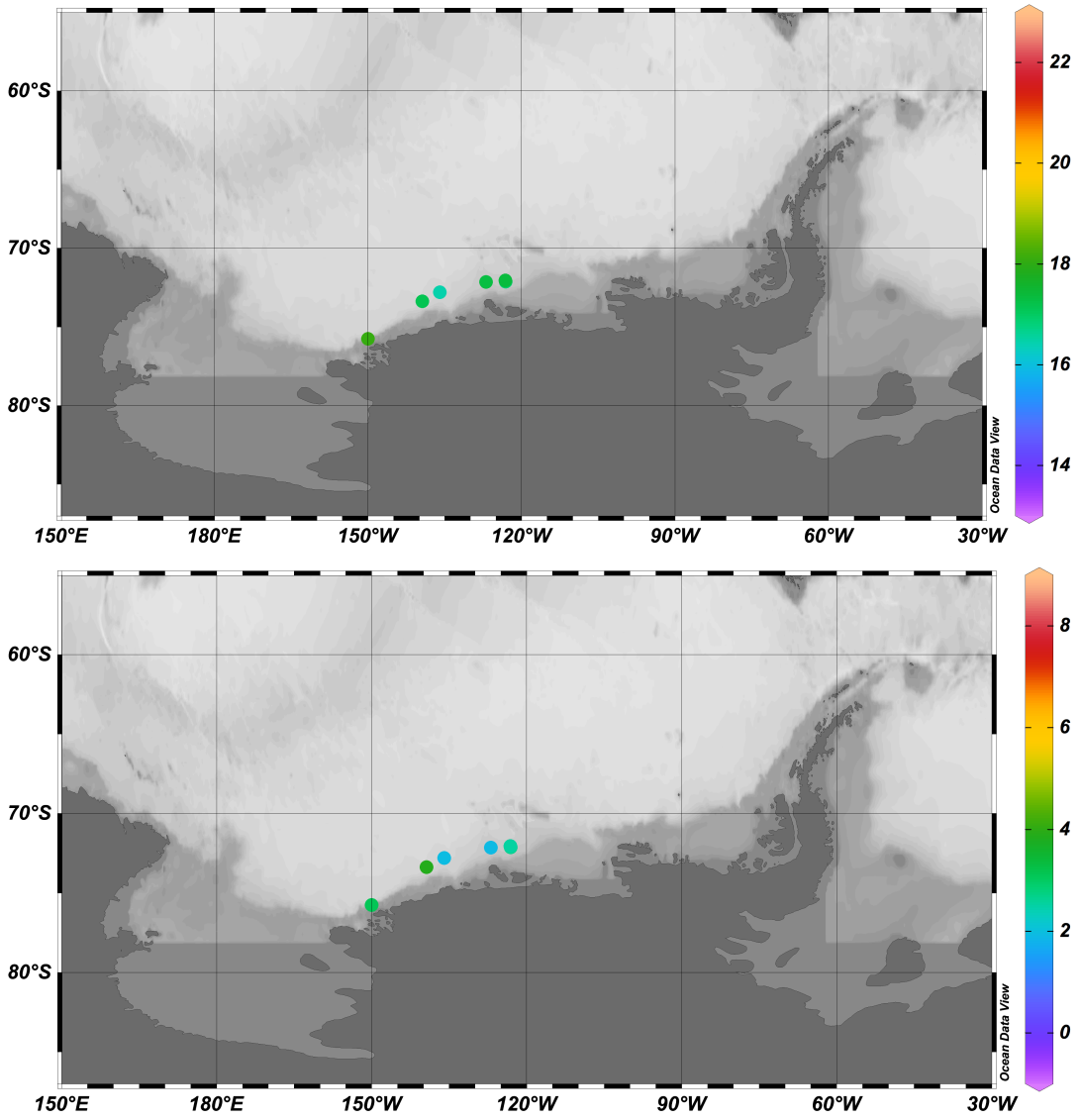

Figure 2.S3. Spatial variation in $\delta^{15}N$ values of Pro (top) and Phe (bottom) values for Ross seals. Figures were produced in Ocean Data View 4.7.4 (Schlitzer 2015).

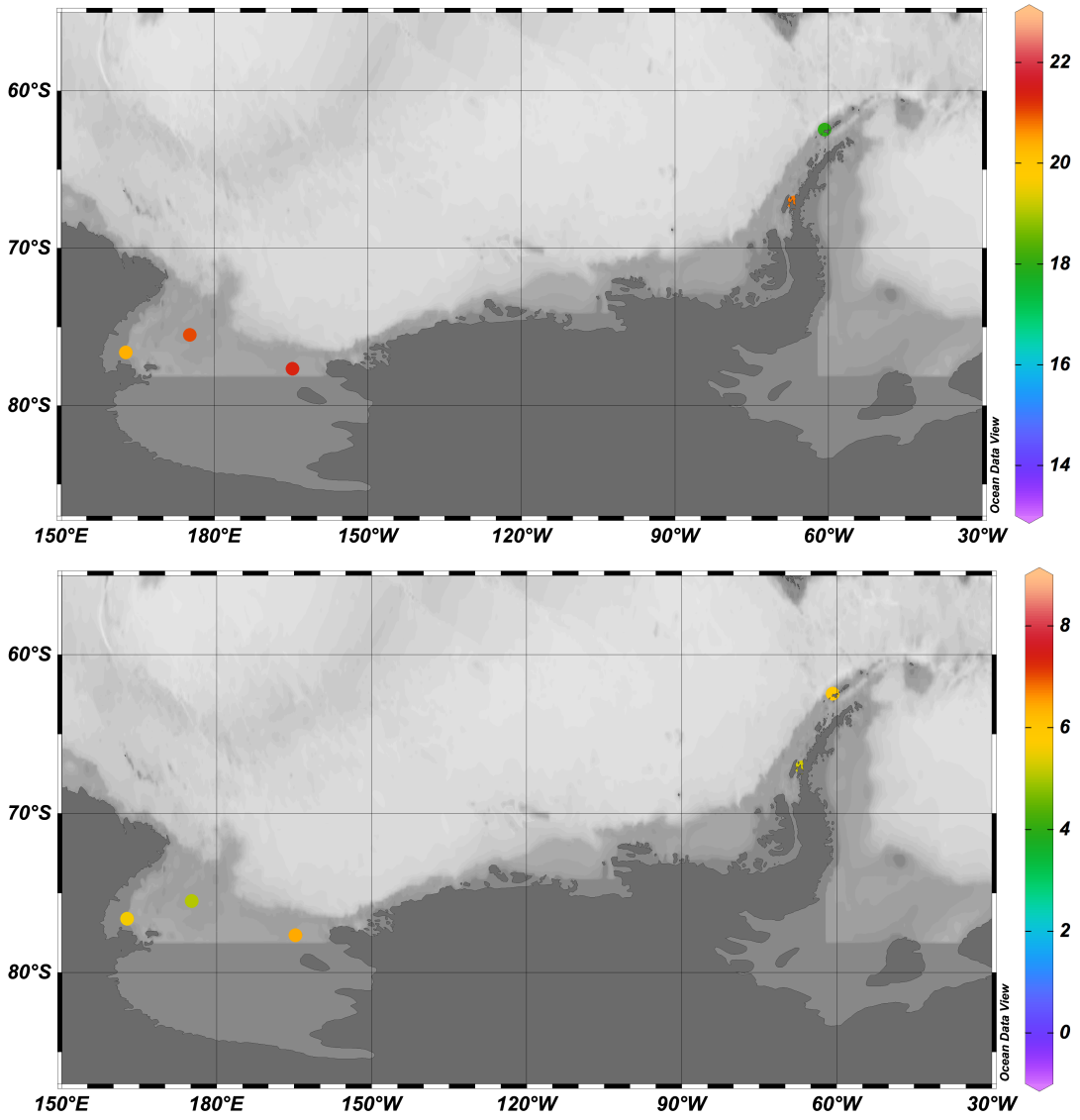

Figure 2.S4. Spatial variation in $\delta^{15}N$ values of Pro (top) and Phe (bottom) values for Weddell seals. Figures were produced in Ocean Data View 4.7.4 (Schlitzer 2015).

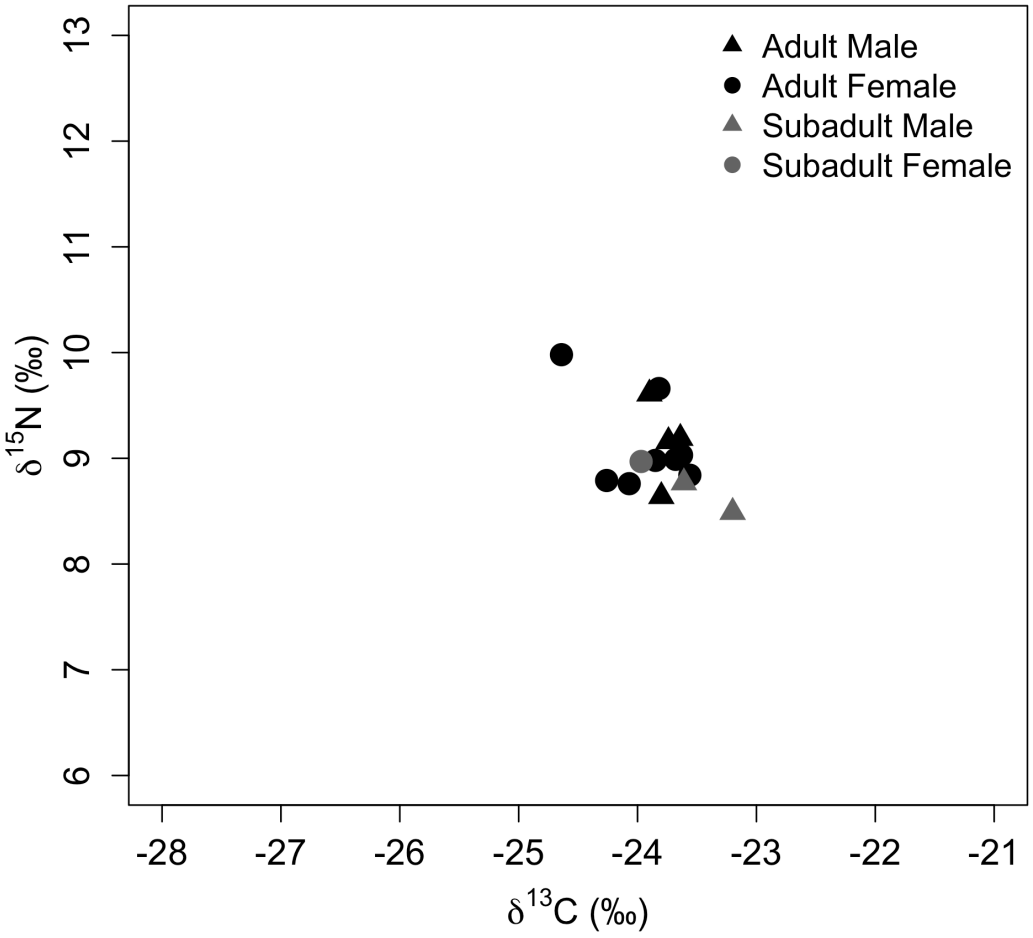

Figure 2.S5. Bulk $\delta^{13}C$ and $\delta^{15}N$ for Ross Seals. Age class and gender are indicated with colors (medium grey for subadults and black for adults) and shapes (triangles and circles for males and females, correspondingly).

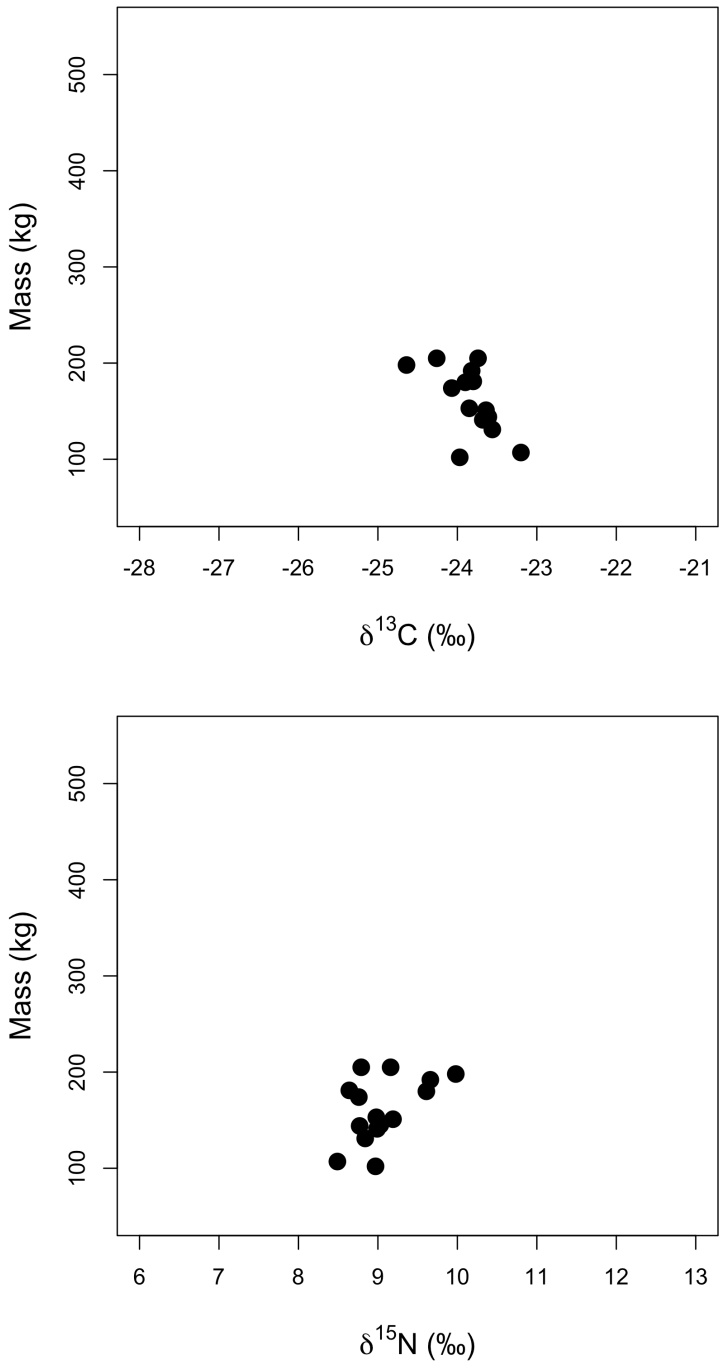

Figure 2.S6. Mass (kg) versus bulk $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values for Ross Seals.

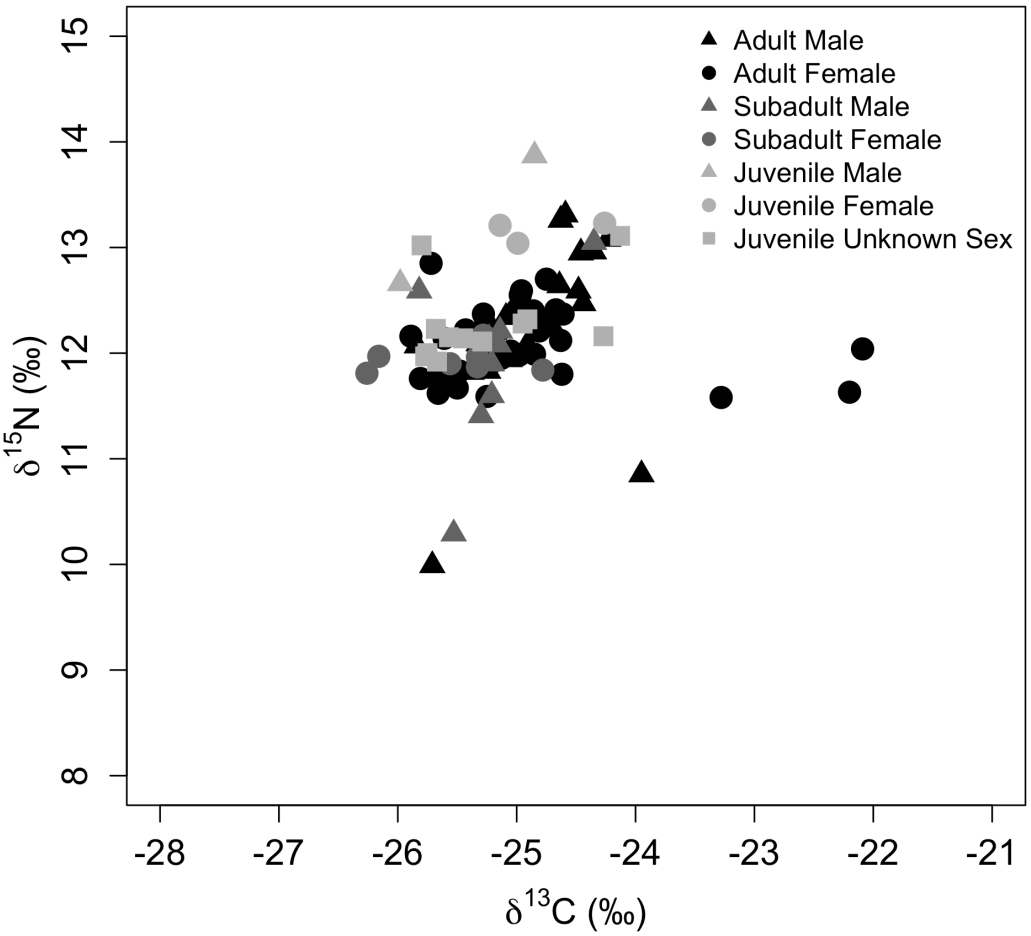

Figure 2.S7. Bulk $\delta^{13}C$ and $\delta^{15}N$ for Weddell Seals. Age class and gender are indicated with colors (light grey for juveniles, medium grey for subadults, and black for adults) and shapes (triangles, circles, and squares for males, females, and unknown sex, correspondingly).

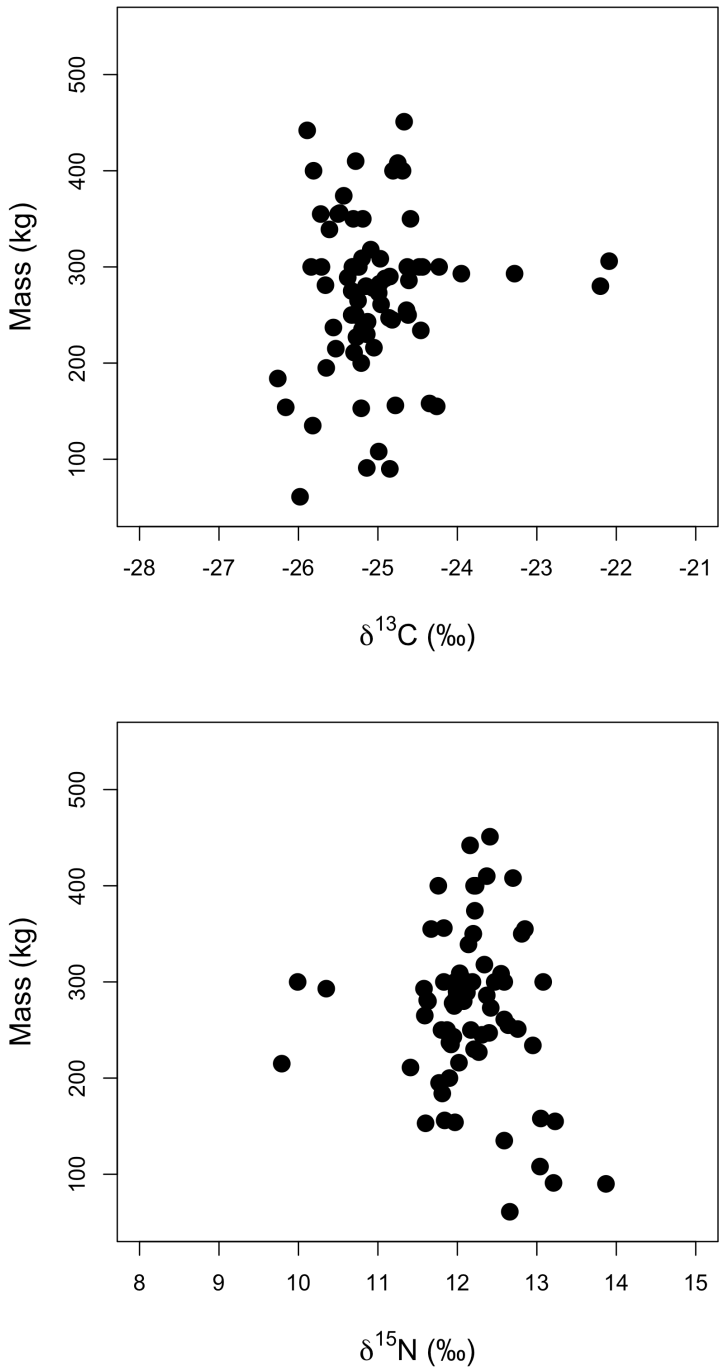

Figure 2.S8. Mass (kg) versus bulk $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values of Weddell Seals.

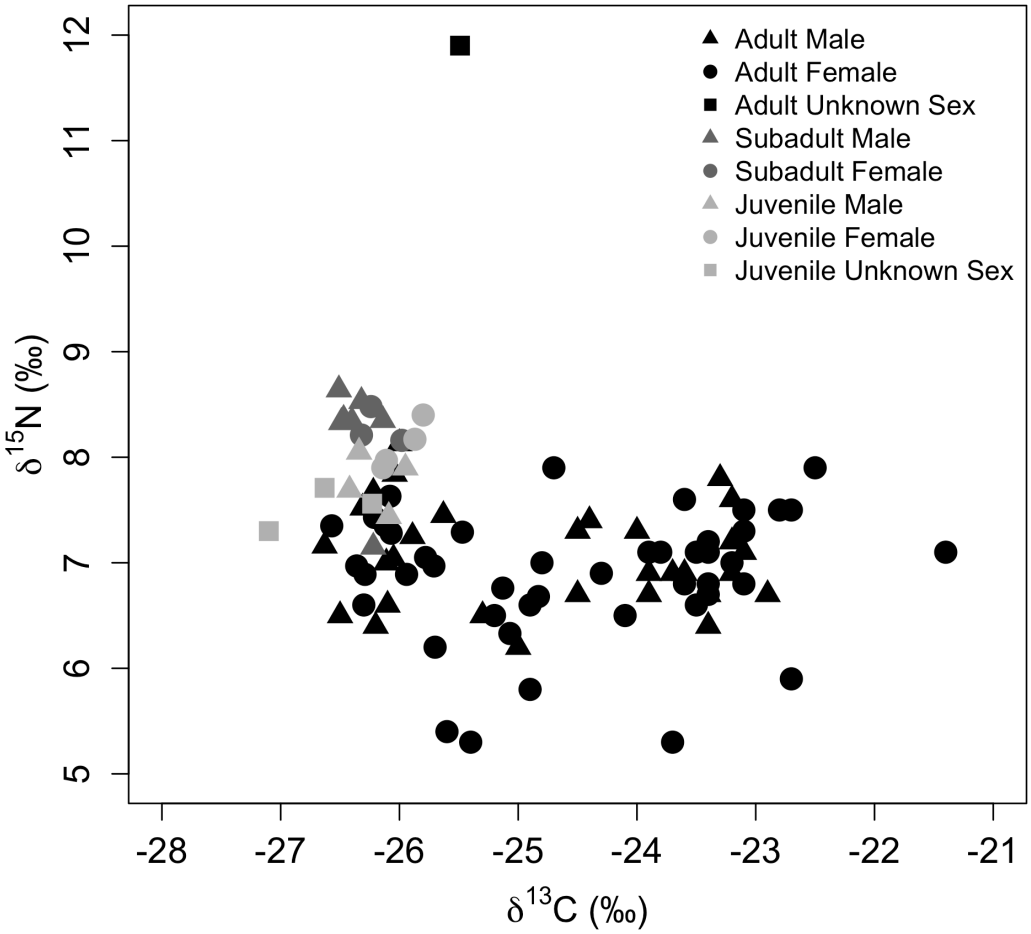

Figure 2.S9. Bulk $\delta^{13}C$ and $\delta^{15}N$ for Crabeater Seals. Age class and gender are indicated with colors (light grey for juveniles, medium grey for subadults, and black for adults) and shapes (triangles, circles, and squares for males, females, and unknown sex, correspondingly).

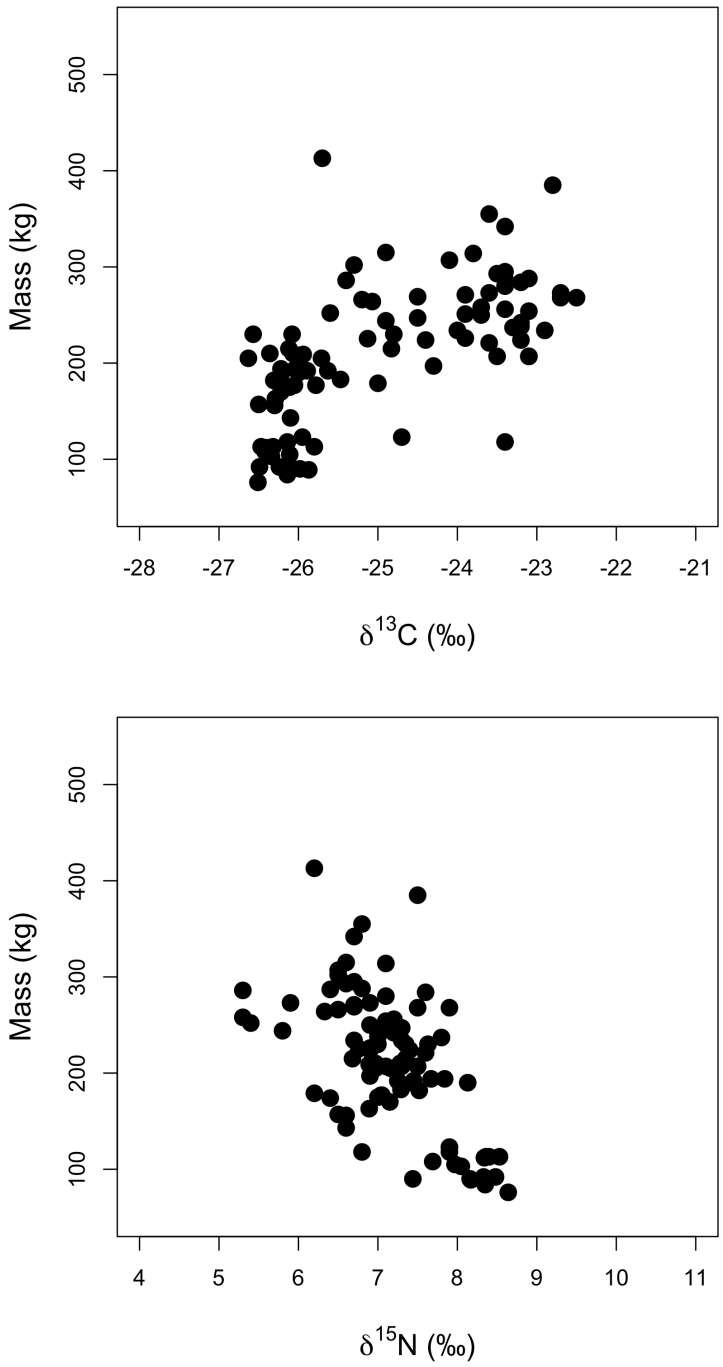

Figure 2.S10. Mass (kg) versus bulk $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) values of crabeater Seals.

Table 2.S1. Sample information for Antarctic Seals. In cases where multiple sample types were obtained from a seal, we indicate the tissue from which isotopic values were used in figures and statistical analyses. Negative latitude and longitude indicate degrees south and west, respectively. Abbreviations: DD, decimal degrees; WB, whole blood; RBCs, red blood cells; F, female; M, male; na, information not available; Su, summer; Sp, spring; F, fall; W, winter; Oden, *RV Oden* cruises; MCM, McMurdo Station region; WAP, West Antarctic Peninsula area; Ad, adult; Sub, subadult; Juv, juvenile; Lat, latitude; Long, longitude.

Species	Sample ID	Source	Season	Sample Type	Age Class	Sex	Weight (kg)	Lat (DD)	Long (DD)
Crabeater	C02	*Oden*	Su 2010/11	Clot	Ad	F	163	-68.6	-102.3
	C03	*Oden*	Su 2008/09	WB	Sub	F	na	-70.6	-107.0
	C03	*Oden*	Su 2010/11	Clot	Ad	F	210	-68.6	-102.5
	C04	*Oden*	Su 2008/09	WB	Sub	M	92	-70.6	-107.0
	C06	*Oden*	Su 2008/09	WB	Sub	M	76	-71.1	-110.5
	C07	*Oden*	Su 2008/09	WB	Sub	F	92	-71.1	-110.5
	C07	*Oden*	Su 2010/11	Hair	Ad	F	205	-69.5	-103.7
	C10	*Oden*	Su 2010/11	Hair	Ad	F	225.4	-69.5	-103.7
	C11	*Oden*	Su 2010/11	Hair	Ad	F	264	-69.5	-103.7
	C14	*Oden*	Su 2010/11	Clot	Ad	F	215	-70.1	-107.4
	C15	*Oden*	Su 2010/11	WB	Sub	M	170	-70.1	-107.4
	C20	*Oden*	Su 2008/09	WB	Ad	M	190	-72.6	-116.0
	C20	*Oden*	Su 2010/11	RBCs	Juv	M	90	-72.7	-114.2
	C21	*Oden*	Su 2008/09	Clot	Sub	M	112	-72.6	-116.0
	C21	*Oden*	Su 2010/11	RBCs	Juv	M	103	-72.7	-114.2
	C22	*Oden*	Su 2008/09	Clot	Sub	M	113	-72.6	-116.0
	C32	*Oden*	Su 2008/09	WB	Ad	F	230	-70.2	-119.9
	C33	*Oden*	Su 2008/09	WB	Ad	M	194	-70.2	-119.9
	C43	*Oden*	Su 2008/09	WB	Ad	F	190	-69.4	-125.3
	C44	*Oden*	Su 2008/09	WB	Ad	M	182	-69.4	-125.3
	C45	*Oden*	Su 2008/09	WB	Ad	F	230	-70.2	-133.5
	C46	*Oden*	Su 2008/09	WB	Sub	F	90	-72.5	-146.5
	C47	*Oden*	Su 2008/09	WB	Ad	M	192	-74.4	-150.7
	C48	*Oden*	Su 2008/09	WB	Ad	F	177	-74.4	-150.7

C50	*Oden*	Su 2008/09	WB	Sub	M	84	-75.4	-151.3
C51	*Oden*	Su 2008/09	WB	Ad	F	210	-75.4	-151.3
C52	*Oden*	Su 2008/09	WB	Ad	F	183	-75.4	-151.3
C143	*Oden*	Su 2010/11	WB	Juv	F	105	-72.1	-119.7
C144	*Oden*	Su 2010/11	WB	Juv	F	118	-72.1	-119.7
C153	*Oden*	Su 2010/11	WB	Ad	M	192	-72.1	-123.5
C154	*Oden*	Su 2010/11	WB	Ad	M	177	-72.1	-123.5
C155	*Oden*	Su 2010/11	Hair	Juv	M	108	-72.2	-126.7
C156	*Oden*	Su 2010/11	WB	Juv	M	123	-72.2	-126.7
C157	*Oden*	Su 2010/11	WB	Juv	F	113	-72.2	-126.7
C158	*Oden*	Su 2010/11	WB	Juv	F	89	-72.2	-126.7
C173	*Oden*	Su 2010/11	WB	Ad	F	209	-72.8	-135.6
C174	*Oden*	Su 2010/11	WB	Ad	M	175	-75.3	-139.5
C175	*Oden*	Su 2010/11	Hair	Ad	F	215	-73.3	-139.5
C176	*Oden*	Su 2010/11	WB	Ad	M	205	-73.3	-139.5
C177	*Oden*	Su 2010/11	WB	Ad	M	194	-75.8	-150.0
Cr 1	MCM	Su 2009/10	Hair	Juv	na	na	-77.6	166.2
Cr Royds	MCM	Su 2009/10	Hair	Juv	na	na	-77.6	166.2
Cr 2	MCM	Su 2009/10	Hair	Juv	na	na	-77.6	166.2
CS11-01	MCM	Su 2010/11	WB	Ad	na	na	-77.7	166.5
G001	Hückstädt et al. (2012a)	F 2001	Whisker	Ad	F	na	-67.3	-67.6
G003	Hückstädt et al. (2012a)	F 2001	Whisker	Ad	F	258	-67.3	-67.6
G004	Hückstädt et al. (2012a)	F 2001	Whisker	Ad	M	342	-69.2	-72.3
G005	Hückstädt et al. (2012a)	F 2001	Whisker	Ad	F	293	-69.3	-72.4
G006	Hückstädt et al. (2012a)	F 2001	Whisker	Ad	F	413	-69.3	-72.5
G007	Hückstädt	F 2001	Whisker	Ad	M	287	-69.3	-72.5

		et al. (2012a)							
	G008	Hückstädt et al. (2012a)	F 2001	Whisker	Ad	F	355	-69.1	-72.4
	G009	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	M	179	-67.7	-69.3
	G010	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	F	307	-68.1	-70.4
	G012	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	F	288	-68.1	-70.2
	G013	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	M	234	-68.1	-70.2
	G014	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	M	284	-68.1	-70.1
	G015	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	M	234	-67.2	-70.2
	G016	Hückstädt et al. (2012a)	W 2001	Whisker	Ad	F	273	-67.4	-70.9
	G017	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	118	-66.4	-66.8
	G018	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	157	-66.8	-66.8
	G019	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	156	-66.8	-66.8
	G020	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	143	-66.6	-67.5
	G021	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	271	-66.6	-67.5
	G022	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	268	-67.4	-67.7
	G023	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	174	-67.6	-68.2
	G024	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	256	-67.6	-69.0
	G026	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	266	-67.6	-69.0

G027	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	226	-66.6	-67.5
G028	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	314	-68.5	-69.8
G029	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	242	-68.7	-70.0
G030	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	M	250	-66.6	-67.5
G031	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	385	-66.3	-66.6
G032	Hückstädt et al. (2012a)	F 2002	Whisker	Ad	F	230	-68.8	-69.9
G033	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	F	268	-66.3	-66.7
G034	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	F	295	-66.5	-67.1
G035	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	F	238	-66.4	-66.9
G036	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	F	207	-66.4	-66.9
G038	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	273	-67.2	-70.6
G039	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	247	-68.6	-76.0
G040	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	302	-68.5	-75.8
G041	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	269	-68.1	-75.0
G042	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	224	-68.0	-74.9
G043	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	224	-68.0	-74.8
G044	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	F	280	-65.7	-68.7
G045	Hückstädt et al.	W 2002	Whisker	Ad	F	221	-65.6	-68.6

		(2012a)							
	G046	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	237	-65.5	-68.5
	G047	Hückstädt et al. (2012a)	W 2002	Whisker	Ad	M	254	-65.7	-68.5
	G102	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	286	-67.2	-66.9
	G104	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	197	-67.2	-66.9
	G105	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	251	-67.2	-66.8
	G106	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	207	-67.2	-66.8
	G107	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	315	-67.0	-67.4
	G108	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	207	-67.2	-66.8
	G110	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	123	-67.1	-66.8
	G112	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	252	-65.2	-64.2
	G113	Hückstädt et al. (2012a)	F 2007	Whisker	Ad	F	244	-66.1	-65.4
	W02	*Oden*	Su 2008/09	WB	Sub	M	113	-71.7	-112.2
Weddell	W01	*Oden*	Su 2010/11	Hair	Ad	M	251	-72.6	-115.1
	W02	*Oden*	Su 2010/11	Hair	Ad	F	300	-72.6	-115.1
	W04	*Oden*	Su 2010/11	Clot	Ad	F	400	-72.8	-114.4
	W06	*Oden*	Su 2010/11	Clot	Ad	M	400	-72.9	-114.2
	W10	*Oden*	Su 2008/09	WB	Sub	F	156	-77.3	-165.5
	W11	*Oden*	Su 2008/09	WB	Sub	M	153	-77.3	-165.5
	W12	*Oden*	Su 2008/09	WB	Ad	M	318	-77.3	-165.5
	W14	*Oden*	Su 2008/09	WB	Ad	M	288	-77.3	-165.5
	W15	*Oden*	Su 2008/09	WB	Sub	M	211	-77.3	-165.5
	W17	*Oden*	Su	WB	Ad	M	278	-77.3	-165.5

			2008/09						
	W19	*Oden*	Su 2008/09	WB	Ad	F	309	-77.3	-165.5
	W103	*Oden*	Su 2010/11	WB	Ad	M	300	-72.6	-115.1
	W112	*Oden*	Su 2010/11	Hair	Ad	M	350	-72.9	-114.0
	W113	*Oden*	Su 2010/11	WB	Ad	M	255	-72.9	-114.0
	W116	*Oden*	Su 2010/11	WB	Ad	M	300	-71.7	-115.5
	W117	*Oden*	Su 2010/11	WB	Ad	F	290	-71.7	-115.5
	W118	*Oden*	Su 2010/11	WB	Ad	F	216	-71.7	-115.5
	W130	*Oden*	Su 2010/11	WB	Sub	M	158	-72.5	-116.6
	W133	*Oden*	Su 2010/11	WB	Ad	M	300	-72.5	-116.6
	W136	*Oden*	Su 2010/11	WB	Ad	F	235	-72.9	-116.9
	W137	*Oden*	Su 2010/11	WB	Ad	F	243	-72.9	-116.9
	W155	*Oden*	Su 2010/11	WB	Juv	F	155	-72.1	-119.2
	W157	*Oden*	Su 2010/11	WB	Juv	F	108	-72.1	-119.2
	W174	*Oden*	Su 2010/11	WB	Ad	F	250	-72.1	-119.7
	W175	*Oden*	Su 2010/11	WB	Ad	M	300	-72.1	-119.7
	W176	*Oden*	Su 2010/11	WB	Ad	M	na	-72.1	-119.7
	W177	*Oden*	Su 2010/11	WB	Ad	M	234	-72.1	-119.7
	W182	*Oden*	Su 2010/11	Hair	Sub	M	215	-72.8	-135.8
	W185	*Oden*	Su 2010/11	WB	Ad	F	400	-75.5	-184.9
	W186	*Oden*	Su 2010/11	WB	Sub	F	154	-75.5	-184.9
	W208	*Oden*	Su 2010/11	WB	Sub	M	135	-78.7	-164.2
	W209	*Oden*	Su 2010/11	WB	Juv	M	61	-78.7	-164.2
	W214	*Oden*	Su 2010/11	WB	Sub	F	184	-77.6	-166.3
	W216	*Oden*	Su 2010/11	WB	Juv	F	91	-77.6	-166.3
	W219	*Oden*	Su 2010/11	WB	Sub	F	237	-77.7	-164.7
	W220	*Oden*	Su 2010/11	WB	Ad	F	261	-77.7	-164.7
	W222	*Oden*	Su 2010/11	WB	Ad	M	350	-77.7	-164.7
	W223	*Oden*	Su 2010/11	WB	Juv	M	90	-77.7	-164.7
	WS10-	MCM	Su 2009/10	RBCs	Ad	F	308.5	-75.8	162.8

	11								
	WS10-12	MCM	Su 2009/10	RBCs	Ad	F	282.5	-75.8	162.8
	WS10-13	MCM	Su 2009/10	RBCs	Ad	F	245	-75.8	162.8
	WS10-17	MCM	Su 2009/10	RBCs	Ad	F	356	-76.5	162.8
	WS10-18	MCM	Su 2009/10	RBCs	Ad	F	265	-76.5	162.8
	WS11-11	MCM	Su 2010/11	WB	Ad	F	281	-76.6	162.7
	WS11-12	MCM	Su 2010/11	WB	Ad	F	355	-77.9	166.8
	WS11-13	MCM	Su 2010/11	WB	Ad	F	247	-76.9	162.5
	WS11-14	MCM	Su 2010/11	WB	Ad	F	286	-76.6	162.7
	WS11-15	MCM	Su 2010/11	WB	Ad	F	195	-77.2	163.5
	WS12-11	MCM	Su 2011/12	RBCs	Ad	F	273	-76.9	162.8
	WS12-12	MCM	Su 2011/12	RBCs	Ad	F	374	-77.9	166.8
	WS12-13	MCM	Su 2011/12	RBCs	Ad	F	410	-77.9	166.8
	WS12-14	MCM	Su 2011/12	RBCs	Ad	M	227	-76.1	162.4
	WS12-15	MCM	Su 2011/12	RBCs	Ad	M	289	-76.5	162.7
	WS12-22	MCM	Sp 2012	WB	Ad	F	451	-77.7	166.5
	WS12-23	MCM	Sp 2012	WB	Ad	F	442	-77.7	166.9
	WS12-24	MCM	Sp 2012	WB	Ad	F	339	-77.7	166.8
	WS12-25	MCM	Sp 2012	WB	Ad	F	355	-77.7	166.9
	WS12-26	MCM	Sp 2012	WB	Ad	F	408	-77.7	166.7
	G103	WAP	F 2007	Serum	Ad	F	306	-67.2	-66.9
	G111	WAP	F 2007	Plasma	Ad	F	280	-67.1	-66.8
	LW11-03	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-05	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-06	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-07	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-08	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-09	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7

	LW11-10	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-11	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-12	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-13	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-14	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW11-15	MCM	Su 2010/11	WB	Juv	na	na	-74.9	163.7
	LW15-01	MCM	Sp 2015	WB	Ad	M	300	-77.8	166.8
	LW15-02	MCM	Sp 2015	WB	Sub	M	280	-77.8	166.8
	LW15-03	MCM	Sp 2015	WB	Ad	M	300	-77.8	166.8
	LW15-04	MCM	Sp 2015	WB	Ad	M	300	-77.8	166.8
	LW15-05	MCM	Sp 2015	WB	Ad	M	300	-77.8	166.8
	LW15-06	MCM	Sp 2015	WB	Ad	M	300	-77.7	166.4
	LW15-07	MCM	Sp 2015	WB	Ad	F	350	-77.7	166.4
	LW15-08	MCM	Sp 2015	WB	Sub	F	250	-77.8	166.8
	LW15-09	MCM	Sp 2015	WB	Sub	F	275	-77.7	166.3
	LW15-10	MCM	Sp 2015	WB	Sub	M	230	-77.7	166.4
	LW15-11	MCM	Sp 2015	WB	Sub	F	250	-77.7	166.4
	LW15-12	MCM	Sp 2015	WB	Sub	M	200	-77.7	166.4
	W006	WAP	Su 2009/10	Whisker	Ad	M	293	-62.5	-60.8
	W013	WAP	Su 2009/10	Whisker	Ad	F	293	-62.5	-60.8
Ross	R01	*Oden*	Su 2008/09	WB	Sub	M	107	-69.4	-125.3
	R101	*Oden*	Su 2010/11	WB	Ad	M	180	-72.1	-123.2
	R102	*Oden*	Su 2010/11	WB	Ad	F	145	-72.2	-123.2
	R103	*Oden*	Su 2010/11	WB	Sub	F	102	-72.1	-123.1
	R104	*Oden*	Su 2010/11	WB	Ad	M	205	-72.1	-123.5
	R105	*Oden*	Su 2010/11	WB	Ad	M	151	-72.2	-126.9
	R106	*Oden*	Su 2010/11	WB	Ad	F	174	-72.1	-127.0

	R107	*Oden*	Su 2010/11	WB	Ad	F	131	-72.2	-127.6
	R108	*Oden*	Su 2010/11	WB	Ad	F	198	-72.2	-132.9
	R109	*Oden*	Su 2010/11	WB	Ad	F	153	-72.2	-133.0
	R110	*Oden*	Su 2010/11	Hair	Ad	F	205	-72.9	-137.1
	R111	*Oden*	Su 2010/11	WB	Sub	M	144	-72.8	-136.0
	R112	*Oden*	Su 2010/11	WB	Ad	F	192	-73.4	-139.4
	R113	*Oden*	Su 2010/11	WB	Ad	F	141	-73.3	-139.4
	R114	*Oden*	Su 2010/11	WB	Ad	M	181	-75.8	-150.0

Table 2.S2. Effect of lipid extraction on isotopic values of crabeater, Weddell, and Ross seals. Effect of lipid extraction on isotopic values. Sample ID as in Table 2.S1. Abbreviations: WB, whole blood without lipid extraction; LE, whole blood with lipid extraction. The difference in isotopic value between whole blood samples with and without lipid extraction is reported. The difference is 0.0 ± 0.1 ‰ and 0.2 ± 0.1 ‰ for $\delta^{13}C$ and $\delta^{15}N$, respectively. The mean offset between the isotopic values with and without lipid extraction do not exceed the instrument error of 0.2 ‰ for both $\delta^{13}C$ and $\delta^{15}N$ values.

Species	Sample ID	Year	Sample Type	$\delta^{13}C$ (‰)	LE $\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	LE $\delta^{15}N$ (‰)	$\delta^{13}C$ – LE $\delta^{13}C$ (‰)	$\delta^{15}N$ – LE $\delta^{15}N$ (‰)
Crabeater	C03	2008	WB	-26.3	-26.5	8.2	8.0	0.2	0.2
	C06	2008	WB	-26.5	-26.6	8.6	8.5	0.1	0.1
	C07	2008	WB	-26.2	-26.3	8.5	8.3	0.1	0.2
	C20	2008	WB	-26.0	-26.0	8.1	7.9	0.0	0.2
	C46	2008	WB	-26.0	-26.0	8.2	8.1	0.0	0.1
	C52	2008	WB	-25.5	-25.7	7.3	7.1	0.2	0.2
	C153	2010	WB	-25.9	-25.9	7.3	7.2	0.0	0.1
	C154	2010	WB	-26.1	-26.1	7.0	6.9	0.0	0.1
	C176	2010	WB	-26.6	-26.7	7.2	7.0	0.1	0.2
Weddell	W12	2008	WB	-25.1	-25.1	12.3	12.1	0.0	0.2
	W15	2008	WB	-25.3	-25.3	11.4	11.2	0.0	0.2
	W117	2010	WB	-24.9	-24.9	12.0	11.8	0.0	0.2
	W216	2010	WB	-25.1	-25.2	13.2	13.1	0.1	0.1
	W223	2010	WB	-24.9	-24.9	13.9	13.8	0.0	0.1
Ross	R01	2008	WB	-23.2	-23.2	8.5	8.4	0.0	0.1
	R101	2010	WB	-23.9	-23.9	9.6	9.4	0.0	0.2
	R102	2010	WB	-23.6	-23.7	9.0	8.8	0.1	0.2
	R103	2010	WB	-24.0	-24.0	9.0	8.8	0.0	0.2
	R108	2010	WB	-24.6	-24.7	10.0	9.8	0.1	0.2
	R112	2010	WB	-23.8	-23.8	9.7	9.6	0.0	0.1
	R114	2010	WB	-23.7	-23.7	8.6	8.5	0.0	0.1

Table 2.S3. Bulk $\delta^{13}C$ and $\delta^{15}N$ values of crabeater, Weddell, and Ross seals for multiple tissue types. These isotopic values are used to calculate the isotopic offsets between different tissue types, see Table 2.S4 below. Abbreviations are as in Tables 2.S1.

Species	ID	Year	WB		Clot		RBCs		Hair	
			$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Crabeater	C14	Su 2010/11			-26.1	7.3			-23.7	6.4
	C143	Su 2010/11	-26.1	8.0					-24.5	7.5
	C157	Su 2010/11	-25.8	8.4					-24.6	8.7
	C158	Su 2010/11	-25.9	8.2					-24.4	8.0
	C173	Su 2010/11	-25.9	6.9					-24.2	6.6
	C174	Su 2010/11	-26.1	7.0	-26.1	6.8			-24.4	7.5
	C176	Su 2010/11	-26.6	7.2			-26.8	6.9		
	C02	Su 2010/11			-26.3	6.9			-24.7	7.1
	C20	Su 2010/11					-26.1	7.4	-25.0	7.0
	C21	Su 2010/11					-26.3	8.1	-24.9	7.3
	C03	Su 2010/11			-26.4	7.0			-24.2	7.0
Weddell	WS12-22	Sp 2012	-24.7	12.4			-24.4	12.1		
	WS12-23	Sp 2012	-25.9	12.2			-25.3	11.7		
	WS12-24	Sp 2012	-25.6	12.1			-25.5	12.1		
	WS12-25	Sp 2012	-25.7	12.9			-25.0	12.0		
	WS12-26	Sp 2012	-24.8	12.7			-24.7	12.5		
	W116	Su 2010/11	-24.5	12.6					-23.2	12.9
	W117	Su 2010/11	-24.9	12.0					-23.3	12.7
	W118	Su 2010/11	-25.1	12.0	-24.9	11.9				
	W130	Su 2010/11	-24.4	13.1			-24.4	13.0		
	W133	Su 2010/11	-24.4	12.5					-23.0	13.1
	W136	Su 2010/11	-25.2	11.9	-25.3	12.0				
	W137	Su 2010/11	-25.1	12.0			-25.1	11.9	-23.6	12.8
	W176	Su	-24.3	13.0					-22.9	13.0

		2010/11								
	W208	Su 2010/11	-25.8	12.6			-25.9	12.4		
	W216	Su 2010/11	-25.1	13.2	-25.0	13.2				
	W219	Su 2010/11	-25.6	11.9	-25.4	11.9				
	W220	Su 2010/11	-25.0	12.6	-25.0	12.4				
	W04	Su 2010/11			-24.8	12.2			-23.5	12.6
	W06	Su 2010/11			-24.7	12.2			-23.5	12.2
Ross	R101	Su 2010/11	-23.9	9.6					-22.6	10.3
	R103	Su 2010/11	-24.0	9.0					-22.8	11.0
	R105	Su 2010/11	-23.6	9.2					-22.4	10.1
	R107	Su 2010/11	-23.6	8.8					-22.4	10.5
	R108	Su 2010/11	-24.6	10.0					-23.0	10.8

Table 2.S4. Calculated isotopic offsets between different tissue types for crabeater, Weddell, and Ross seals. Abbreviations are as in Tables 2.S1. If a calculated mean offset is ≤ 0.2 ‰, then the offset between the two tissue types is considered insignificant (less than instrumental error).

Species	Offset Type	Sample ID	$\delta^{13}C$ Offset (‰)	$\delta^{15}N$ Offset (‰)	Mean $\delta^{13}C$ Offset (‰)	Mean $\delta^{15}N$ Offset (‰)
Crabeater	WB – Clot	C174	0.0	0.2	0.0	0.2
	WB – RBCs	C176	0.2	0.2	0.2	0.2
	WB – Hair	C143	-1.6	0.4	-1.6	0.0
		C157	-1.2	-0.3		
		C158	-1.5	0.2		
		C173	-1.7	0.3		
		C174	-1.7	-0.5		
	Clot – Hair	C14	-2.4	0.9	-2.0	0.0
		C174	-1.7	-0.7		
		C2	-1.5	-0.2		
		C3	-2.1	0.0		
	RBCs – Hair	C20	-1.1	0.4	-1.3	0.6
		C21	-1.5	0.8		
Weddell	WB – Clot	W118	-0.2	0.1	-0.1	0.1
		W136	0.1	-0.1		
		W216	-0.1	0.0		
		W219	-0.2	0.0		
		W220	0.0	0.2		
	WB – RBCs	WS12-22	-0.2	0.3	-0.2	0.3
		WS12-23	-0.6	0.4		
		WS12-24	-0.2	0.1		
		WS12-25	-0.7	0.9		
		WS12-26	-0.1	0.2		
		W130	0.1	0.1		
		W137	0.0	0.0		
		W208	0.0	0.2		
	WB – Hair	W116	-1.3	-0.3	-1.4	-0.5
		W117	-1.5	-0.7		
		W133	-1.4	-0.6		
		W137	-1.5	-0.9		
		W176	-1.4	0.0		
	Clot – Hair	W4	-1.3	-0.4	-1.2	-0.2
		W6	-1.2	0.0		
	RBCs – Hair	W137	-1.5	-0.9	-1.5	-0.9

Ross	WB – Hair	R101 R103 R105 R107 R108	-1.3 -1.2 -1.2 -1.2 -1.6	-0.7 -2.0 -0.9 -1.6 -0.8	-1.3	-1.2

Table 2.S5. Bulk $\delta^{13}C$ and $\delta^{15}N$ values of Weddell seals for multiple blood sample types. These isotopic values are used to calculate the isotopic offsets between these different sample types, see Table 2.S6 below. Abbreviations are as in Tables 2.S1.

ID	Year	WB		Plasma		Serum		RBCs	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
LW15-01	Sp 2015	-25.8	12.1	-26.4	12.3	-26.2	12.7		
LW15-02	Sp 2015	-25.2	12.1	-25.6	13.0	-25.3	13.4		
LW15-03	Sp 2015	-25.3	12.1	-25.7	12.7	-25.5	13.1		
LW15-11	Sp 2015	-25.3	12.2	-26.2	12.8	-25.8	13.3		
LW15-12	Sp 2015	-25.2	11.9	-25.8	12.8	-25.5	13.3		
WS12-22	Sp 2012	-24.7	12.4					-24.4	12.1
WS12-23	Sp 2012	-25.9	12.2					-25.3	11.7
WS12-24	Sp 2012	-25.6	12.1					-25.5	12.1
WS12-25	Sp 2012	-25.7	12.9					-25.0	12.0
WS12-26	Sp 2012	-24.8	12.7					-24.7	12.5
W130	Su 2010/11	-24.4	13.1					-24.4	13.0
W137	Su 2010/11	-25.1	12.0					-25.1	11.9
W208	Su 2010/11	-25.8	12.6					-25.9	12.4

Table 2.S6. Calculated isotopic offsets between different blood sample types for Weddell seals. Abbreviations are as in Tables 2.S1. If a calculated mean offset is ≤ 0.2 ‰, then the offset between the two sample types is considered insignificant (less than instrumental error).

Offset Type	Sample ID	$\delta^{13}C$ Offset (‰)	$\delta^{15}N$ Offset (‰)	Mean $\delta^{13}C$ Offset (‰)	Mean $\delta^{15}N$ Offset (‰)
Plasma – Serum	LW15-01	-0.2	-0.4	-0.3	-0.4
	LW15-02	-0.3	-0.4		
	LW15-03	-0.2	-0.4		
	LW15-11	-0.3	-0.5		
	LW15-12	-0.3	-0.5		
WB – Serum	LW15-01	0.4	-0.6	0.3	-1.1
	LW15-02	0.2	-1.3		
	LW15-03	0.1	-1.0		
	LW15-11	0.5	-1.2		
	LW15-12	0.3	-1.4		
WB – Plasma	LW15-01	0.5	-0.2	0.6	-0.7
	LW15-02	0.4	-0.9		
	LW15-03	0.4	-0.6		
	LW15-11	0.9	-0.7		
	LW15-12	0.6	-0.9		
WB – RBCs	WS12-22	-0.3	0.3	-0.2	0.3
	WS12-23	-0.6	0.5		
	WS12-24	-0.1	0.0		
	WS12-25	-0.7	0.9		
	WS12-26	-0.1	0.2		
	W130	0.1	0.1		
	W137	0.0	0.0		
	W208	0.0	0.2		

Table 2.S7. Bulk $\delta^{13}C$ and $\delta^{15}N$ values of crabeater, Weddell, and Ross seals. Note, bulk $\delta^{13}C$ and $\delta^{15}N$ values are reported for the original measurement (Orig.) and with a correction to whole blood (Corr.) if the sample is a tissue type with a significant isotopic offset from whole blood. Isotopic offset between whole blood and the given sample type are reported in Tables S4 and S6, above. Atomic C:N ratios are from the original measurements. Samples with an asterisk are from Hückstädt et al. (2012a); all other data are from this study. Abbreviations are as in Table 2.S1.

Species	Sample ID	Season	Sample Type	Orig. $\delta^{13}C$ (‰)	Orig. $\delta^{15}N$ (‰)	Corr. $\delta^{13}C$ (‰)	Corr. $\delta^{15}N$ (‰)	Atomic C:N
Crabeater	C02	Su 2010/11	Clot	-26.3	6.9	–	–	3.8
	C03	Su 2008/09	WB	-26.3	8.2	–	–	3.9
	C03	Su 2010/11	Clot	-26.4	7.0	–	–	3.8
	C04	Su 2008/09	WB	-26.5	8.3	–	–	4.0
	C06	Su 2008/09	WB	-26.5	8.6	–	–	3.9
	C07	Su 2008/09	WB	-26.2	8.5	–	–	3.9
	C07	Su 2010/11	Hair	-24.1	7.0	-25.7	–	3.4
	C10	Su 2010/11	Hair	-23.5	6.8	-25.1	–	3.4
	C11	Su 2010/11	Hair	-23.5	6.3	-25.1	–	3.4
	C14	Su 2010/11	Clot	-26.1	7.4	–	–	3.9
	C15	Su 2010/11	WB	-26.2	7.2	–	–	3.9
	C20	Su 2008/09	WB	-26.0	8.1	–	–	3.9
	C20	Su 2010/11	RBCs	-26.1	7.4	–	–	3.8
	C21	Su 2008/09	Clot	-26.4	8.3	–	–	3.9
	C21	Su 2010/11	RBCs	-26.3	8.1	–	–	3.9
	C22	Su 2008/09	Clot	-26.5	8.4	–	–	3.9
	C32	Su 2008/09	WB	-26.1	7.6	–	–	3.9
	C33	Su 2008/09	WB	-26.0	7.8	–	–	3.8
	C43	Su 2008/09	WB	-26.2	7.4	–	–	3.9
	C44	Su 2008/09	WB	-26.3	7.5	–	–	3.9
	C45	Su 2008/09	WB	-26.6	7.4	–	–	3.9
	C46	Su 2008/09	WB	-26.0	8.2	–	–	3.8
	C47	Su 2008/09	WB	-25.6	7.5	–	–	3.9
	C48	Su 2008/09	WB	-25.8	7.1	–	–	4.0
	C50	Su 2008/09	WB	-26.1	8.4	–	–	4.0
	C51	Su 2008/09	WB	-26.1	7.3	–	–	3.8
	C52	Su 2008/09	WB	-25.5	7.3	–	–	3.8
	C143	Su 2010/11	WB	-26.1	8.0	–	–	3.9
	C144	Su 2010/11	WB	-26.1	7.9	–	–	3.9
	C153	Su 2010/11	WB	-25.9	7.3	–	–	3.9
	C154	Su 2010/11	WB	-26.1	7.0	–	–	3.9
	C155	Su 2010/11	Hair	-24.8	7.7	-26.4	–	3.4
	C156	Su 2010/11	WB	-26.0	7.9	–	–	3.9
	C157	Su 2010/11	WB	-25.8	8.4	–	–	4.0
	C158	Su 2010/11	WB	-25.9	8.2	–	–	4.0
	C173	Su 2010/11	WB	-25.9	6.9	–	–	3.9
	C174	Su 2010/11	WB	-26.1	7.0	–	–	3.9
	C175	Su 2010/11	Hair	-23.2	6.7	-24.8	–	3.4
	C176	Su 2010/11	WB	-26.6	7.2	–	–	3.9
	C177	Su 2010/11	WB	-26.2	7.7	–	–	3.9
	Cr-1	Su 2009/10	Hair	-25.0	7.7	-26.6	–	3.4
	Cr-CR	Su 2009/10	Hair	-24.6	7.6	-26.2	–	3.4
	Cr-2	Su 2009/10	Hair	-25.5	7.3	-27.1	–	3.4
	CS11-01	Su 2010/11	WB	-25.5	11.9	–	–	4.0

G001*	F 2001	Whisker	-19.8	7.1	-21.4	–	3.4
G003*	F 2001	Whisker	-22.1	5.3	-23.7	–	3.5
G004*	F 2001	Whisker	-21.8	6.7	-23.4	–	3.5
G005*	F 2001	Whisker	-21.9	6.6	-23.5	–	3.5
G006*	F 2001	Whisker	-24.1	6.2	-25.7	–	3.5
G007*	F 2001	Whisker	-21.8	6.4	-23.4	–	3.4
G008*	F 2001	Whisker	-22.0	6.8	-23.6	–	3.4
G009*	W 2001	Whisker	-23.4	6.2	-25.0	–	3.4
G010*	W 2001	Whisker	-22.5	6.5	-24.1	–	3.4
G012*	W 2001	Whisker	-21.5	6.8	-23.1	–	3.5
G013*	W 2001	Whisker	-21.3	6.7	-22.9	–	3.5
G014*	W 2001	Whisker	-21.6	7.6	-23.2	–	3.4
G015*	W 2001	Whisker	-22.4	7.3	-24.0	–	3.5
G016*	W 2001	Whisker	-21.1	5.9	-22.7	–	3.5
G017*	F 2002	Whisker	-21.8	6.8	-23.4	–	3.3
G018*	F 2002	Whisker	-24.9	6.5	-26.5	–	3.3
G019*	F 2002	Whisker	-24.7	6.6	-26.3	–	3.3
G020*	F 2002	Whisker	-24.5	6.6	-26.1	–	3.3
G021*	F 2002	Whisker	-22.3	6.7	-23.9	–	3.4
G022*	F 2002	Whisker	-20.9	7.9	-22.5	–	3.4
G023*	F 2002	Whisker	-24.6	6.4	-26.2	–	3.3
G024*	F 2002	Whisker	-21.8	7.2	-23.4	–	3.3
G026*	F 2002	Whisker	-23.6	6.5	-25.2	–	3.3
G027*	F 2002	Whisker	-22.3	6.9	-23.9	–	3.3
G028*	F 2002	Whisker	-22.2	7.1	-23.8	–	3.3
G029*	F 2002	Whisker	-21.6	7.2	-23.2	–	3.3
G030*	F 2002	Whisker	-22.1	6.9	-23.7	–	3.3
G031*	F 2002	Whisker	-21.2	7.5	-22.8	–	3.3
G032*	F 2002	Whisker	-23.2	7.0	-24.8	–	3.3
G033*	W 2002	Whisker	-21.1	7.5	-22.7	–	3.3
G034*	W 2002	Whisker	-21.8	6.7	-23.4	–	3.3
G035*	W 2002	Whisker	-21.6	7.0	-23.2	–	3.3
G036*	W 2002	Whisker	-21.5	7.3	-23.1	–	3.4
G038*	W 2002	Whisker	-22.0	6.9	-23.6	–	3.4
G039*	W 2002	Whisker	-22.9	7.3	-24.5	–	3.4
G040*	W 2002	Whisker	-23.7	6.5	-25.3	–	3.4
G041*	W 2002	Whisker	-22.9	6.7	-24.5	–	3.4
G042*	W 2002	Whisker	-21.6	6.9	-23.2	–	3.5
G043*	W 2002	Whisker	-22.8	7.4	-24.4	–	3.4
G044*	W 2002	Whisker	-21.8	7.1	-23.4	–	3.5
G045*	W 2002	Whisker	-22.0	7.6	-23.6	–	3.4
G046*	W 2002	Whisker	-21.7	7.8	-23.3	–	3.4
G047*	W 2002	Whisker	-21.5	7.1	-23.1	–	3.5
G102*	F 2007	Whisker	-23.8	5.3	-25.4	–	na
G104*	F 2007	Whisker	-22.7	6.9	-24.3	–	3.4
G105*	F 2007	Whisker	-22.3	7.1	-23.9	–	na
G106*	F 2007	Whisker	-21.9	7.1	-23.5	–	3.5
G107*	F 2007	Whisker	-23.3	6.6	-24.9	–	na
G108*	F 2007	Whisker	-21.5	7.5	-23.1	–	3.4
G110*	F 2007	Whisker	-23.1	7.9	-24.7	–	na
G112*	F 2007	Whisker	-24.0	5.4	-25.6	–	3.4
G113*	F 2007	Whisker	-23.3	5.8	-24.9	–	3.5
W02	Su 2008/09	WB	-26.3	8.5	–	–	4.0

Weddell	W01	Su 2010/11	Hair	-23.2	13.3	-24.6	12.8	3.5
	W02	Su 2010/11	Hair	-23.2	12.6	-24.6	12.1	3.5
	W04	Su 2010/11	Clot	-24.8	12.2	–	–	3.9
	W06	Su 2010/11	Clot	-24.7	12.2	–	–	3.9
	W10	Su 2008/09	WB	-24.8	11.8	–	–	3.9
	W11	Su 2008/09	WB	-25.2	11.6	–	–	4.0
	W12	Su 2008/09	WB	-25.1	12.3	–	–	3.9
	W14	Su 2008/09	WB	-24.9	12.1	–	–	3.9
	W15	Su 2008/09	WB	-25.3	11.4	–	–	3.9
	W17	Su 2008/09	WB	-25.1	11.9	–	–	4.0
	W19	Su 2008/09	WB	-25.2	12.0	–	–	3.9
	W103	Su 2010/11	WB	-25.7	10.0	–	–	3.9
	W112	Su 2010/11	Hair	-23.2	13.3	-24.6	12.8	3.5
	W113	Su 2010/11	WB	-24.6	12.6	–	–	4.0
	W116	Su 2010/11	WB	-24.5	12.6	–	–	3.9
	W117	Su 2010/11	WB	-24.9	12.0	–	–	4.0
	W118	Su 2010/11	WB	-25.1	12.0	–	–	4.0
	W130	Su 2010/11	WB	-24.4	13.1	–	–	3.9
	W133	Su 2010/11	WB	-24.4	12.5	–	–	3.9
	W136	Su 2010/11	WB	-25.2	11.9	–	–	4.0
	W137	Su 2010/11	WB	-25.1	12.0	–	–	3.9
	W155	Su 2010/11	WB	-24.3	13.2	–	–	4.0
	W157	Su 2010/11	WB	-25.0	13.0	–	–	4.0
	W174	Su 2010/11	WB	-24.6	11.8	–	–	3.9
	W175	Su 2010/11	WB	-24.2	13.1	–	–	4.0
	W176	Su 2010/11	WB	-24.4	13.0	–	–	3.9
	W177	Su 2010/11	WB	-24.5	13.0	–	–	3.9
	W182	Su 2010/11	Hair	-24.1	10.3	-25.5	9.8	3.5
	W185	Su 2010/11	WB	-25.8	11.8	–	–	3.9
	W186	Su 2010/11	WB	-26.2	12.0	–	–	3.9
	W208	Su 2010/11	WB	-25.8	12.6	–	–	3.9
	W209	Su 2010/11	WB	-26.0	12.7	–	–	3.9
	W214	Su 2010/11	WB	-26.3	11.8	–	–	4.0
	W216	Su 2010/11	WB	-25.1	13.2	–	–	4.0
	W219	Su 2010/11	WB	-25.6	11.9	–	–	4.0
	W220	Su 2010/11	WB	-25.0	12.6	–	–	4.0
	W222	Su 2010/11	WB	-25.2	12.2	–	–	3.9
	W223	Su 2010/11	WB	-24.9	13.9	–	–	4.1
	WS10-11	Su 2009/10	RBC	-25.0	12.3	–	12.6	3.9
	WS10-12	Su 2009/10	RBC	-25.0	11.7	–	12.0	3.8
	WS10-13	Su 2009/10	RBC	-24.8	12.0	–	12.3	3.9
	WS10-17	Su 2009/10	RBC	-25.5	11.5	–	11.8	4.0
	WS10-18	Su 2009/10	RBC	-25.3	11.3	–	11.6	3.8
	WS11-11	Su 2010/11	WB	-25.7	11.6	–	–	4.0
	WS11-12	Su 2010/11	WB	-25.5	11.7	–	–	3.9
	WS11-13	Su 2010/11	WB	-24.9	12.4	–	–	3.9
	WS11-14	Su 2010/11	WB	-24.6	12.4	–	–	3.9
	WS11-15	Su 2010/11	WB	-25.7	11.8	–	–	4.0
	WS12-11	Su 2011/12	RBC	-25.0	12.1	–	12.4	3.9
	WS12-12	Su 2011/12	RBC	-25.4	11.9	–	12.2	3.9
	WS12-13	Su 2011/12	RBC	-25.3	12.1	–	12.4	3.9
	WS12-14	Su 2011/12	RBC	-25.3	12.0	–	12.3	3.8
	WS12-15	Su 2011/12	RBC	-25.4	11.8	–	12.1	3.9

	WS12-22	Sp 2012	WB	-24.7	12.4	–	–	4.1
	WS12-23	Sp 2012	WB	-25.9	12.2	–	–	4.3
	WS12-24	Sp 2012	WB	-25.6	12.1	–	–	4.1
	WS12-25	Sp 2012	WB	-25.7	12.9	–	–	4.4
	WS12-26	Sp 2012	WB	-24.8	12.7	–	–	4.0
	G103	F 2007	Serum	-22.4	13.1	-22.1	12.0	4.3
	G111	F 2007	Plasma	-22.8	12.3	-22.2	11.6	4.2
	LW11-03	Su 2010/11	WB	-24.3	12.2	–	–	3.9
	LW11-05	Su 2010/11	WB	-25.7	12.2	–	–	3.9
	LW11-06	Su 2010/11	WB	-25.8	12.0	–	–	3.9
	LW11-07	Su 2010/11	WB	-25.6	12.2	–	–	3.9
	LW11-08	Su 2010/11	WB	-24.9	12.3	–	–	3.9
	LW11-09	Su 2010/11	WB	-25.0	12.3	–	–	3.9
	LW11-10	Su 2010/11	WB	-25.7	11.9	–	–	3.9
	LW11-11	Su 2010/11	WB	-24.1	13.1	–	–	3.9
	LW11-12	Su 2010/11	WB	-25.8	12.0	–	–	3.9
	LW11-13	Su 2010/11	WB	-25.3	12.1	–	–	3.9
	LW11-14	Su 2010/11	WB	-25.5	12.1	–	–	3.9
	LW11-15	Su 2010/11	WB	-25.8	13.0	–	–	4.1
	LW15-01	Sp 2015	WB	-25.8	12.1	–	–	4.2
	LW15-02	Sp 2015	WB	-25.2	12.1	–	–	3.9
	LW15-03	Sp 2015	WB	-25.3	12.1	–	–	3.9
	LW15-04	Sp 2015	WB	-25.3	12.0	–	–	3.9
	LW15-05	Sp 2015	WB	-25.3	12.2	–	–	3.9
	LW15-06	Sp 2015	WB	-25.2	11.8	–	–	4.0
	LW15-07	Sp 2015	WB	-25.3	12.2	–	–	4.0
	LW15-08	Sp 2015	WB	-25.3	11.9	–	–	3.9
	LW15-09	Sp 2015	WB	-25.3	12.0	–	–	3.9
	LW15-10	Sp 2015	WB	-25.1	12.2	–	–	3.9
	LW15-11	Sp 2015	WB	-25.3	12.2	–	–	3.9
	LW15-12	Sp 2015	WB	-25.2	11.9	–	–	4.0
	W006	Su 2009/10	Whisker	-22.6	10.9	-24.0	10.4	3.4
	W013	Su 2009/10	Whisker	-21.9	12.1	-23.3	11.6	3.4
Ross	R01	Su 2008/09	WB	-23.2	8.5	–	–	3.9
	R101	Su 2010/11	WB	-23.9	9.6	–	–	3.9
	R102	Su 2010/11	WB	-23.6	9.0	–	–	4.0
	R103	Su 2010/11	WB	-24.0	9.0	–	–	4.0
	R104	Su 2010/11	WB	-23.7	9.2	–	–	4.0
	R105	Su 2010/11	WB	-23.6	9.2	–	–	4.0
	R106	Su 2010/11	WB	-24.1	8.8	–	–	3.9
	R107	Su 2010/11	WB	-23.6	8.8	–	–	3.9
	R108	Su 2010/11	WB	-24.6	10.0	–	–	4.0
	R109	Su 2010/11	WB	-23.9	9.0	–	–	4.0
	R110	Su 2010/11	Hair	-23.0	10.0	-24.3	8.8	3.5
	R111	Su 2010/11	WB	-23.6	8.8	–	–	4.0
	R112	Su 2010/11	WB	-23.8	9.7	–	–	3.9
	R113	Su 2010/11	WB	-23.7	9.0	–	–	4.0
	R114	Su 2010/11	WB	-23.8	8.6	–	–	4.0

Table 2.S8. Amino acid $\delta^{15}N$ values for crabeater, Ross, and Weddell seals. Values are reported as the mean ± one standard deviation for the injections on the GC/C/IRMS. For crabeater seals, whole blood (C06, C44, C177) and plasma (G112, G105, and G110) samples were analyzed. All Ross seal samples analyzed for amino acid $\delta^{15}N$ values were whole blood. For Weddell seals, whole blood (W185, W220, and WS11-11), plasma (G111), and sample from the first segment nearest the whisker base, 0.0-0.5 cm, (W006 and W013) were used for CSIA. Abbreviation: na, not available.

Species	Sample ID	Amino Acid	Injections	$\delta^{15}N$ (‰)
Crabeater	C06	Alanine	3	13.7 ± 0.3
	C06	Glycine	3	8.5 ± 0.1
	C06	Threonine	3	-21.9 ± 0.6
	C06	Serine	3	7.0 ± 0.5
	C06	Valine	3	14.9 ± 0.3
	C06	Leucine	3	13.9 ± 0.2
	C06	Isoleucine	3	12.8 ± 0.2
	C06	Proline	3	15.7 ± 0.4
	C06	Aspartic	3	11.0 ± 0.3
	C06	Glutamic acid	3	15.1 ± 0.4
	C06	Phenylalanine	3	6.8 ± 0.3
	C06	Lysine	3	5.5 ± 0.6
	G112	Alanine	3	12.0 ± 0.7
	G112	Glycine	3	0.6 ± 0.1
	G112	Threonine	3	-20.7 ± 0.1
	G112	Serine	3	1.9 ± 0.2
	G112	Valine	3	13.5 ± 0.2
	G112	Leucine	3	11.8 ± 0.6
	G112	Isoleucine	3	11.6 ± 1.0
	G112	Proline	3	15.5 ± 0.6
	G112	Aspartic	3	9.9 ± 0.2
	G112	Glutamic acid	3	15.0 ± 0.4
	G112	Phenylalanine	3	4.3 ± 0.1
	G112	Lysine	2	4.5 ± 0.2
	C44	Alanine	3	14.3 ± 0.4
	C44	Glycine	3	4.7 ± 0.4
	C44	Threonine	3	-25.4 ± 0.4
	C44	Serine	3	4.2 ± 0.2
	C44	Valine	3	15.1 ± 0.5
	C44	Leucine	3	13.4 ± 0.5
	C44	Isoleucine	3	12.2 ± 0.1
	C44	Proline	3	14.7 ± 0.3
	C44	Aspartic	3	9.3 ± 0.2
	C44	Glutamic acid	3	15.0 ± 0.2
	C44	Phenylalanine	3	5.8 ± 0.2
	C44	Lysine	3	4.9 ± 0.3
	G105	Alanine	3	13.3 ± 0.4
	G105	Glycine	3	1.6 ± 0.3
	G105	Threonine	3	-19.6 ± 0.4
	G105	Serine	3	2.5 ± 0.3
	G105	Valine	3	14.4 ± 0.5
	G105	Leucine	3	12.7 ± 0.1
	G105	Isoleucine	3	11.5 ± 0.6
	G105	Proline	3	16.5 ± 0.5

	G105	Aspartic	3	10.4 ± 0.0
	G105	Glutamic acid	3	15.2 ± 0.3
	G105	Phenylalanine	3	4.7 ± 0.2
	G105	Lysine	3	5.3 ± 0.5
	C177	Alanine	4	14.6 ± 0.4
	C177	Glycine	4	3.9 ± 0.4
	C177	Threonine	4	-26.1 ± 0.8
	C177	Serine	4	5.2 ± 0.6
	C177	Valine	4	15.7 ± 0.8
	C177	Leucine	4	14.4 ± 0.5
	C177	Isoleucine	4	12.6 ± 0.7
	C177	Proline	4	15.7 ± 0.5
	C177	Aspartic	4	9.8 ± 0.1
	C177	Glutamic acid	4	14.4 ± 0.3
	C177	Phenylalanine	4	5.4 ± 0.4
	C177	Lysine	4	5.1 ± 0.5
	G110	Alanine	3	13.4 ± 0.1
	G110	Glycine	3	3.4 ± 0.1
	G110	Threonine	3	-23.4 ± 0.3
	G110	Serine	3	4.7 ± 0.5
	G110	Valine	3	15.8 ± 0.3
	G110	Leucine	3	13.5 ± 0.2
	G110	Isoleucine	3	12.3 ± 0.4
	G110	Proline	3	15.8 ± 0.3
	G110	Aspartic	3	10.4 ± 0.4
	G110	Glutamic acid	3	14.8 ± 0.4
	G110	Phenylalanine	3	4.1 ± 0.5
	G110	Lysine	3	5.0 ± 0.2
Ross	R101	Alanine	3	20.3 ± 0.3
	R101	Glycine	3	2.9 ± 0.2
	R101	Threonine	3	-29.2 ± 0.2
	R101	Serine	3	4.4 ± 0.7
	R101	Valine	3	21.5 ± 0.1
	R101	Leucine	3	19.9 ± 0.3
	R101	Isoleucine	3	20.1 ± 1.0
	R101	Proline	3	17.3 ± 0.3
	R101	Aspartic	3	15.9 ± 0.1
	R101	Glutamic acid	3	18.3 ± 0.7
	R101	Phenylalanine	3	2.5 ± 0.2
	R101	Lysine	na	Na
	R103	Alanine	3	18.5 ± 0.3
	R103	Glycine	3	5.1 ± 0.4
	R103	Threonine	3	-27.4 ± 0.7
	R103	Serine	3	5.4 ± 0.8
	R103	Valine	3	20.0 ± 0.4
	R103	Leucine	3	18.6 ± 0.3
	R103	Isoleucine	3	15.7 ± 0.6
	R103	Proline	3	16.9 ± 0.6
	R103	Aspartic	3	13.9 ± 0.2
	R103	Glutamic acid	3	17.2 ± 0.6
	R103	Phenylalanine	3	2.6 ± 0.4
	R103	Lysine	3	1.8 ± 0.4
	R106	Alanine	3	18.8 ± 0.1

	R106	Glycine	3	5.7 ± 0.3
	R106	Threonine	3	-27.5 ± 0.3
	R106	Serine	3	5.8 ± 0.4
	R106	Valine	3	19.3 ± 0.4
	R106	Leucine	3	17.9 ± 0.3
	R106	Isoleucine	3	18.8 ± 0.7
	R106	Proline	3	17.3 ± 0.2
	R106	Aspartic	3	14.0 ± 0.2
	R106	Glutamic acid	3	16.9 ± 0.3
	R106	Phenylalanine	3	1.9 ± 0.2
	R106	Lysine	3	2.5 ± 0.4
	R111	Alanine	3	18. 6 ± 0.3
	R111	Glycine	3	5.2 ± 0.1
	R111	Threonine	3	-28.0 ± 0.1
	R111	Serine	3	5.7 ± 0.3
	R111	Valine	3	19.7 ± 0.3
	R111	Leucine	3	18.2 ± 0.3
	R111	Isoleucine	3	18.4 ± 0.7
	R111	Proline	3	16.4 ± 0.9
	R111	Aspartic	3	13.6 ± 0.2
	R111	Glutamic acid	3	17.6 ± 0.3
	R111	Phenylalanine	3	1.9 ± 0.1
	R111	Lysine	3	3.4 ± 0.2
	R112	Alanine	3	19.2 ± 0.5
	R112	Glycine	3	4.8 ± 0.5
	R112	Threonine	3	-28.0 ± 0.7
	R112	Serine	3	4.7 ± 0.4
	R112	Valine	3	19.7 ± 0.1
	R112	Leucine	3	18.2 ± 0.1
	R112	Isoleucine	2	17.7 ± 0.6
	R112	Proline	3	17.1 ± 0.6
	R112	Aspartic	3	14.3 ± 0.4
	R112	Glutamic acid	3	17.6 ± 0.5
	R112	Phenylalanine	3	3.9 ± 0.2
	R112	Lysine	3	3.1 ± 0.4
	R114	Alanine	3	17.6 ± 0.4
	R114	Glycine	3	5.9 ± 0.3
	R114	Threonine	3	-25.9 ± 0.2
	R114	Serine	3	5.9 ± 0.8
	R114	Valine	3	19.0 ± 0.4
	R114	Leucine	3	17.5 ± 0.4
	R114	Isoleucine	na	Na
	R114	Proline	3	18.1 ± 0.8
	R114	Aspartic	3	12.9 ± 0.2
	R114	Glutamic acid	3	17.5 ± 0.8
	R114	Phenylalanine	3	3.1 ± 0.3
	R114	Lysine	2	3.3 ± 0.1
Weddell	G111	Alanine	3	18.9 ± 0.4
	G111	Glycine	3	5.0 ± 0.4
	G111	Threonine	3	-22.1 ± 0.6
	G111	Serine	3	8.6 ± 0.1
	G111	Valine	3	22.9 ± 0.5
	G111	Leucine	3	20.8 ± 0.4

G111	Isoleucine	3	19.6 ± 0.6
G111	Proline	3	20.8 ± 0.9
G111	Aspartic	3	16.7 ± 0.5
G111	Glutamic acid	3	20.4 ± 0.5
G111	Phenylalanine	3	5.3 ± 0.4
G111	Lysine	3	6.7 ± 0.4
W006	Alanine	3	20.7 ± 0.2
W006	Glycine	3	2.1 ± 0.1
W006	Threonine	3	-29.4 ± 0.3
W006	Serine	3	6.7 ± 0.2
W006	Valine	3	24.0 ± 0.5
W006	Leucine	3	21.7 ± 0.4
W006	Isoleucine	3	21.4 ± 0.9
W006	Proline	3	18.0 ± 0.1
W006	Aspartic	3	12.8 ± 0.1
W006	Glutamic acid	3	20.8 ± 0.2
W006	Phenylalanine	3	5.9 ± 0.5
W006	Lysine	1	3.1
W013	Alanine	3	22.1 ± 0.1
W013	Glycine	3	2.3 ± 0.1
W013	Threonine	3	-31.9 ± 0.3
W013	Serine	3	8.0 ± 0.2
W013	Valine	3	25.5 ± 0.5
W013	Leucine	3	23.5 ± 0.1
W013	Isoleucine	3	24.0 ± 0.2
W013	Proline	3	18.5 ± 0.2
W013	Aspartic	3	14.2 ± 0.1
W013	Glutamic acid	3	22.2 ± 0.2
W013	Phenylalanine	3	5.9 ± 0.1
W013	Lysine	2	3.6 ± 0.8
W185	Alanine	3	22.8 ± 0.1
W185	Glycine	3	6.9 ± 0.9
W185	Threonine	3	-29.9 ± 0.4
W185	Serine	3	9.0 ± 0.5
W185	Valine	3	24.2 ± 0.4
W185	Leucine	3	22.6 ± 0.4
W185	Isoleucine	3	21.7 ± 0.6
W185	Proline	3	21.0 ± 0.1
W185	Aspartic	3	17.2 ± 0.2
W185	Glutamic acid	3	20.7 ± 0.4
W185	Phenylalanine	3	5.0 ± 0.0
W185	Lysine	3	5.4 ± 0.4
W220	Alanine	3	23.1 ± 0.1
W220	Glycine	3	9.4 ± 0.3
W220	Threonine	3	-27.9 ± 0.3
W220	Serine	3	10.9 ± 0.3
W220	Valine	3	25.0 ± 0.6
W220	Leucine	3	23.3 ± 0.2
W220	Isoleucine	3	22.8 ± 1.0
W220	Proline	3	21.3 ± 0.7
W220	Aspartic	3	18.6 ± 0.1
W220	Glutamic acid	3	22.3 ± 0.2
W220	Phenylalanine	3	6.4 ± 0.1

	W220	Lysine	3	6.8 ± 0.8
	WS11-11	Alanine	3	22.5 ± 0.1
	WS11-11	Glycine	3	7.0 ± 0.9
	WS11-11	Threonine	3	-28.3 ± 0.3
	WS11-11	Serine	3	9.2 ± 0.5
	WS11-11	Valine	3	24.6 ± 0.3
	WS11-11	Leucine	3	22.6 ± 0.3
	WS11-11	Isoleucine	3	21.7 ± 0.9
	WS11-11	Proline	3	20.4 ± 0.9
	WS11-11	Aspartic	3	17.5 ± 0.5
	WS11-11	Glutamic acid	3	21.5 ± 0.3
	WS11-11	Phenylalanine	3	5.6 ± 0.2
	WS11-11	Lysine	3	5.8 ± 0.5

Table 2.S9. Results of one-way ANOVA Bonferroni post-hoc comparisons for amino acid $\delta^{15}N$ data for the three seal species. Significant *p*-values are < 0.05.

Amino Acid	ANOVA Post-hoc *p*-values	Comparison
Ala	<0.001	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	0.003	Ross vs. Weddell
Gly	–	Crabeater vs. Ross
	–	Crabeater vs. Weddell
	–	Ross vs. Weddell
Thr	0.01	Crabeater vs. Ross
	0.006	Crabeater vs. Weddell
	–	Ross vs. Weddell
Ser	–	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	0.002	Ross vs. Weddell
Val	<0.001	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	<0.001	Ross vs. Weddell
Leu	<0.001	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	<0.001	Ross vs. Weddell
Ile	<0.001	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	<0.001	Ross vs. Weddell
Pro	0.03	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	<0.001	Ross vs. Weddell
Asp	<0.001	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	–	Ross vs. Weddell
Glu	<0.001	Crabeater vs. Ross
	<0.001	Crabeater vs. Weddell
	<0.001	Ross vs. Weddell
Phe	<0.001	Crabeater vs. Ross
	–	Crabeater vs. Weddell
	<0.001	Ross vs. Weddell
Lys	0.009	Crabeater vs. Ross
	–	Crabeater vs. Weddell
	0.005	Ross vs. Weddell

Table 2.S10. Bulk $\delta^{13}C$ and $\delta^{15}N$ values of crabeater, Weddell, and Ross seals from the literature. Note, bulk $\delta^{13}C$ and $\delta^{15}N$ values are reported for the original measurement (Orig.) and with a correction to whole blood (Corr.) if the sample is a tissue type with a significant isotopic offset from whole blood. Isotopic offset between whole blood and the given sample type are reported in Tables S4 and S6, above. Abbreviations: RBCs, red blood cells; F, female; M, male; na, information not available; NDR, no dive records; RS, Ross Sea; AS, Amundsen Sea; MCM, McMurdo; *n*, sample size.

Species	Sample Type	*n*	Sex	Age Class	Area	Orig. $\delta^{13}C$ (‰)	Orig. $\delta^{15}N$ (‰)	Corr. $\delta^{13}C$ (‰)	Corr. $\delta^{15}N$ (‰)	Source
Ross	Serum	21	M	na	RS/AS	24.3 ± 0.4	10.6 ± 0.6	-24.0 ± 0.4	9.5 ± 0.4	Zhao et al. (2004)
	Serum	12	F	na	RS/AS	-24.0 ± 0.4	10.0 ± 0.5	-23.7 ± 0.4	8.9 ± 0.5	Zhao et al. (2004)
	Hair	1	M	na	RS	-22.3	10.4	-23.6	9.2	Aubail et al. (2011)
Weddell	Serum	17	M	na	RS/AS	-24.6 ± 0.6	13.3 ± 0.8	-24.3 ± 0.6	12.2 ± 0.8	Zhao et al. (2004)
	Serum	16	F	na	RS/AS	-25.3 ± 0.9	12.5 ± 1.1	-25.0 ± 0.9	11.4 ± 1.1	Zhao et al. (2004)
	Serum	22	na	Adult	RS/AS	-24.9 ± 0.8	13.0 ± 0.9	-24.6 ± 0.8	11.9 ± 0.9	Zhao et al. (2004)
	Serum	4	na	Subadult	RS/AS	-25.5 ± 0.9	11.5 ± 1.1	-25.2 ± 0.9	10.4 ± 1.1	Zhao et al. (2004)
	Serum	6	na	Juvenile	RS/AS	-24.8 ± 1.0	13.1 ± 1.0	-24.5 ± 1.0	12.0 ± 1.0	Zhao et al. (2004)
	Serum	1	na	Pup	RS/AS	-25.2	13.4	-24.9	12.3	Zhao et al. (2004)
	Plasma	12	na	Adult	RS	-25.5 ± 0.1	13.1 ± 0.2	-24.9 ± 0.1	12.4 ± 0.2	Burns et al. (1998)
	Plasma	6	na	Deep-diving yearling	RS	-25.4 ± 0.2	12.6 ± 0.2	-24.8 ± 0.2	11.9 ± 0.2	Burns et al. (1998)
	Plasma	4	na	NDR yearling	RS	-25.1 ± 0.2	12.9 ± 0.1	-24.5 ± 0.2	12.2 ± 0.1	Burns et al. (1998)
	Plasma	4	na	Shallow-diving yearling	RS	-23.5 ± 0.1	13.3 ± 0.1	-22.9 ± 0.1	12.6 ± 0.1	Burns et al. (1998)
	Plasma	16	na	Pup	RS	-26.0 ± 0.2	13.8 ± 0.1	-25.4 ± 0.2	13.1 ± 0.1	Burns et al. (1998)
	Hair	12	na	na	RS	-23.2 ± 0.1	13.5 ± 0.2	-24.6 ± 0.1	13.0 ± 0.2	Aubail et al.

	RBCs	116	na	na	RS	-25.2 ± 0.3	12.0± 0.3	-25.2 ± 0.3	12.3 ± 0.3	(2011) Goetz et al. (2017)
Crabeater	Serum	26	M	na	RS/AS	-26.7 ± 0.9	8.2 ± 0.5	-26.4 ± 0.9	7.1 ± 0.5	Zhao et al. (2004)
	Serum	15	F	na	RS/AS	-26.5 ± 1.2	8.4 ± 0.4	-26.2 ± 1.2	7.3 ± 0.4	Zhao et al. (2004)
	Serum	30	na	Adult	RS/AS	-26.5 ± 1.0	8.4 ± 0.6	-26.2 ± 1.0	7.3 ± 0.6	Zhao et al. (2004)
	Serum	4	na	Subadult	RS/AS	-26.1 ± 1.2	8.4 ± 0.3	-25.8 ± 1.2	7.3 ± 0.3	Zhao et al. (2004)
	Serum	3	na	Juvenile	RS/AS	-27.2 ± 1.2	8.0 ± 0.1	-26.9 ± 1.2	7.9 ± 0.1	Zhao et al. (2004)
	Serum	4	na	Pup	RS/AS	-27.4 ± 0.4	7.7 ± 0.1	-27.1 ± 0.4	6.6 ± 0.1	Zhao et al. (2004)
	Hair	33	na	na	RS	-24.3 ± 0.1	7.7 ± 0.1	-25.9 ± 0.1	7.7 ± 0.1	Aubail et al. (2011)

REFERENCES

Aubail A, Teilmann J, Dietz R, Rigét F, Harkonen T, Karlsson O, Rosing-Asvid A, Caurant F (2011) Investigation of mercury concentrations in fur of phocid seals using stable isotopes as tracers of trophic levels and geographic regions. Polar Biol 34:1411-1420

Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biol 19:272-282

Goetz KT, Burns JM, Hückstädt LA, Shero MR, Costa DP (2017) Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. Deep Sea Res II 140:36-44

Hückstädt LA, Burns JM, Koch PL, McDonald BI, Crocker DE, Costa DP (2012a) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287-301

Zhao L, Castellini MA, Mau TL, Trumble SJ (2004) Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biol 27:368-373

BULK AND COMPOUND-SPECIFIC ISOTOPE ANALYSES OF SEAL MUMMIES REVEAL THE VULNERABILITIES OF ANTARCTIC SEALS TO CLIMATE CHANGE

ABSTRACT

Anthropogenic climate change is rapidly altering polar systems. Studying a species' responses to past climate events provides insights into their present vulnerabilities. Evidence has suggested that sea ice duration and extent likely increased in the Ross Sea over the Holocene. We used bulk stable carbon and nitrogen isotope ($\delta^{13}C$ and $\delta^{15}N$, respectively) analyses of ~ 700 subfossil Antarctic seals from the Ross Sea, complimented by isotopic analysis of individual amino acids, to investigate biological and biogeochemical responses to Holocene climate change. Bulk isotope values of Weddell seals (*Leptonychotes weddellii*) decrease around 800 YBP ($\delta^{13}C$ by ~ 1.5 ‰ and $\delta^{15}N$ by ~ 3 ‰). Similarly, bulk $\delta^{15}N$ values of subfossil southern elephant seals (SES) are higher than modern SES. These isotopic transitions could result from a drop in primary productivity, a switch to lower trophic level prey, or both. In contrast, crabeater seals (*Lobodon carcinophagus*) show no temporal change in their bulk isotope values, but do show greater isotopic variability in the past, indicating more diverse foraging habits. Amino acid $\delta^{15}N$ analysis allows discrimination between trophic switching and baseline shifts in $\delta^{15}N$ values. Weddell seal and SES amino acid $\delta^{15}N$ values point to a late Holocene

baseline drop of ~ 3 ‰, consistent with higher past productivity. Crabeater seal amino acid $\delta^{15}N$ values indicate diets consisting of more fish and use of a different Ross Sea region than the Weddell seals. Our findings indicate that crabeater seals and SES may have a higher adaptive capacities and lower sensitivities to climate change than Weddell seals.

INTRODUCTION

West Antarctica, the Southern Ocean region from the Ross to the Weddell Sea, is presently experiencing some of the most profound and rapid climate change on Earth (Meredith & King 2005, Ducklow et al. 2007, 2012, Stammerjohn et al. 2012). However, considerable variation in climate change exists across this area. For instance, while the West Antarctic Peninsula (WAP) is experiencing some of the most rapid warming in the world since the mid-20th century (e.g., about 7% sea ice extent reduction per decade), sea ice extent in the Ross Sea has increased by approximately 5% per decade (Kwok and Comiso et al. 2002, Parkinson 2002, Smith et al. 2007).

The Ross Sea is the southernmost and likely most pristine sea in the world. It is unique for having a broad and relatively deep continental shelf, the largest ice shelf in Antarctica, multiple significant polynyas, considerable sea ice generation, a site of bottom water formation, and high primary productivity rates (Arrigo and van Dijken 2003, Smith et al. 2007). The high production and oceanography of the Ross Sea lead to this region being an important carbon sink and habitat for abundant and diverse

upper trophic level animals (Arrigo and van Dijken 2003, Smith et al. 2007, Arrigo et al. 2008a). In recent years, the Ross Sea has become an important site for harvesting Antarctic toothfish (*Dissostichus mawsoni*) with uncertain impacts on the biota (Ainley and Siniff 2009). Considering this system's unique response to anthropogenic climate change, role in biogeochemical cycles, productive food web, and fisheries interests, an understanding of the likely physical, chemical, and biological responses of the Ross Sea to continued anthropogenic climate change is needed. An examination of past climate events in the Ross Sea and their effects on this ecosystem provides this information.

Prior studies have offered some insights on climate change in the Ross Sea during the Holocene, although the findings are not always consistent. Like today, climate trends in the Ross Sea have differed from those of other Antarctic regions in the past (Steig et al. 2000). Considerable variability in the Wilson Piedmont Glacier on the coast of the western Ross Sea during the Holocene, 11,700 years before present (YBP) to modern times, has been discovered (Hall and Denton 2002). The glacier retreated during the early (11,700 to 8,200 YBP) and mid Holocene (8,200 to 4,200 YBP), following the Last Glacial Maximum, but then advanced in the late Holocene (4,200 to 0 YBP), which culminated less than 250 years ago (Hall and Denton 2002, Walker et al. 2012). Storm-formed, raised beaches dating to between 6,500 and 800 YBP occur on the Victoria Land Coast (VLC), along the western Ross Sea, showing that liquid water reached the coast during this time, whereas today the coast is locked with landfast ice (Bamberg 2007). This study also reports a transition

from open water to ice-push beach features in the VLC in the late Holocene (Bamberg 2007). In support of these findings, other studies suggest a cooling trend during the late Holocene (Masson et al. 2000, Stenni et al. 2002, Bertler et al. 2011, Rhodes et al. 2012). Analyses of ice cores taken from the Victoria Lower Glacier and Mount Erebus Saddle, both in the western Ross Sea coastal region, reveal a time of rapid cooling in this area with the onset of the Little Ice Age (LIA), a period from about 720 to 170 YBP (Bertler et al. 2011, Rhodes et al. 2012).

Along with geologic findings, biological evidence points to a less icy Ross Sea earlier in the Holocene. Southern elephant seals (SES, *Mirounga leonina*) have a Subantarctic distribution in modern times (Le Boeuf and Laws 1994). However, a large Antarctic breeding colony (> 200,000 individuals) is represented along the VLC during the Holocene until it crashes at ~ 1,000 YBP, becoming extinct by ~ 500 YBP (Hall et al. 2006, de Bruyn et al. 2009, 2014). As SES require beaches with open water access for breeding and molting (Laws 1960, Gales and Burton 1989), their past inhabitation of the VLC indicates that this region had considerably less landfast ice and likely a smaller sea ice extent and duration earlier in the Holocene than it does today. In sum, both geologic and biologic evidence point to the VLC being less icy between approximately 6,500 and 1,000 YBP than it is at modern times.

The consequences of these past climate events on the Ross Sea ecosystem were likely broad and variable, affecting organisms from primary producers to top predators. For instance, at the bottom of Antarctic food webs, phytoplankton production may increase if reduced sea ice cover alleviates the light limitation on

their growth (Arrigo and van Dijken 2003, Smith et al. 2007). An enhanced supply of iron, typically a limiting micronutrient in the Southern Ocean, would also likely increase phytoplankton production and could result from a number of environmental changes, such as increased inputs from melting sea ice (Sedwick and DiTullio 1997, Lannuzel et al. 2010), melting glaciers (Raiswell et al. 2006), upwelling of Circumpolar Deep Water (CDW) (Klunder et al. 2011), or floating icebergs (Raiswell et al. 2008, Raiswell 2011, Shaw et al. 2011).

Top predators respond to climate change in several ways, such as by altering behavior (e.g. foraging, reproduction, or migration) to survive and reproduce within a changed environment, expanding or shifting their range, remaining within their altered environment, but utilizing a contracted habitat, or becoming extinct (Walther et al. 2002, Parmesan et al. 2006). To date, our understanding of how pinnipeds will respond to anthropogenic climate change is limited. Siniff (2008) suggests ice-dependent species, i.e., crabeater (*Lobodon carcinophagus*), Weddell (*Leptonychotes weddellii*), Ross (*Ommatophoca rossii*), and leopard (*Hydrurga leptonyx*) seals, will experience net negative effects, while ice-tolerant species, SES and Antarctic fur seals (*Arctocephalus gazella*), will experience net positive and net neutral effects, respectively, from modern climate change. Likewise, the results of Costa et al. (2010) indicate that the environment of the WAP is changing in favor of SES due to their preference for foraging in CDW and lack of dependence on sea ice, while it changes in disfavor of crabeater and Weddell seals since these species require sea ice for foraging and breeding.

Isotopic analyses of nitrogen (N) and carbon (C) allow for the examination of past environmental change and the subsequent responses by biota. The N isotope ($\delta^{15}N$) value of a predator is indicative of its trophic position since tissues become enriched in ^{15}N by about 3 to 5 ‰ with each trophic step (primary producers to herbivores to carnivores) due to the preferential loss of ^{14}N during amino acid metabolism and egestion (Minagawa and Wada 1984). However, a predator's $\delta^{15}N$ value is not only affected by its diet and trophic position, but also by the $\delta^{15}N$ value of the base of the food web, i.e., primary producers in marine systems. Baseline or "source" $\delta^{15}N$ values ($\delta^{15}N_{baseline}$) may vary in space and time due to several factors (Graham et al. 2010, Chapter 1). The Southern Ocean is a high nutrient-low, chlorophyll (HNLC) region, a place in which low iron concentrations and light availability limit primary productivity, resulting in a large pool of available macronutrients, such as NO_3^- (Arrigo and van Dijken 2003, Smith et al. 2007). The $\delta^{15}N$ value of NO_3^- used by phytoplankton and the degree of N drawdown, associated with the rate of primary productivity, are the main drivers of $\delta^{15}N_{baseline}$ in the Southern Ocean (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1).

In contrast to nitrogen, carbon isotope ($\delta^{13}C$) values show little trophic level ^{13}C-enrichment, but they are useful for inferring the sources of primary production (Peterson and Fry 1987). The $\delta^{13}C$ values of primary producers ($\delta^{13}C_{baseline}$) reflect a number of factors: dissolved inorganic carbon $\delta^{13}C$ values, $[CO_2]_{aq}$, temperature, plant and cell size and geometry, internal biological parameters (e.g., growth rate), and CO_2 drawdown (reviewed in McMahon et al. 2013a). Importantly, in the

Southern Ocean, studies have shown decreasing $\delta^{13}C$ values with increasing latitude due to decreasing sea surface temperatures (Rau et al. 1989, Graham et al. 2010, Quillfeldt et al. 2010, Chapter 1). For both nitrogen and carbon, spatial and temporal variations in driving forces will in turn generate spatial and temporal variations in $\delta^{15}N_{baseline}$ and $\delta^{13}C_{baseline}$ values (e.g., Schell et al. 1998).

By complementing isotopic analysis of bulk material from predators with that of amino acids, we are able to disentangle trophic and baseline effects (McClelland and Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). Since $\delta^{15}N$ values of source amino acids become minimally ^{15}N-enriched with each trophic step, while those of trophic amino acids become heavily ^{15}N-enriched, $\delta^{15}N$ measurements of these amino acids can be used to tease apart the contributions of a change in baseline $\delta^{15}N$ values, diet, or both on the predator $\delta^{15}N$ pattern (McClelland and Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). Glutamic acid + glutamine (Glu) and phenylalanine (Phe) have been commonly considered the most representative trophic and source amino acids, respectively (McClelland and Montoya 2002, Popp et al. 2007, Chikaraishi et al. 2009). More recently, however, proline (Pro) has been shown to be a reliable trophic amino acid and to enable more accurate trophic position calculations for upper trophic level organisms, since the ^{15}N-enrichment factors for different trophic steps are less variable than those for Glu (McMahon et al., data unpublished). Measurements of $\delta^{13}C$ values for essential amino acids (i.e., threonine, leucine, isoleucine, valine, Phe), which animals must obtain from their diet, are useful for deciphering sources of carbon, since they typically vary among primary producer

communities, are recorded in consumer tissues, and are nearly unmodified with food chain steps (Hayes 2001, Scott et al. 2006, McMahon et al. 2015). Phe $\delta^{13}C$ values are considered most indicative of source carbon. For nonessential amino acids, animals can either biosynthesize them *de novo* (using a bulk C pool) or route them from their dietary protein, making their interpretation complicated but perhaps meaningfully related to dietary protein quantity and quality (Howland et al. 2003, McMahon et al. 2010, McMahon et al. 2015).

We performed bulk and compound (amino acid) – specific isotope analysis (CSIA) of subfossil crabeater, Weddell, leopard, and SES specimens in order to gain information on the climate events that occurred in the Ross Sea over the mid-to-late Holocene, considered the period of 6,000 to 0 YBP in the following text, and the ways in which species, from phytoplankton to seals, responded to them. Our findings reveal the sensitivities and adaptive capacities of these four Antarctic seal species to environmental change, and indicate their potential responses to anthropogenic climate change. Furthermore, this study also provides insight into how continued warming will likely affect the biogeochemistry (e.g., elemental cycles and primary production) of the Ross Sea.

MATERIALS AND METHODS

Sample collection

Fossil seal samples were collected during the austral summers of 2006/07, 2012/13, and 2013/14 in Antarctica in the Dry Valleys and along the Victoria Land Coast (especially Inexpressible Island on Terra Nova Bay), Antarctica (Fig. 3.1). Since this region experiences unusually dry and cold conditions, carcasses are well-preserved, potentially for several thousand years, and therefore have unchanged isotopic compositions in most cases. Samples were collected from over 728 seal specimens. The sampled species were crabeater, Weddell, leopard, and southern elephant seals. Latitude and longitude of each specimen was recorded and several photographs were taken of the carcass. Bone and carcass weathering states were determined (indices were developed by Dr. Laura Niven, Kwasi Gilbert, and Jon Nye). Several samples were gathered from the carcasses. Most commonly, bone was collected, followed by skin and fur; nails, teeth, and whiskers were not frequently available for sampling, but taken when possible. Samples were collected with ethanol-cleaned tools, stored in Whirl-Pak bags, and refrigerated (~ 4 °C).

Species identification

When possible, species identification of each specimen was conducted in the field via examination of teeth or bones with features unique to the four pinniped species. Additionally, colleagues at the University of Durham in the United Kingdom extracted and analyzed DNA from many subfossil seal samples, described below, to confirm or establish the species identification.

Sample preparation for bulk and compound-specific isotope analyses

Preparation of bone samples was based on established procedures and by preliminary method testing in the lab (DeNiro 1987, Ambrose 1990). Bone fragments (50 -100 mg) were weighed into a vial (BD Falcon 15 mL centrifuge tubes, polypropylene) and acidified (to remove bone mineral, sedimentary carbonates, and fulvic acids) by the addition of 5 mL HCl (0.5 M) at room temperature. The acid was removed approximately three days later. If the samples did not appear completely decalcified (i.e., remains inflexible), a fresh aliquot of acid was added every 24 hours until the bone was decalcified, leaving behind bone collagen. Upon decalcification, the collagen was rinsed five times with Milli-Q water (Thermo Fisher Scientific, Inc.), neutralizing the sample, and 5 mL NaOH (0.1 M) was added to the samples, which were then kept at room temperature, further purifying the bone collagen by removing humic acids. A fresh aliquot of 0.1 M NaOH was added to the sample every 24 hours until the sample was nearly white. Again, the material was rinsed five times with Milli-Q water; then, it was refrigerated until the lipid extraction procedure. Lipids were removed via an accelerated solvent extraction with 100% petroleum ether (Dionex ASE 200 Accelerated Solvent Extractor: 1500 psi; 60°C; 3 cycles).

Since bone was the most common sample type available. As bone integrates diet over the largest period among the sample types collected (i.e., the animal's lifespan), we analyzed bone from each specimen when available. Hair (fur) samples were analyzed from specimens if no bone had been collected. For some specimens (n = 15), both bone and fur were analyzed to determine the isotopic offset between these

different tissues. We were unable to develop a protein purification method for skin samples to achieve reliable bulk isotope values.

Hair samples, between 10 and 20 hairs with their follicles removed, were prepared for isotopic analysis by first washing with Milli-Q water. Then, lipids were removed via three rinses with petroleum ether in an ultrasonic bath (Thermo Fisher Scientific, Inc.) for 15 minutes each time, and other exogenous material was eliminated with alternating treatments of acid (0.5 M HCl) and base (0.1 M NaOH) until the solution was clear. After each acid or base treatment, five rinses with Milli-Q water were performed.

Bulk stable isotope analysis

For all bone (n = 554) and hair (n = 45) samples approximately 1 mg and 0.5 mg of sample, respectively, was weighed into tin cups (Costech, 3x5 mm) for elemental analysis-isotope ratio mass spectrometry (EA-IRMS). This analysis was performed at the Stable Isotope Lab (SIL) at the University of California (UC) Santa Cruz on a Carlo Erba EA 1108 elemental analyzer coupled to a Thermo-Finnigan Delta^{Plus} XP isotope ratio mass spectrometer. $\delta^{15}N$ values were referenced to an AIR standard, and $\delta^{13}C$ values were referenced to a V-PDB standard. Gelatin standard replicates were analyzed in each instrument session in order to correct for variations in mass across samples and in instrument drift. Comparisons of standards resulted in standard deviations that were ≤0.2 ‰ for both $\delta^{15}N$ and $\delta^{13}C$ values (7 standards analyzed at the start of each session, and a standard analyzed after every 8 samples).

Compound-specific isotope analysis

CSIA was performed at UC Santa Cruz via gas chromatography-isotope ratio mass spectrometry (GC-IRMS). Amino acid $\delta^{15}N$ analysis was performed on 12, 22, and 11 subfossil specimens of crabeater, Weddell, and southern elephant seals, respectively. For crabeater, Weddell, and southern elephant seals, amino acid $\delta^{13}C$ measurements were conducted on 4, 3, and 4 subfossil specimens, correspondingly. No amino acid isotope analyses were performed on leopard seals since no significant variation was found with their bulk isotope values, discussed below.

All samples were prepared for GC-IRMS analysis using the method described in detail by McCarthy et al. (2007), Hannides et al. (2009), and McCarthy et al. (2013). In brief, samples were hydrolyzed (6 N HCl for 20 hr at 110 °C), purified using cation-exchange chromatography, turned into trifluoroacetic anhydride (TFAA) derivatives, further purified via solvent extraction with a 3.5 mL chloroform and 2 mL P-buffer (KH_2PO_4 + Na_2HPO_4 in Milli-Q water, pH 7) solution, and re-derivatized. Samples were stored in a -20 °C freezer in a 1:3 TFAA:DCM (methylene chloride) mixture until the day of instrumental analysis. Immediately before the analysis, the TFAA:DCM mixture was evaporated under N_2 and samples were diluted in ethyl acetate.

The amino acid N and C isotope compositions of all samples were determined with a Thermo Trace GC coupled to a Thermo-Finnigan Delta^{Plus} XP isotope-ratio-monitoring mass spectrometer (oxidation furnace at 980 ºC (N) or 940 ºC (C) and reduction furnace at 650 ºC (N) or 630 ºC (C)). The column used for $\delta^{15}N$ analyses was a SGE Analytical Science BPX5 column 60 m by 0.32 mm with a 1 μm film

thickness. An Agilent DB-5 column 50 m by 0.32 mm with a 0.52 μm film thickness was used for $\delta^{13}C$ analyses. The injector temperature was 250 ºC with a split He flow of 2 mL/min. The GC temperature program for $\delta^{15}N$ analysis was: initial temp = 70 ºC hold for 1 min; ramp 1 = 10 ºC /min to 185 ºC, hold for 2 min; ramp 2 = 2 ºC/min to 200 ºC, hold for 10 min; ramp 3 = 30 ºC/min to 300 ºC, hold for 6 min. The GC temperature program for $\delta^{13}C$ analysis was: initial temp = 75 ºC hold for 2 min; ramp 1 = 4 ºC /min to 90 ºC, hold for 4 min; ramp 2 = 4 ºC/min to 185 ºC, hold for 5 min; ramp 3 = 10 ºC/min to 250 ºC, hold for 2 min; ramp 4 = 20 ºC/min to 300 ºC, hold for 5 min. Directly measured amino acid $\delta^{15}N$ values were corrected via bracketing external standards, described in McCarthy et al. (2013), while amino acid $\delta^{13}C$ values were determined from the measured values of amino acid derivatives following the approach of Silfer et al. (1991). The $\delta^{15}N$ and $\delta^{13}C$ values of 11 amino acids could be quantified for most samples: alanine (Ala), glycine (Gly), threonine (Thr), serine (Ser), valine (Val), leucine (Leu), isoleucine (Ile), Pro, aspartic acid + asparagine (Asp), Glu, Phe, and lysine (Lys).

Sample preparation for radiocarbon analysis

When possible, skin samples from a specimen were analyzed for radiocarbon (^{14}C), but when skin was unavailable, bone was analyzed instead. Prior to ^{14}C analysis, skin samples were manually cleaned to remove visible sand and dried in an oven. Bone samples required more extensive preparation to isolate collagen and eliminate contaminants.

Bone samples were prepared for ^{14}C according to an established laboratory protocol. First, between 150 and 200 mg of bone was weighed and ground into a coarse powder via a mortar and pestel (pre-cleaned with ethanol). Then, the material was transferred into a vial (BD Falcon 15 mL centrifuge tubes, polypropylene) for processing to isolate highly pure collagen. Ground bone was decalcified via the addition of 7 mL of HCl (0.5 M), agitation with a vortex, and storage at room temperature. Decalcifying samples were checked after 48 hours and if their decalcification was incomplete, the HCl was refreshed. Subsequently, the HCl was refreshed every 24 hours until decalcification appeared complete at which time the collagen was rinsed five times with Milli-Q water and 7 mL NaOH (0.1 M) was added at room temperature. After 24 hours, the NaOH was removed and the samples were rinsed five times with Milli-Q water. A final application of 7 mL of HCl (0.5 M) for 24 hours was performed to ensure complete decalcification, which was followed by five Milli-Q water rinses. Samples were kept frozen at -20 °C until the next preparatory step.

The bone collagen was gelatinized via the addition of 7 mL HCl (0.05 M) after being transferred to 10 mL borosilicate culture tubes (Fisherbrand). Samples were heated in the HCl solution at 58 °C on a hot plate for 48 hours. Immediately after stopping the gelatinization the samples were filtered (Whatman glass microfiber filters, grade 934-AH circles, particle retention 1.5 μm), retaining the filtrate, which was transferred to borosilicate culture tubes. Lastly, samples were dried via a vacuum

concentrator centrifugal evaporator system (Jouan RC 10-10) with liquid N_2 and water traps. At this point, the nearly pure collagen from bone was obtained.

Radiocarbon analysis

After pretreatment, about 20 mg of each bone or skin sample was sent to the National Ocean Sciences Accelerator Mass Spectrometry Facility (NOSAMS) at Woods Hole Oceanographic Institution (WHOI) for ^{14}C analysis. Skin samples received further pretreatment to remove organic contaminants at NOASAMS (repeated acid-base rinse cycles until rinsing solutions were clear). NOSAMS used their organic combustion method to graphitize the samples, which were then pressed into target cartridge and loaded into the Accelerator Mass Spectrometer (AMS) for analysis. Samples were analyzed on either a 3 MV Tandetron or 500 kV Pelletron system. NBS Oxalic Acid I (NIST-SRM-4990) was the primary standard used for ^{14}C measurements, and process blank materials were analyzed during each instrument session. The blank materials were the Fourth International Radiocarbon Intercomparison (FIRI) A and B woods, as well as acetanilide (CE Elantech). Upon receiving the data, ^{14}C ages were calibrated with CALIB 7.0.1, the Marine13 calibration database (Reimer et al. 2013), using the delta-*R* value of 791 +/- 121 (Hall et al. 2010). Calendar ages were reported as the midpoint of the one standard deviation range. The correction for the applied reservoir effect was verified via radiocarbon analysis of Weddell seal specimens from the Ross Sea that were of known age as they were collected during particular expeditions in the early 1900s. Additionally, an effect of contamination on the ^{14}C data was disregarded since

preparation and analysis of standards resulted in ^{14}C measurements that had offsets from the known ages of the materials that were within instrument error.

Sample preparation for ancient DNA analysis

All ancient DNA (aDNA) work was conducted in a dedicated aDNA laboratory at Durham University, using strict protocols to prevent and detect contamination. Briefly, this included one-way movement of reagents, samples, and personnel from the aDNA to the modern DNA lab, decontamination using 50% bleach and/or UV sterilization, use of filter tips, and inclusion of extraction and negative controls every 10 to 20 samples.

Ancient DNA was extracted from skin, bone, and hair samples. For bone and skin samples, an approximately 1 cm x 1 cm section of sample was removed using a rotary saw with disposable blades. These were homogenized in a Retsch MM 200 mill in stainless steel canisters cleaned with Virkon disinfectant, 50% bleach, and rinsed in 95% ethanol. Hair samples were cut into ~ 5 mm portions using a sterile blade.

aDNA extraction and amplification

First, samples were digested overnight at 37 °C in 750 uL of solution of 0.5% SDS, 0.425 M EDTA (pH 8.0), 0.1 M Tris-HCl (pH 8.0), and 0.77 mg/mL Proteinase K. Following digestion, 3 mL of PB Buffer (QIAgen) was added to each sample, along with up to 50 uL of 3 M sodium acetate (pH 5.2) to adjust the pH for purification with the Qiaquick spin filter kit. Purification was conducted according to manufacturer directions; however, additional spins were required to bind the entire

sample to the column. Elution was performed twice using 70 uL of EB buffer, which was incubated at 37 °C for 5 min.

Polymerase chain reaction (PCR) was carried out to amplify an approximately 180 bp fragment of the mitochondrial control region, using primers aSealCR1F (5'-GCATTAACGGTTTGCCCCAT-3') and aSealCR1R (5'-GGTACACGTTTCACAAGGGT-3'), which were designed in the program Primer3 (Koressaar and Remm 2007, Untergasser et al. 2012) from 200 ancient southern elephant seal (sampled from the VLC; de Bruyn et al. 2009), 135 modern crabeater seal (Curtis et al. 2009), 83 modern Weddell seal (Curtis et al. 2009), and 2 modern leopard seal sequences from Genbank. This region carries several diagnostic sites that differ among the four species, thus facilitating species identification. PCR reactions were conducted in a total volume of 25 µl, which included 2 µl DNA, as well as 0.02 units of AmpliTaqGold, 1X AmpliTaq Gold buffer II, 2.5 mM $MgCl_2$, 0.2 mM each dNTP, and 0.4 µM each primer. The thermocycler program used was 94 °C for 8 min, then 45 cycles of 94 °C for 30 s, 50 °C for 30 s, and 72 °C for 30 s, followed by a further extension step of 72 °C for 7 min. PCR products were visualized on a 2% agarose gel stained with ethidium bromide. In total, DNA extraction was attempted for 536 samples and was performed successfully for 468 samples.

Species identification from aDNA analysis

We developed a restriction digest test to conduct an initial screen for species identification. Positive PCR products (20 uL) were cleaned via a standard ethanol precipitation procedure: 10% of 3 M sodium acetate (pH 5.2) and 1 mL of chilled

100% ethanol was added to each sample, which was then incubated overnight at -20 °C. Samples were spun for 15 min and then the ethanol was discarded and 1 mL of chilled 70% ethanol was added. Samples were spun for another 15 min, the ethanol was discarded, and the samples were dried for 45 min at 50 °C in a SpeedVac DNA concentrator. Next, 15 uL of EB buffer, preheated to 55 °C, was added to each sample and the samples were subsequently incubated at 55 °C for a further 10 min in order for elution.

Restriction digests were carried out using 1x Cutsmart Buffer (New England Biolabs), 7.5 uL of cleaned PCR product, and 0.5 uL BstE-II HF enzyme (New England Biolabs). Reactions were incubated at 37 °C for 30 min and terminated by the addition of 5 uL of gel loading buffer, following manufacturer instructions. The resulting products were run at 90 V for 3 hr on a 2.5% agarose gel stained with ethidium bromide. *In silico* tests via the program, Geneious v9.0 (Kearse et al. 2012), suggested that this restriction digest would result in the production of two fragments of 100 and 80 bp in length for approximately 80% of the crabeater seal sequences available on Genbank. However, up to 2% of ancient southern elephant seals shared this site and would also be cut since no perfect species-specific restriction site could be found within the sequences available on Genbank (for this site or any other mitochondrial region) that would be short enough to reliably amplify aDNA. Any cut PCR product was assumed to be a crabeater seal, and any uncut product was sent for Sanger sequencing in the forward direction at Durham University's DBS Genomics facility.

Resulting sequences were visually inspected and manually edited in Geneious and then compared against the Genbank database using the BLAST tool to provide initial species assignments. The highest scoring hit was accepted as long as the e-value was below 1×10^{-20} and the sequence identity was greater than 95%. DNA sequences from Genbank, described above, were added to those obtained from our study. Sequences for northern elephant seal (*Mirounga angustirostris*), Mediterranean monk seal (*Monachus monachus*), Ross seal (*Ommatophoca rossii*) and bearded seal (*Erignathus barbatus*) were included as outgroups. MAFFT v7 (Katoh et al. 2002) was used to align the sequences and the best-fit model of nucleotide evolution was investigated using jModelTest v2 (Darriba et al. 2012). A neighbor-joining tree was built in Geneious with 1,000 bootstraps and principle component analysis (PCA) was conducted in the program GenAlEx (Peakall and Smouse 2006, 2012). Results (not shown) displayed all putative and known crabeater seal individuals grouping together in a monophyletic group with a bootstrap support of 89. Similarly, all northern and southern elephant seals grouped together with bootstrap support of 67, and Ross seals grouped together with support of 96. Leopard seals and Weddell seals grouped together in a single clade with a bootstrap support of 76, but these species are known to have a close evolutionary history (Dasmahapatra et al. 2009, Fulton and Strobeck 2010). PCA was able to successfully separate all species – both individuals of known identity and those with putative assignments – thus confirming previous initial BLAST species assignments. These species assignments have also been largely confirmed through morphological identification of preserved remains (e.g. teeth, body

size). Additionally, eight individuals were tested two to three times with the restriction digest test and Sanger sequencing, and the results were consistent in each case.

Data analysis

To examine temporal trends in the isotopic values of Antarctic pinnipeds, we include modern data from the species. Modern crabeater seal isotope data for Ross Sea specimens were derived from Chapter 2. Multiple data sources were used for modern Weddell seal isotope values and, in all cases, the animals were sampled in the Ross Sea: Goetz et al. (2017), Chapter 2, and Hückstädt et al. (2017). Samples from Hückstädt et al. (2017) were obtained from skins of Weddell seals, hunted approximately 100 years ago, that have remained in explorer huts around the Ross Sea. The temporal trend of leopard seal isotope values was constructed using modern data from specimens sampled in the region of the eastern Ross Sea and western Amundsen Sea (Zhao et al. 2004) and in Prydz Bay, East Antarctica (Hall-Aspland et al. 2005). For SES, subfossil isotope values were compared to modern data from animals sampled throughout the Subantarctic region. Since this species only rarely appears in the Ross Sea today isotopic values were not available for modern animals in the region. Modern SES data were derived from: Lewis et al. (2006), Eder et al. (2010), Martin et al. (2011), Newland et al. (2011), Hückstädt et al. (2012a), and van den Hoff (pers. comm.).

To account for isotopic offsets between different tissues we developed corrections to apply to bulk isotope values of blood or hair samples such that they

were adjusted to represent bone material for crabeater and Weddell seals. Corrections were developed by determining the bulk isotope differences between samples of blood, including various components of blood, and hair, see Chapter 2, as well as the bulk isotope differences between hair and bone, presented in Table 3.S1-3.S2. We were unable to determine such offsets for leopard seals and SES due to a lack of the necessary tissues. For these two species we have applied the calculated Weddell seal isotope corrections since leopard seals and SES are known to be at a more similar trophic position to that of Weddell seals than crabeater seals (Rau et al. 1992, Zhao et al. 2004, Chapter 2). Thus, leopard seals and SES may be more metabolically similar to Weddell seals than crabeater seals (Ernest et al. 2003).

All data analyses were done in R statistical software (R Core Team, 2014). Before performing all statistical analyses any test assumptions were considered. If an assumption was violated and data were transformed, then this has been noted in the following text. An effect of age class on isotope patterns was assessed via a one-way analysis of variance (ANOVA) on Box-Cox transformed (Box and Cox, 1964) bulk isotope data for crabeater and Weddell seals to evaluate differences in $\delta^{15}N$ and $\delta^{13}C$ values between different age classes. In the field, an age class of pup (< 1-year-old), subadult/yearling (approximately 1- to 2-years-old), or adult (≥ 2-years-old) was noted when possible for crabeater and Weddell seals. For Weddell seals, we broke their isotopic data into a group with calendar ages ≤ 788 YBP and one with calendar ages > 788 YBP, which has been determined to be a likely point of transition in

baseline isotope values as described below, conducting a one-way ANOVA with each group.

In establishing temporal trends in the bulk $\delta^{15}N$ and $\delta^{13}C$ values for all seal species, for subfossils we used data only from bone samples, the material analyzed in most cases for subfossil animals, so that the time represented by each subfossil isotope datum was more consistent. The temporal trends in bulk isotope values for all species were evaluated via linear or logarithmic regression analysis. For each species, an F-test for equality of variance was conducted to compare the variability in the bulk isotope values of subfossil specimens to that of the modern specimens. However, this test was not done for SES since modern Ross Sea SES tissues were not available for bulk isotope analysis. A linear regression analysis was performed to evaluate a relationship between bulk $\delta^{15}N$ and $\delta^{13}C$ values of most modern SES. Additionally, a two-way student's *t*-test was used to examine whether the bulk isotope values of subfossil SES were statistically equivalent to those of modern SES with isotopic values most similar to them. Since the bulk isotope values of subfossil SES appeared to cluster into two groups a two-way student's *t*-test was also performed to assess this variation. A one-way ANOVA was used on the Box-Cox transformed (Box and Cox, 1964) bulk isotope data for subfossil specimens to evaluate differences in $\delta^{15}N$ and $\delta^{13}C$ values between species.

Like the bulk isotope values, a linear or logarithmic regression analysis was carried out to explore temporal trends in the $\delta^{15}N$ values of certain amino acids, Pro and Phe, for crabeater seals, Weddell seals, and SES. An F-test for equality of

variance was also completed for crabeater and Weddell seals to compare the variances in the Pro and Phe $\delta^{15}N$ values of subfossil specimens to those of modern specimens. This comparison was not done for SES since modern Ross Sea SES tissues were not available for amino acid isotope analysis. A two-way student's *t*-test was conducted to assess the variation between Phe $\delta^{15}N$ values of two groups of subfossil crabeater seals: one with high trophic positions (≥ 3.8) and high bulk $\delta^{15}N$ values (> 15 ‰) and another with low trophic positions (≤ 3.1) and low bulk $\delta^{15}N$ values (< 10 ‰). Additionally, a k-means cluster analysis was used to compare two groups of subfossil SES specimens from their Phe $\delta^{15}N$ and $\delta^{13}C$ values since the amino acid isotope values for this species appeared to separate into two clear clusters. Linear regression analyses were conducted to determine whether the Phe isotope values of SES were related to the SES bulk isotope values for both carbon and nitrogen.

Trophic positions were calculated for subfossil specimens of all species using the method described in Chapter 2. In brief, trophic positions were calculated based on Chikaraishi et al. (2009), but using Pro for Glu as the trophic amino acid, suggested by McMahon et al. (data unpublished). Trophic positions were calculated as follows:

$$TP = (\delta^{15}N_{Pro} - \delta^{15}N_{Phe} - \beta_{Pro/Phe})/TDF_{Pro} + 1$$

Here, TP, $\beta_{Pro/Phe}$, and TDF_{Pro} are the trophic position, isotope difference between Pro and Phe in primary producers (3.1 ‰), and trophic discrimination factor (4.5 ‰), respectively (McMahon and McCarthy 2016). Note, the calculated TP may

be an underestimate, since TDF_{Pro} values vary across species and tissue types, and published TDF_{Pro} values are limited (McMahon and McCarthy 2016). For crabeater, Weddell, and southern elephant seals, temporal trends in TPs were determined, which included TPs of modern specimens that were obtained from Chapter 2. These trends were assessed via linear or logarithmic regression analysis. Additionally, the variability in the trophic positions of subfossil specimens was compared to that of modern specimens via a F-test for equality of variance for crabeater and Weddell seals. Trophic positions of subfossil specimens were compared between crabeater, Weddell, and southern elephant seals via a one-way ANOVA on Box-Cox transformed data. The same analysis was also performed upon splitting the crabeater seal data into two groups – one with high trophic positions (≥ 3.8 ‰) and another with low trophic positions (≤ 3.1 ‰) – since the wide range of trophic positions for subfossil crabeater seals suggests two ecologically distinct groups.

A k-means cluster analysis was used to compare four groups of subfossil specimens from their Phe $\delta^{15}N$ and $\delta^{13}C$ values. Note, we selected individual crabeater seals that had bulk $\delta^{15}N$ values spanning the wide range observed and individual SES specimens that had bulk $\delta^{13}C$ values covering the full range measured.

RESULTS

Influence of age class on isotopic patterns

We examined whether isotopic differences between age classes could have accounted for variation in the bulk or amino acid isotope data of Antarctic seal species. Many of the pinniped specimens appeared to be yearlings or subadults at their time of death. For both crabeater and Weddell seals, age class was noted when possible during our sample collection (Table 3.S3). We find no significant differences in the bulk $\delta^{15}N$ and $\delta^{13}C$ values of different age classes (i.e., pup, subadult/yearling, adult, $p > 0.05$ from a one-way ANOVA) for both crabeater and Weddell seals.

Temporal trends in bulk $\delta^{15}N$ values of ice-dependent Antarctic seal species

For bulk $\delta^{15}N$ measurements, the variability of subfossil crabeater seals (standard deviation of 1.9 ‰) is not significantly different from that of modern crabeater seals (standard deviation of 1.4 ‰) from the Ross Sea ($p > 0.05$ from a F-test for equality of variance) (Fig. 3.2 and Table 3.S3). One modern crabeater seal has a bulk $\delta^{15}N$ value of 11.9 ‰, which is notably higher than the bulk $\delta^{15}N$ values of all other modern crabeater seals from West Antarctica. Without this individual, the range in bulk $\delta^{15}N$ values for modern crabeater seals from the Ross Sea is 7.1 ‰ to 8.4 ‰ ($n = 9$) and the range for modern crabeater seals from all of West Antarctica is 5.3 ‰ to 8.6 ‰ ($n = 97$), see Chapter 2. Only four out of 97 West Antarctic modern crabeater seals have bulk $\delta^{15}N$ values greater than or equal to 9 ‰. In comparison, subfossil crabeater seals have a range of bulk $\delta^{15}N$ values (5.3 ‰ to 17.1 ‰, $n = 337$) and proportion of bulk $\delta^{15}N$ values exceeding or equal to 9 ‰ (121 out of 337 individuals) that are both greater than those observed for modern specimens. Across the time series, bulk $\delta^{15}N$ values of crabeater seals shift, declining significantly with

decreasing calendar age ($p = 0.05$ and $R^2 = 0.03$ from a linear regression analysis). This shift appears to be recent, occurring within the last 200 years.

For leopard seals, the variability in bulk $\delta^{15}N$ measurements for subfossil specimens does not differ significantly from that of modern specimens ($p > 0.05$ from a F-test for equality of variance). Additionally, bulk $\delta^{15}N$ values show no significant trend over the mid-to-late Holocene ($p > 0.05$ from both linear and logarithmic regression analyses) (Fig. 3.S1 and Table 3.S3).

The variability in the bulk $\delta^{15}N$ values of the mummified Weddell seals is greater than that of modern animals ($p < 0.001$ from an F-test for equality of variance, Fig. 3.3 and Table 3.S3). Mummified Weddell seal specimens have bulk $\delta^{15}N$ values with a mean ± standard deviation of 15.1 ± 1.3 ‰ (range of 11.3 to 18.3 ‰, $n = 198$), while that of modern Weddell seal specimens is 13.1 ± 0.4 ‰ (range of 12.3 to 14.8 ‰, $n = 157$). Furthermore, Weddell seal bulk $\delta^{15}N$ values appear to be relatively stable from the mid Holocene to about 680 YBP at which time they begin to decline. A logarithmic regression analysis reveals the trend is significant ($p < 0.001$, $R^2 = 0.6$). From about 680 to 4,679 YBP bulk $\delta^{15}N$ values of subfossil Weddell seals are fairly consistent at 15.8 ± 1.1 ‰ ($n = 68$). Bulk $\delta^{15}N$ values of Weddell seals decline considerably after 680 YBP, dropping by 2.7 ‰ from the mean bulk $\delta^{15}N$ value of earlier Holocene times to that of modern times.

Temporal trends in bulk $\delta^{13}C$ values of ice-dependent Antarctic seal species

No significant differences occur between the bulk $\delta^{13}C$ value variation of subfossil specimens and that of modern specimens for either crabeater or leopard

seals ($p > 0.05$ from a F-test for equality of variance in both cases), and no significant temporal trends in bulk $\delta^{13}C$ values for these species have been found ($p > 0.05$ from linear and logarithmic regression analyses for crabeater and leopard) (Fig. 3.S2-3.S3 and Table 3.S3). The variability in the bulk $\delta^{13}C$ values of the mummified Weddell seals is greater than that of modern animals ($p < 0.001$ from an F-test for equality of variance), as is the case for bulk $\delta^{15}N$ values (Fig. 3.4 and Table 3.S3). The Weddell seal bulk $\delta^{13}C$ values begin to drop around 1,200 YBP, earlier than the bulk $\delta^{15}N$ values. A logarithmic regression analysis indicates this temporal trend is significant ($p < 0.001$, $R^2 = 0.1$). The magnitude of the decline in bulk $\delta^{13}C$ values of subfossil Weddell seals is less than that for nitrogen, dropping by about 1.4 ‰ from the bulk $\delta^{13}C$ value of specimens from the period before 1,200 YBP (1,209 to 4,679 YBP; -21.0 ± 1.0, $n = 26$) to that of modern specimens (-22.4 ± 0.4, $n = 157$).

Bulk isotope values over the modern era and Holocene for southern elephant seals

No significant temporal trends are observed for the bulk $\delta^{15}N$ and $\delta^{13}C$ values of subfossil SES, spanning a period of 3187 to 416 YBP ($p > 0.05$ from a linear regression analysis). The comparison of subfossil SES isotope values to those of modern SES from locations throughout the Antarctic and Subantarctic yields significant results. Excluding isotopic data from a small subset of modern SES, those known to have been foraging in coastal polynyas off East Antarctica, a significant linear relationship exists between bulk $\delta^{15}N$ and $\delta^{13}C$ values for modern SES (Fig. 3.5

and Table 3.S3). In this relationship, $\delta^{15}N$ values significantly decrease with decreasing $\delta^{13}C$ values ($p < 0.001$ and $R^2 = 0.8$ from a linear regression analysis).

A decrease in both bulk $\delta^{15}N$ and $\delta^{13}C$ values of modern SES occurs when animals forage closer to Antarctica (Fig. 3.5). Animals known to have closely approached the continent from satellite tracking data are among those with the lowest bulk $\delta^{15}N$ and $\delta^{13}C$ values. A unique group of modern SES has low bulk $\delta^{13}C$ values, but high bulk $\delta^{15}N$ values. These animals are known from satellite tracking or other data to have visited coastal polynyas, productivity hot spots, along the East Antarctic coast in Prydz Bay or Vincennes Bay.

Subfossil SES from the VLC have bulk $\delta^{15}N$ and $\delta^{13}C$ values that seem most similar to those of the modern SES that forage in the East Antarctic coastal polynyas. Indeed, the bulk $\delta^{15}N$ and $\delta^{13}C$ values of these two groups are statistically equivalent (student's *t*-test, $p > 0.05$). However, SES subfossil specimens have a wide spread of isotopic values, especially for carbon. For $\delta^{15}N$, the range in values is 13.3 ‰ to 16.7 ‰ (15.1 ± 1.1 ‰, $n = 28$). Values range from -22.7 ‰ to -16.6 ‰ for $\delta^{13}C$ (-19.6 ± 1.3 ‰, $n = 28$).

Bulk isotope comparison among all Antarctic seal subfossil species

Bulk isotope values vary significantly among several species (Fig. 3.6 and Table 3.S3). Bulk $\delta^{15}N$ values of crabeater seals (8.2 ± 1.9 ‰, $n = 337$) are significantly lower than all other pinniped species ($p < 0.001$ for all Bonferroni post-hoc comparisons). Yet, some crabeater seal subfossil specimens ($n = 7$), interestingly,

have very high bulk $\delta^{15}N$ values (> 15 ‰), comparable to those of subfossil SES and Weddell seals. Southern elephant seals (15.1 ± 1.1 ‰, $n = 28$) have similar $\delta^{15}N$ values to those of Weddell seals (15.2 ± 1.4 ‰, $n = 164$) and leopard seals (14.1 ± 1.9 ‰, $n = 25$). Weddell seal $\delta^{15}N$ values are significantly higher than leopard seal $\delta^{15}N$ values ($p = 0.03$ from a Bonferroni post-hoc comparison). All seal species have significantly different $\delta^{13}C$ values, except Weddell and leopard seals, which have similar values of -21.7 ± 1.0 ‰ ($n = 164$) and -22.0 ± 0.9 ‰ ($n = 25$), respectively. Crabeater seals have the lowest $\delta^{13}C$ values (-23.0 ± 0.8 ‰, $n = 337$), while SES have the highest $\delta^{13}C$ values (-19.6 ± 1.3 ‰, $n = 28$). Intriguingly, comparison of isotopic data for all subfossil specimens, encompassing all four pinniped species, shows two groups of SES. Some SES specimens have $\delta^{13}C$ values (< -19.7 ‰, $n = 14$) that overlap with data from the other pinniped species, although their $\delta^{13}C$ values remain statistically different from those of the other three species ($p < 0.001$ from Bonferroni post-hoc comparison in all cases). The other SES specimens have $\delta^{13}C$ values largely unique from any other seal species from the Ross Sea (≥ -19.7 ‰, $n = 14$). While their $\delta^{15}N$ values are not significantly different, the $\delta^{13}C$ values of the two groups of SES (-20.5 ± 0.9 ‰ and -18.7 ± 1.1 ‰) do vary significantly ($p < 0.001$ from a student's *t*-test).

Patterns in amino acid $\delta^{15}N$ values for crabeater seals

Crabeater seal $\delta^{15}N$ values of Pro and Phe show no significant shift across the time series, but the former does experience temporal change in regards to variance

(Figs. 3.7, 3.S4, and 3.S5, Table 3.S4). Phe $\delta^{15}N$ values across approximately the last 3,000 years are consistent at 5.8 ± 1.2 ‰ (n = 15). In contrast, the variance of Pro $\delta^{15}N$ values seems to decline after about 200 YBP and is significantly greater for subfossil specimens than modern seals (p = 0.04 from an F-test for equality of variance). For subfossil and modern crabeater seals Pro $\delta^{15}N$ values are 19.2 ± 4.3 ‰ (range from 13.7 to 25.1 ‰, n = 12) and 15.4 ± 0.6 ‰ (range from 14.7 to 15.7 ‰, n = 3), respectively. Like Pro, the trophic positions of crabeater seals show no significant shift over the late Holocene, but their variance declines, after approximately 200 YBP (Fig. 3.8). Indeed, the variability in the trophic positions of subfossil crabeater seal specimens is significantly greater than that of modern individuals (p = 0.04 from an F-test of equality of variances). The trophic positions of mummified and modern crabeater seals are 3.3 ± 0.8 (range from 2.2 to 4.5, n = 12) and 2.4 ± 0.2 (range from 2.3 to 2.6, n = 3), correspondingly. Among the subfossil specimens that have been analyzed for amino acid $\delta^{15}N$ values, crabeater seals cluster into a group with low trophic positions (≤ 3.1), as well as low bulk $\delta^{15}N$ values (< 10 ‰), and another group with high trophic positions (≥ 3.8) in addition to high bulk $\delta^{15}N$ values (> 15 ‰). Interestingly, Phe $\delta^{15}N$ values differ significantly between these two groups with measurements of 4.9 ± 1.0 ‰ (n = 7) for the low trophic position group and 6.8 ± 0.6 ‰ (n = 5) for the high trophic level group (p < 0.001 from a two-way student's t-test).

Patterns in amino acid $\delta^{15}N$ values for Weddell seals

For the subset of Weddell seal specimens analyzed for amino acid $\delta^{15}N$ values, a significant trend in $\delta^{15}N$ values has been found for both Pro and Phe from a logarithmic regression analysis (p-values of < 0.001 and 0.003, respectively; R^2 values of 0.5 and 0.3, correspondingly; Figs. 3.9, 3.S4, and 3.S5, Table 3.S4). Like the bulk $\delta^{15}N$ trend, $\delta^{15}N$ values of Pro and Phe decline with decreasing calendar age. From 4,679 to 788 YBP $\delta^{15}N$ values of Pro and Phe are fairly consistent at 24.8 ± 1.2 ‰ (n = 16) and 8.8 ± 0.9 ‰ (n = 16), correspondingly. Their values decrease after this period, reducing to 20.9 ± 0.5 ‰ (n =3) and 5.7 ± 0.7 ‰ (n =3) for Pro and Phe $\delta^{15}N$ values, respectively, by modern times. Thus, during the late Holocene, $\delta^{15}N$ values of Pro drop by about 3.9 ‰ and those of Phe decrease by approximately 3.1 ‰, greater than the drop for all Weddell seal bulk $\delta^{15}N$ values (2.7 ‰). Lastly, the trophic position of Weddell seals does not vary significantly across approximately the last 5,000 years (Fig. 3.S6).

Patterns in amino acid $\delta^{15}N$ values for southern elephant seals

Across the late Holocene, $\delta^{15}N$ values of Phe significantly decline with decreasing calendar age (p = 0.03 and R^2 = 0.3 from a linear regression analysis) whereas $\delta^{15}N$ values of Pro do not shift significantly for subfossil SES with $p > 0.05$ from a linear regression analysis (Figs. 3.10, 3.S4, and 3.S5, Table 3.S4). Recall, the time series of SES does not include modern data since it is not available for Ross Sea SES and covers the time period of 3187 to 493 YBP. The linear relationship indicates that Phe $\delta^{15}N$ values decrease by about 3 ‰ with decreasing calendar age across the

late Holocene. For animals that have overlapping bulk $\delta^{13}C$ values with those of other true Antarctic seal species, having bulk $\delta^{13}C$ less than -19.7 ‰, a significant decline in Phe $\delta^{15}N$ values occurs from 3187 to 513 YBP ($p = 0.05$ and $R^2 = 0.5$ from a linear regression analysis), decreasing by about 2 ‰ over this period. The $\delta^{15}N$ values of Pro are 26.3 ± 1.8 ‰ ($n = 11$) for the late Holocene. The trophic position of subfossil SES does not significantly change during this time period, like the Pro $\delta^{15}N$ values, remaining relatively constant at 4.6 ± 0.2 ($n = 11$) with $p > 0.05$ from a linear regression analysis (Fig. 3.S7). Lastly, we expect spatial differences among animals to be most clearly revealed by $\delta^{15}N$ and $\delta^{13}C$ data from Phe since Phe is both a source amino acid for nitrogen and an essential amino acid for carbon, discussed above. Subfossil SES cluster into two groups according to their Phe $\delta^{15}N$ and $\delta^{13}C$ data, representing the isotopic baselines of subfossil SES, from a k-means cluster analysis (Fig. 3.S8). One group (cluster 1) has high $\delta^{15}N_{baseline}$ and low $\delta^{13}C_{baseline}$ with its centroid having Phe $\delta^{15}N$ and $\delta^{13}C$ values of 8.5 ± 0.8 ‰ and -29.0 ± 0.7 ‰, respectively. The other group (cluster 2) has low $\delta^{15}N_{baseline}$ and high $\delta^{13}C_{baseline}$ with its centroid having Phe $\delta^{15}N$ and $\delta^{13}C$ values of 4.8 ± 0.1 ‰ and -24.8 ± 1.4 ‰, correspondingly. Note, a significant positive relationship exists between Phe and bulk $\delta^{15}N$ values ($p < 0.001$ and $R^2 = 0.7$ from a linear regression analysis). Although a relationship between Phe and bulk $\delta^{13}C$ values from a linear regression analysis is not significant ($p > 0.05$), the sample size for the Phe $\delta^{13}C$ analysis is low ($n = 4$) whereas the sample size for the Phe $\delta^{15}N$ analysis is higher ($n = 11$). Notably, subfossil SES

with high Phe $\delta^{13}C$ values (> -25 ‰) also have high bulk $\delta^{13}C$ values (≥ -19.7 ‰) that are largely distinct from those of other Ross Sea pinniped species, and subfossil SES with low Phe $\delta^{13}C$ values (< -28 ‰) also have low bulk $\delta^{13}C$ values (< -19.7 ‰) that overlap with the bulk $\delta^{13}C$ values of other Ross Sea seal species.

Trophic positions of subfossil Antarctic seals

The trophic positions of crabeater, Weddell, and SES subfossils differ significantly (Fig. 3.S9). From the Bonferroni post-hoc comparisons, the significant differences have *p*-values of less than or equal to 0.001 in all cases. Trophic positions of the subfossil specimens decrease as follows: SES (4.6 ± 0.2 ‰, $n = 11$) > Weddell seal (3.9 ± 0.3 ‰, $n = 22$) > crabeater seal (3.3 ± 0.8 ‰, $n = 12$). To further investigate differences in trophic level between the subfossil species, we have divided the crabeater seal subfossils into two groups since they show significant variation in their trophic positions, described above: a high trophic level group (≥ 3.8) and a low trophic level group (≤ 3.1). After this segregation, the trophic positions of the subfossil specimens are significantly different between all species, except Weddell seals and the crabeater seals with high trophic positions, as well as high bulk and Phe $\delta^{15}N$ values. The observed significant differences have *p*-values of less than or equal to 0.01 in each case (Bonferroni post-hoc comparisons). The trophic positions of the subfossil specimens decrease as follows: SES (4.6 ± 0.2 ‰, $n = 11$) > high trophic level crabeater seals (4.1 ± 0.3 ‰, $n = 5$) and Weddell seals (3.9 ± 0.3 ‰, $n = 22$) > low trophic level crabeater seals (2.8 ± 0.3 ‰, $n = 7$).

Comparison of amino acid Phe $\delta^{15}N$ and $\delta^{13}C$ values for subfossil seal species

As mentioned previously, Phe $\delta^{15}N$ and $\delta^{13}C$ data indicate spatial differences among animals. A k-means cluster analysis produces four groups of subfossil specimens from their Phe $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 3.11 and Table 3.S4 and 3.S5). The Weddell seal exclusive group (cluster 1) had the highest Phe $\delta^{15}N$ values and lowest Phe $\delta^{13}C$ values with its centroid at 10.1 ± 0.1 ‰ (*n* =2) and -30.3 ± 0.1 ‰ (*n* =2) for $\delta^{15}N$ and $\delta^{13}C$ values, respectively. Cluster 2, which consists of one Weddell seal, two high trophic level crabeater seals, and two high $\delta^{15}N_{baseline}$ /low $\delta^{13}C_{baseline}$ SES specimens, has slightly lower Phe $\delta^{15}N$ values (8.0 ± 0.8 ‰, *n* =5) than cluster 1, and similar Phe $\delta^{13}C$ values (-29.1 ± 0.4 ‰, *n* =5) to that cluster. Cluster 3, comprising of two low trophic level crabeater seals, has the lowest Phe $\delta^{15}N$ values (4.6 ± 0.7 ‰, *n* =2) that are similar to those of cluster 4, exclusively low $\delta^{15}N_{baseline}$ /high $\delta^{13}C_{baseline}$ SES (4.8 ± 0.1 ‰, *n* =2). Cluster 4 has the highest Phe $\delta^{13}C$ values (-24.8 ± 1.4 ‰, *n* =2), while cluster 3 had intermediate Phe $\delta^{13}C$ values (-28.0 ± 0.6 ‰, *n* =2) relative to all subfossil specimens.

DISCUSSION

As mentioned above, we have explored whether age class drives any isotopic variation observed for Antarctic seals. Bulk isotope values do not differ significantly between different age classes for crabeater or Weddell seals. Prior work that examines the variation in bulk isotope values among age classes for modern

individuals of these species (Chapter 2) suggests such variation cannot account for the observed isotope patterns of our subfossils, discussed below. For crabeater and Weddell seals, the greatest offsets between the bulk $\delta^{15}N$ values of any two age classes are 1.3 ‰ and 0.7 ‰ (Chapter 2), respectively, both less than the variations observed for the subfossil specimens, described later. The largest offset between the bulk $\delta^{13}C$ values of any two crabeater seal age classes is 1.7 ‰, while no significant variation in bulk $\delta^{13}C$ values among different age classes is noted for Weddell seals (Chapter 2). No significant trends in bulk $\delta^{13}C$ values of subfossil crabeater seals occur, however. Thus, we conclude that the isotopic variations discovered for subfossil Antarctic seals are not driven by isotopic differences between age classes.

Temporal trends in foraging strategies of Antarctic seals

In constructing the crabeater seal temporal trend for bulk nitrogen isotopes, a modern individual had an unusually high bulk $\delta^{15}N$ value. However, this result is not surprising given the atypical behavior of this individual, which was discovered amongst a group of Weddell seals in landfast ice at the foot of the Erebus Ice Tongue in the western Ross Sea. Likely, its uniquely high bulk $\delta^{15}N$ value indicates that this individual has been regularly using a foraging strategy more similar to that of Weddell seals, consuming fish more heavily than krill. Only 4 % of modern crabeater seals from West Antarctica have a bulk $\delta^{15}N$ value exceedingly or equivalent to 9 ‰ and, thus, the animal – with a bulk $\delta^{15}N$ value of 11.9 ‰ – is clearly unusual. In contrast, it is striking that 36 % bone samples from subfossil crabeater seals have bulk $\delta^{15}N$ values greater than or equal to 9 ‰.

The considerably greater percent of subfossil crabeater seals with high bulk $\delta^{15}N$ values than that of modern crabeater seals suggests a greater proportion of high tropic level prey in the crabeater seal diet earlier in the Holocene than at present. The significant drop in bulk $\delta^{15}N$ values of modern crabeater seals relative to their conspecifics in the earlier Holocene might suggest a decrease in trophic level, a $\delta^{15}N$ baseline drop, or both. The results of the crabeater amino acid $\delta^{15}N$ analysis show no baseline shift; Phe $\delta^{15}N$ values are stable across the last 3,000 years. Pro $\delta^{15}N$ values are remarkably variable among subfossil crabeater seal specimens, which is not observed in modern animals. Indeed, the variance in Pro $\delta^{15}N$ values for subfossil crabeater seals is significantly greater than that for modern crabeater seals. The variability in Pro $\delta^{15}N$ values, along with consistency in Phe $\delta^{15}N$ values, across the late Holocene results in a wide range of offsets between Pro and Phe $\delta^{15}N$ values (ranging from 8.6 to 18.9 ‰), which is indicative of trophic position (Chikaraishi et al. 2009, McMahon and McCarthy 2016). Thus, the trophic positions of Ross Sea crabeater seals are highly variable earlier in the Holocene and become considerably less variable in modern times, after about 200 YBP.

The amino acid $\delta^{15}N$ analysis reveals solely a trophic effect on crabeater seal bulk $\delta^{15}N$ values. Those bulk data show that for about a third of crabeater subfossil specimens (with bulk $\delta^{15}N$ values greater than or equal to 9 ‰), fish or some other higher tropic level prey make up a greater portion of the diet than that for modern animals. This third of the subfossil crabeater seal population has a diet consisting of

roughly 25 % to 100 % fish (75 % to 0 % Antarctic krill) using a simple two-source mixing model (Fry 2006) with bulk $\delta^{15}N$ values of subfossil crabeater seals, fish (an average for Ross Sea fish species presented in Goetz et al. 2017), and Antarctic krill (Pinkerton et al. 2013). Repeating this scenario, but substituting bulk $\delta^{15}N$ values of crystal krill (*Euphausia crystallorophias*, Pinkerton et al. 2013) for Antarctic krill, produces a crabeater seal diet composed of approximately 0 % to 100 % fish (100 % to 0 % crystal krill). Seventeen subfossil crabeater seals have bulk $\delta^{15}N$ values comparable to those of modern Weddell seals (> 11.5 ‰) and, thus, are heavily or entirely consuming high trophic level prey, such as Antarctic silverfish or Antarctic toothfish. In contrast, fish species compose only 8 % to 25 % of crabeater seal diets, today (Hückstädt et al. 2012a).

The dietary flexibility we observe in subfossil crabeater seals is, perhaps, surprising given the specialized dentition of crabeater seals, which are optimal for capturing krill (Siniff 1991). Perhaps the selective pressure for the unique, curved, five-cusped post-canine teeth of crabeater seals is episodic and, over time, has not consistently driven dietary choices. For instance, the evolution of high-crowned molars (hypsodonty) in horses has been considered an adaptation that evolved in response to increased dental wear resulting from increased dietary abrasion due to diet or habitat changes (Mihlbachler et al. 2011). Although a strong correlation exists between mesowear score (indicative of dietary abrasion) and crown height in horses, Mihlbachler et al. (2011) have found that most fossil equids have highly variable mesowear scores, which are typically well below extreme values that reflect a highly

abrasive diet. MacFadden et al. (1999) have documented a similar pattern in their more focused isotopic and tooth wear study of ancient equids from Florida; horses with hypsodont teeth show a very wide range of diets. These results suggest that selection for high-crowned molars is episodic and that hypsodonty, despite being an adaption for dietary abrasion, enables a species to increase its dietary breadth, using both high- and low-abrasion diets (MacFadden et al. 2009, Mihlbachler et al. 2011). As in horses, perhaps selection for the unique molars of modern crabeater seals has been weak or absent for most of their history, being driven by limited time intervals with heavy selection pressure due to conditions strongly favoring predation on krill. The molars of present day crabeater seals may reflect an increase in dietary breadth to include krill as well as fish and squid, not obligate consumption of a specialized krill diet.

The recent shift in crabeater seals from diets with a considerable fish contribution (with some animals heavily focusing on larger fish or other high trophic level prey) to diets consisting almost exclusively of krill may reflect an increase in the availability of euphausiids to Ross Sea predators. Prior work has presented the "krill surplus hypothesis" as an explanation for a transition in Antarctic predators from fish- to krill-heavy diets (Laws 1977, 1985). Harvesting of krill predators, such as baleen whales and fur seals (*Arctocephalus tropicalis* and *Arctocephalus gazella*), has been hypothesized to result in an excess of krill and, thus, greater availability of this prey resource to other predators, such as penguins and unexploited seals (Laws 1977, 1985). Emslie and Patterson (2007) show a significant decline in the recent past in

both $\delta^{15}N$ and $\delta^{13}C$ values of Adélie penguin (*Pygoscelis adeliae*) eggshells from abandoned and active colonies in the Ross Sea, West Antarctic Peninsula (WAP), and East Antarctica. The authors suggest a krill surplus as an explanation for the dramatic shift in penguin isotope values, indicating a sharp transition from fish- to krill-heavy diets for this species. Other studies, likewise, note top-down effects on krill abundance shaping trophic interactions in the Antarctic (Fraser et al. 1992, Ainley et al. 2009, Trathan et al. 2012, Surma et al. 2014).

Our isotopic results indicate that crabeater seals have switched to krill-heavy diets within the last 200 years, but the trigger for this shift is unclear. The timeframe of the crabeater seal dietary shift coincides with the onset of sealing and whaling. Hunting of fur seals began in the late 1700s in Subantarctic islands of the Atlantic sector of the Southern Ocean, quickly spread throughout the Subantarctic and Antarctic, began a decline in the 1820s due to heavy fur seal depletion, and ceased by the 1950s (Hoffman 2017). Harvesting of baleen whales did not begin in the Southern Ocean until the late 1800s, initially occurring in the regions south of New Zealand, Australia, South Africa, and South America (Hoffman 2017). It peaked in the 1900s with heavy whaling taking place in the WAP and nearby Subantarctic islands, as well as considerable hunting ensuing at other sites, including the Ross Sea (Hoffman 2017). The International Whaling Commission imposed a moratorium on whaling in the 1980s (Hoffman 2017). Thus, a surplus in euphausiids in response to human removal of krill predators is a plausible, yet uncertain, explanation for an increase in

the importance of krill in crabeater seal diets. Along with harvesting, climate is an important driver of krill biomass.

Changing climate and oceanic conditions have considerable effects on the abundances and community compositions of phytoplankton and zooplankton, including krill (Arrigo and van Dijken 2003, Atkinson et al. 2004, Smetacek and Nicol 2005, Azzali et al. 2006, Nicol 2006, Arrigo et al. 2008b, Loeb et al. 2009, Montes-Hugo et al. 2009). For instance, a dramatic warming trend in the WAP appears to be driving a decline in krill abundance and, correspondingly, an increase in other zooplankton taxa, notably salps (*Salpa thompsoni*) (Loeb et al. 1997, Atkinson et al. 2004, Ducklow et al. 2007, Schofield et al. 2010). Trends in climate conditions in the Ross Sea are strikingly different than those of the WAP during the last century (Kwok and Comiso et al. 2002, Parkinson 2002, Smith et al. 2007, Stammerjohn et al. 2012). Unlike the WAP region, the Ross Sea has been experiencing an increasing trend in sea ice cover and a decreasing trend in the length of the ice-free season since approximately the mid-20th century (Kwok and Comiso et al. 2002, Parkinson 2002, Smith et al. 2007, Stammerjohn et al. 2012). Although the trend in euphausiid abundance over the last century is unclear for the Ross Sea, given our understanding of interactions between sea ice dynamics and krill abundance, perhaps, the recent climate trends in this region are not causing considerable declines in krill biomass, as is occurring in the WAP. Azzali et al. (2006) show relatively stable krill biomass in the Ross Sea across three sampling periods, November 1994, December 1994, and December 1997, when the sampling region has full or partial ice cover. For the krill

species *Euphausia superba* and *E. crystallaphorophias*, biomass is 44 % to 56 % and 26 % to 33 %, respectively, less in January 2000, a time of little ice cover in the sampling area, than the krill biomass of the three sampling periods in the 1990s. In regards to our finding of a temporal change in crabeater seal foraging behavior, perhaps, a combination of both bottom-up and top-down controls enable historically high krill availability in the Ross Sea, encouraging focused predation on krill by crabeater seals in modern times.

A further consideration is that a crabeater seal foraging strategy of capturing both krill and fish in landfast ice may have been present throughout the late Holocene, but has been become less prevalent in modern times relative to the strategy of capturing almost exclusively krill in pack ice. This shift may have been trigged by an environmental change within the recent past. Unlike crabeater seals, Weddell seals are capable of foraging in landfast ice since they have evolved dentition and behavior to maintain breathing holes in the ice (Laws 1977). Foraging in landfast regions by crabeater seals is likely possible since they use Weddell seal breathing holes. Indeed, the sole modern crabeater seal, which had a particularly high bulk $\delta^{15}N$ value, found in nearshore landfast ice was among Weddell seals. An increase in sea ice in the VLC during the late Holocene may have reduced habitat for crabeater seals moving with Weddell seals and consuming a diet more similar to that of Weddell seals than the krill-dominant diet of pack ice crabeater seals. Consequently, today, almost all crabeater seals are found in pack ice regions, heavily consuming krill. Possible

environmental changes in the VLC occurring during the Holocene are discussed further below.

Leopard seal isotope data do not suggest a transition in the foraging behavior or in the environmental conditions of the leopard seal habitat over the mid-to-late Holocene. However, our sample size (n = 26) for this species is low, reducing the temporal resolution for the leopard seal isotope trend and, perhaps, hindering our observation of a change in foraging strategy and/or habitat for this species.

Weddell seals show significantly greater variability in bulk $\delta^{15}N$ and $\delta^{13}C$ values of subfossil specimens than that of modern animals, as well as significant decreases after 1,200 YBP in both isotopic values. Possible drivers of these trends could be a transition to lower trophic level prey (e.g., Antarctic toothfish to Antarctic silverfish), a drop in baseline $\delta^{15}N$ values, or both with decreasing calendar age. The amino acid $\delta^{15}N$ data indicate no significant temporal change in the foraging strategy of Weddell seals given the relatively consistent offsets between the $\delta^{15}N$ values of Pro and Phe. The driver of the bulk isotope trends, thus, must be a change in baseline isotope values rather than foraging behavior. Indeed, the significant drop in Phe $\delta^{15}N$ values after approximately 790 YBP reveals a shift in $\delta^{15}N_{baseline}$. The drop in Phe $\delta^{15}N$ values (3.1 ‰) was greater than that observed for bulk material (2.7 ‰), but this discrepancy could be a consequence of the confounding influences of both diet and $\delta^{15}N_{baseline}$ variation on bulk $\delta^{15}N$ values.

To note, the highest Phe $\delta^{15}N$ value for Weddell seals is 10.2 ‰. Surface NO_3^- $\delta^{15}N$ values have been observed to reach 7 ‰ in modern Antarctic continental waters

(DiFiore et al. 2009). Thus, the baseline or Phe $\delta^{15}N$ values could be 7 ‰ with complete nitrate utilization in the modern Ross Sea, less than the highest Weddell seal Phe $\delta^{15}N$ value. However, slight ^{15}N-enrichment for Phe may occur with each trophic step (Chikaraishi et al. 2009). Since Weddell seals are at a trophic position of about four, see Chapter 2, a Phe $\delta^{15}N$ value of 10.2 ‰ indicates a Phe ^{15}N-enrichment of about 0.8 ‰ with each trophic transfer, which is similar to observed Phe ^{15}N-enrichment values (Chikaraishi et al. 2009).

Like Weddell seals, a temporal shift in the diet and trophic position of SES has not occurred over the late Holocene. The consistency of subfossil SES bulk $\delta^{15}N$ and Pro $\delta^{15}N$ values suggests stability in their diet and trophic position in this time period. Also alike the Weddell seal isotope results, Phe $\delta^{15}N$ values of subfossil SES decline with decreasing calendar age during the late Holocene by 3 ‰ and 2 ‰ when considering all SES and those with bulk $\delta^{13}C$ values similar those of true Antarctic pinniped species, respectively. Furthermore, comparison of bulk isotope data of modern SES from throughout the Southern Ocean to that of subfossil SES from the Ross Sea provides additional insights into a possible change in baseline isotope values in the subfossil SES habitat. We find that the bulk $\delta^{15}N$ and $\delta^{13}C$ values of most modern SES are dissimilar from those of many subfossil SES with the exception of one group. Bulk $\delta^{15}N$ and $\delta^{13}C$ values of subfossil SES are similar to modern SES visiting coastal polynyas in East Antarctica, areas known to have high $\delta^{15}N_{baseline}$ (DiFiore et al. 2006, DiFiore et al. 2009, Chapter 1-2). This similarity supports the

subfossil Phe $\delta^{15}N$ trend, indicating that the SES habitat of the earlier Holocene has a high $\delta^{15}N_{baseline}$, exceeding the $\delta^{15}N_{baseline}$ of most foraging regions of modern day SES.

In summary, subfossil crabeater seal isotope data show a recent decline in this species dietary and trophic position variability. The Ross Sea habitat for the majority of crabeater seals in the late Holocene does not seem to have changed considerably during this period. In contrast to crabeater seals, both Weddell seals and SES have not altered their diet or trophic position in the Holocene. However, the bulk and amino acid $\delta^{15}N$ temporal trends of Weddell seals, the shift in SES Phe $\delta^{15}N$ values across the Holocene, and similarity between the bulk isotope values of subfossil SES and those of modern SES foraging in coastal polynyas indicate that the baseline isotope values of the Weddell seal and SES habitat have declined with decreasing calendar age

Distribution of trophic positions across all subfossil seal species

The bulk $\delta^{15}N$ results suggest that the trophic positions of subfossil pinniped species from the Ross Sea are highest for SES and Weddell seals. Leopard seals appear to have a slightly lower trophic position during the mid-to-late Holocene than Weddell seals given the significantly lower bulk $\delta^{15}N$ values of the former than the latter, consistent with expectations from prior research on modern animals (Zhao et al. 2004). Since subfossil leopard seals do not have significantly lower bulk $\delta^{15}N$ values than those of subfossil SES these two species seem to be at a similar trophic position. However, the smaller sample sizes of leopard (n = 25) and southern elephant

(n = 28) seals in the statistical analysis relative to that of Weddell (n = 164) seals may have contributed to the lack of a significant difference between the bulk $\delta^{15}N$ values of leopard seals and SES. The bulk $\delta^{15}N$ data for crabeater seals reveal that this species has the lowest trophic position among these four species during the Holocene, expected according to previous studies of modern seals (Rau et al. 1992, Zhao et al. 2004, and Chapter 2, in review). Yet, some subfossil specimens, approximately seven, of this species are at a trophic position similar to that of Weddell seals and SES given their high bulk $\delta^{15}N$ values.

Trophic positions calculated from the amino acid $\delta^{15}N$ data provide further insights regarding the distribution of trophic positions across seal species of the Ross Sea during the Holocene. The amino acid $\delta^{15}N$ results indicate that SES have the highest trophic position among the species with Weddell seals having a slightly lower trophic position in the Holocene. This finding differs from that suggested by the bulk $\delta^{15}N$ data likely due to the effect of $\delta^{15}N_{baseline}$ variation between Weddell seals and SES, discussed further below. Along with the bulk $\delta^{15}N$ results, amino acid $\delta^{15}N$ data reveal crabeater seals are at the lowest trophic position among Ross Sea pinniped species in the Holocene. However, separating subfossil crabeater seals into two groups given their trophic level variation, we find that a minority of crabeater seals has a high trophic position equivalent to that of Weddell seals.

Overall, we find that several seal species in the Ross Sea have fairly high trophic positions during the mid-to-late Holocene. Some individuals of the crabeater seal population, leopard seals, Weddell seals, and SES all appear to be at trophic

positions between about four and five in the Ross Sea of the recent past. In regards to leopard seals, we are inferring their trophic position given the bulk $\delta^{15}N$ measurements since amino acid $\delta^{15}N$ analysis has not been performed for this species. This result suggests that the Ross Sea has been highly productive during much of the mid-to-late Holocene such that it could support three seal species, as well as some individuals of another seal species, co-occurring in this food web at high trophic positions.

Habitat preferences of Antarctic seals during the Holocene

Bulk $\delta^{15}N$ and $\delta^{13}C$ values, complemented by those of amino acids, provide considerable insights into the habitat preferences of Antarctic seals throughout the Holocene. As described above, the extent of nutrient utilization is a primary driver of $\delta^{15}N_{baseline}$ in the Southern Ocean with $\delta^{15}N$ measurements increasing with more complete nutrient utilization, likely in association with higher productivity (DiFiore et al. 2006, DiFiore et al. 2009, Graham et al. 2010, Chapter 1). The extent of nutrient utilization and, thus, $\delta^{15}N_{baseline}$ values, have been shown to decrease with increasing proximity to Antarctica with the exception of productivity "hot spots," which occur along the coast, often in polynya systems (Arrigo et al. 1998, Arrigo and van Dijken 2004, DiFiore et al. 2006, Arrigo et al. 2008b, DiFiore et al. 2009, Graham et al. 2010, Chapter 1). For $\delta^{13}C_{baseline}$, prior work reveals decreasing values with increasing latitude or nearness to the Antarctic continent due to decreasing sea surface temperatures (Rau et al. 1989, Graham et al. 2010, Quillfeldt et al. 2010, Chapter 1, in review). The isotopic values of Phe best represent $\delta^{15}N_{baseline}$ and $\delta^{13}C_{baseline}$ since it is

an essential amino acid, experiencing little to no trophic fractionation (Larsen et al. 2009, McMahon et al. 2010).

The habitat of most crabeater seals is stable throughout the Holocene given their consistent bulk and amino acid isotope values over the last 3,000 years. Among the pinniped species, crabeater seals have low bulk $\delta^{13}C$ values, indicating that they have largely stayed within the Ross Sea to forage during the Holocene (Fig. 3.6). The Phe $\delta^{13}C$ values of subfossil crabeater support this conclusion since they are relatively low given the range of Phe $\delta^{13}C$ values for all subfossil seal species. Most subfossil crabeater seals have low bulk $\delta^{15}N$ values in comparison to those of subfossil leopard, Weddell, and southern elephant seals, which is partly a consequence of their lower trophic position than the other three species. Phe $\delta^{15}N$ values of these subfossil crabeater seals, represented by the individuals of cluster 3 in Fig. 3.11, have moved within a habitat having a low $\delta^{15}N_{baseline}$. Thus, these crabeater seals appear to have foraged within the Ross Sea, but have not utilized a particularly productive region of this sea, perhaps foraging predominately in pack-ice areas. The minority of crabeater seals that has a high trophic position, individuals of cluster 2 in Fig. 3.11, uses a habitat with a higher Phe $\delta^{15}N$ value than the majority of crabeater seals with lower trophic positions during the late Holocene. Thus, the high trophic level crabeater seals utilize more productive areas of the Ross Sea than low trophic level crabeater seals, likely polynya systems or landfast ice areas where high phytoplankton biomass from blooms has drifted.

The Weddell seal habitat changes over the Holocene, which is discussed below. Weddell seals have likely moved within the Ross Sea throughout the Holocene given their low bulk and Phe $\delta^{13}C$ values, as illustrated in Fig. 3.6 and 3.11. Additionally, in our comparison of the amino acid isotope values of all pinniped species, Weddell seal individuals, dated at times prior to the $\delta^{15}N_{baseline}$ drop, cluster into an exclusively Weddell seal group that has the highest Phe $\delta^{15}N$ values and a group that has the next highest Phe $\delta^{15}N$ values among the four Antarctic seal clusters (cluster 1 in Fig. 3.11). Thus, Weddell seals appear to prefer habitats with the highest $\delta^{15}N_{baseline}$ and, likely, highest productivity rates relative to the habitats of other seal species during the Holocene. Given our understanding of productivity hot spots in the modern Southern Ocean, the favored region of the Weddell seal is probably coastal polynyas or landfast ice areas with high phytoplankton biomass (Arrigo et al. 1998, Arrigo and van Dijken 2004, DiFiore et al. 2006, Arrigo et al. 2008b, DiFiore et al. 2009, Graham et al. 2010, Chapter 1). Note, this habitat is like that of high trophic level crabeater seals.

Comparing the bulk isotope data of modern SES from throughout the Southern Ocean to that of subfossil SES from Victorial Land Coast informs the habitat preferences of the latter. Most data from modern SES show both bulk $\delta^{15}N$ and $\delta^{13}C$ values decreasing with increasing nearness to the Antarctic continent, which parallels spatial patterns of $\delta^{15}N_{baseline}$ and $\delta^{13}C_{baseline}$ in the Southern Ocean. In contrast, modern SES foraging in productive coastal polynyas have distinct bulk $\delta^{15}N$ and $\delta^{13}C$ values that are like those of a large portion of subfossil SES. These modern

SES have high bulk $\delta^{15}N$ values since they are foraging within productivity hot spots and they have low bulk $\delta^{13}C$ values as they are moving in Antarctic coastal waters. The similarity between the bulk isotope values of modern polynya foraging SES and many subfossil SES suggests a preference of productive coastal regions by SES has been common throughout the Holocene. Yet, subfossil SES have a wide range of bulk $\delta^{13}C$ values with some individuals having notably higher values than other Antarctic seal species, indicating that the movements of the SES span an array of latitudes during the Holocene (Fig. 3.6).

The Phe isotope values clarify the habitat preferences of SES in the earlier Holocene. We performed amino acid analysis on tissues from SES representing the extremes of the bulk $\delta^{13}C$ variation. Animals with low bulk $\delta^{13}C$ values also have low Phe $\delta^{13}C$ values and, thus, are likely "Ross Sea foragers." SES with high bulk $\delta^{13}C$ values, likewise, have high Phe $\delta^{13}C$ values, revealing that these animals are "convergence foragers," having spent considerable time foraging outside of the Ross Sea, perhaps in the Antarctic Convergence zone. Ross Sea foragers also have high Phe $\delta^{15}N$ values (cluster 2 in Fig. 3.11), which are similar to those of some crabeater and Weddell seals. This result suggests that these SES, high trophic position crabeater seals, and Weddell seals all have foraged in productive coastal polynyas or landfast ice regions containing high production in the Ross Sea during the Holocene. Convergence foragers have low Phe $\delta^{15}N$ values (cluster 4 in Fig. 3.11) and, thus, a less productive habitat relative to those of high trophic level crabeater seals, Weddell seals, and Ross Sea foraging SES. Since our amino acid isotope values are from

specimens representing the endpoints of variation in subfossil SES, individual with intermediate bulk $\delta^{13}C$ values likely have moved in the region between the productive coastal Ross Sea and the Antarctic Convergence. Additionally, the similarity in bulk isotope values of Ross Sea foraging subfossil SES and modern SES moving within productivity hot spots, as well as the subfossil SES Phe $\delta^{15}N$ trend, indicates that the Ross Sea habitat of SES experienced environmental change during the Holocene.

Environmental changes in the Ross Sea over the mid-to-late Holocene

Weddell seal isotope data show a relatively high and constant $\delta^{15}N_{baseline}$ from about 5,000 to 800 YBP, with values decreasing after 800 YBP and reaching a minimum in modern times. We note that Hückstädt et al. (2017) report a $\delta^{15}N_{baseline}$ drop over the last 100 years for the Ross Sea. As mentioned above, bulk isotope data from Hückstädt et al. (2017) are included in our times series. Along with our bulk isotope data, extending to the mid Holocene, we find an earlier onset of the drop in $\delta^{15}N_{baseline}$ and one of greater magnitude – about 3 ‰ instead of 1 ‰. Thus, our time series extends further into the Holocene, enabling the discovery that at 100 YBP the $\delta^{15}N_{baseline}$ did not begin to decline; rather, it has already been dropping.

The decreasing trend in Weddell seal $\delta^{15}N_{baseline}$ is not observed for leopard and crabeater seals, suggesting stable environmental conditions for the primary habitat of these species during the Holocene. However, use of a high $\delta^{15}N_{baseline}$ foraging zone earlier in the Holocene has been shown for many SES and some crabeater seals, supporting a late Holocene $\delta^{15}N_{baseline}$ transition in areas of the Ross Sea that are important to many species. These productive regions of the Ross Sea,

likely coastal polynyas (or adjacent landfast ice areas), are the strongly preferred foraging habitat of Weddell seals throughout the Holocene. The $\delta^{15}N_{baseline}$ drop in Weddell seals reveals that this habitat, in particular, has changed over the last 5,000 years. Considering our understanding of the key drivers of $\delta^{15}N_{baseline}$ in the Southern Ocean and deep Antarctic waters, productivity and nutrient drawdown likely have declined since about 800 YBP, causing the Weddell seal $\delta^{15}N_{baseline}$ trend. Primary production in the Antarctic is mainly controlled by light and iron limitation (Arrigo and van Dijken 2003, Smith et al. 2007). Sea ice conditions strongly influence the extent of light and iron limitation in the Southern Ocean with less sea ice cover and duration resulting in greater light availability and heightened melting of sea ice or glaciers increasing iron availability (Sedwick and DiTullio 1997, Arrigo and van Dijken 2003, Raiswell et al. 2006, Smith et al. 2007, Lannuzel et al. 2010). If productivity and nutrient drawdown drive the Weddell $\delta^{15}N_{baseline}$ trend, then our results suggest that the Weddell seal habitat experienced higher productivity and, perhaps, more open water earlier in the Holocene than it does at present.

Prior work has explored the changing climate conditions in the Ross Sea region during the Holocene. As noted above, climate trends are variable across the different ice cores obtained from Antarctica (Steig et al. 2000). This is, perhaps, unsurprising, given the opposing trends in climate conditions that have been observed today (Stammerjohn et al. 2012). In this discussion, we focus on climate records from ice cores nearest to our study region.

Multiple studies have reconstructed climate conditions in the mid-to-late Holocene for the Ross Sea via analysis of the Taylor Dome ice core, which is located about 150 km from the western edge of the Ross Sea, south of the VLC. Trends in oxygen isotope ($\delta^{18}O$) and hydrogen isotope (δD) values for this ice core have suggested that following the retreat of the grounded Ross Sea ice sheet, substantial cooling occurred at about 6,000 YBP (Steig et al. 1998, Masson et al. 2000, Steig et al. 2000). After this cooling event, temperatures are variable, but appear to show continued gradual cooling into the late Holocene (Steig et al. 1998, Masson et al. 2000, Steig et al. 2000). From approximately 6,000 YBP to the present, temperatures appear to have cooled by about 2 °C (Steig et al. 1998, 2000). Additionally, more recent studies have suggested a time of more rapid cooling in the western Ross Sea with the onset of the Little Ice Age (LIA), a period from about 720 to 170 YBP (Bertler et al. 2011, Rhodes et al. 2012). Bertler et al. (2011) found that the summer temperatures were about 2 °C colder in the LIA than those of approximately the last 200 years (Modern Era, ME) from isotopic analysis of an ice core obtained from the Victoria Lower Glacier (VLG), which is in the northern Dry Valleys and within our study region. Likewise, Rhodes et al. (2012) concluded that temperatures in the western Ross Sea region were colder – by about 2 °C – during the period of about 520 to 170 YBP than those of approximately the last two centuries via isotopic analysis of an ice core from the Mount Erebus Saddle (MES) on Ross Island. Overall, research to date shows a gradual cooling trend in the mid-to-late Holocene punctuated by likely periods of more rapid cooling at about 6,000 YBP and about 720 YBP, and perhaps

slight warming over the last century or two. All of these ice core proxies are measuring atmospheric temperature, not marine conditions.

Several studies attempt to establish temporal trends in land and sea ice for the Ross Sea region. Along the southern VLC, closest to our sampling localities, Hall and Denton (2002) document the retreat of the Wilson Piedmont Glacier from early to late Holocene, followed by a late Holocene advance, ending about 250 years ago. The glacier has been retreating since the mid-20th century. Storm-formed, raised beaches developed in the middle-to-late Holocene along the VLC from Terra Nova Bay to Explorer's Cove, revealing that open water reached the western Ross Sea coast, unlike today, when landfast sea ice has been locked to much of this coastline, even in summer (Hall and Denton 2002, Bamberg 2007). By around 1,000 YBP, a transition from open water to ice-push beach features takes place in the VLC (Hall and Denton 2002, Bamberg 2007). The occurrence of SES on beaches of the western Ross Sea in the Holocene until approximately 1,000 YBP, when the SES population begins to crash, likewise, indicates the absence of landfast sea ice and perhaps less pack ice earlier in the Holocene, since this species requires beaches with access to open water for molting and breeding (Hall et al. 2006, de Bruyn et al. 2009).

Researchers have further explored patterns in sea ice during the Holocene with geochemical tracers. Concentrations of sodium [Na] in ice cores are used to evaluate past sea ice conditions, but interpretation of [Na] trends is challenging. Na derives either from open water via the bubble bursting mechanism or from frost flowers entrained on the sea ice surface and, thus, indicates either open water or sea

ice (Rankin et al. 2002, Wolff et al. 2003, Rankin et al. 2004, Rhodes et al. 2012). Furthermore, the driving mechanism behind [Na] trends may differ across the Antarctic continent (Sneed et al. 2011). Bertler et al. (2011) and Rhodes et al. (2012) determine that Na in their ice cores originates primarily from open water by confirming that values of Na/Cl and Na^+/SO_4^{2-} are consistent with those of an open water source rather than a sea ice surface source. Rhodes et al. (2012) also note that peaks in [Na] occur in the summer, a time of minimal sea ice cover. Interestingly, Bertler et al. (2011) and Rhodes et al. (2012) have different results. Bertler et al. (2011), working on the VLG, found lower [Na] in the LIA than the ME, suggesting that the colder LIA had greater sea ice cover and/or a shorter ice-free season than the warmer ME. In contrast, Rhodes et al. (2012), working on the MES, observe relatively constant [Na] over the last 500 years. Unfortunately, neither of the published [Na] records from the ice cores most proximal to the VLC document conditions before 1,000 YBP.

Prior to the LIA, the Na record has been reconstructed via analysis of the Taylor Dome ice core, but the driving mechanism (i.e., Na originating from bursting bubbles or from the frost flowers of the sea ice surface) has been unclear. Overall, the record shows fluctuating and relatively low [Na] during the mid-to-late Holocene (Steig et al. 1998, Mayewski et al. 2017). However, a gradually increasing trend in [Na] occurs from about 6,500 YBP to 600 YBP (Steig et al. 2000, Mayewski et al. 2017). Following approximately 600 YBP, a decreasing [Na] trend is observed. Nearby Newall Glacier shows a similar pattern of rising [Na] from 2,000 to 600 YBP,

but [Na] continues to remain high from 600 YBP to the ME (Mayewski et al. 2017). If open water is the primary source for Na trapped in ice earlier in the Holocene, as appears to be the case for the late Holocene (Bertler et al. 2011, Rhodes et al. 2012), then the Taylor Dome ice core indicates more open water from 6,500 to 600 YBP and decreasing open water after about 600 YBP, the latter being relatively consistent with Bertler et al. (2011). However, percentages of sea ice diatoms (*Fragilariopsis curta*), considered to be indicative of seasonal sea ice cover, in two sediment cores from the western Ross Sea show an increasing trend from about 6,000 YBP to 1,000 YBP, possibly supporting the interpretation of the 6,500 YBP to 600 YBP rise in [Na] resulting from increased sea ice area from the frost flower mechanism (Steig et al. 1998). As the [Na] trend for the western Ross Sea during the mid-to-late Holocene exhibits considerable variability and the factors driving [Na] concentration variations have been debated, (Abram et al. 2013), interpretations of the [Na] trend must be taken with caution. In sum, multiple studies suggest an increase in latest Holocene sea ice cover and/or duration with less of a consensus about sea ice conditions earlier in the Holocene.

Some other research points to higher primary productivity earlier in the Holocene than that in modern times. Records of methylsulphonate (MS^-) and methanesulfonic acid (MSA) concentrations, which are indicative of primary productivity from open sea ice, are increasingly used to assess the productivity of Polar Regions (Abram et al. 2013). Rhodes et al. (2012) present MS^- evidence from the MES for a brief interval of higher productivity in the ME, but shallow temporal

depth of this record make it difficult to put this result in context. Steig et al. (1998) report the concentrations of MSA from Taylor Dome spanning the Holocene. MSA concentrations are low before 6,000 YBP, increase sharply at 6,000 YBP and then more gradually until about 2,500 YBP, exhibit more stability from about 2,500 YBP to 1,000 YBP, and begin to drop at about 1,000 YBP (Steig et al. 1998). Overall, the productivity in the western Ross Sea appears to be higher for much of the mid-to-late Holocene than it is for the Modern Era and before 6,000 YBP.

The findings of prior work support and may explain much of our Weddell seal $\delta^{15}N_{baseline}$ trend. Our understanding of the productivity trend in the Holocene given the MSA record from the Taylor Dome ice core suggests high productivity for much of the mid-to-late Holocene, followed by a productivity drop around 1,000 YBP (Steig et al. 1998, Steig et al. 2000). This finding matches well with our Weddell seal $\delta^{15}N_{baseline}$ trend that suggests high productivity since about 5,000 YBP until a drop in productivity commences around 800 YBP. Recent analyses of ice cores from our study region (VCG and MES) do not have sufficient temporal depth to inform changes in sea ice cover and duration over the period of productivity fluctuations in the mid-to-late Holocene. However, given that Bertler et al. (2011) and Rhodes et al. (2012) determine that Na in our study area primarily derives from open water, the Taylor Dome ice core [Na] record suggests gradually increasing open water from the mid Holocene to about 600 YBP at which time sea ice cover and/or duration increase considerably. Since less sea ice cover and duration and increased melting of sea or land ice alleviate the light and iron limitations of phytoplankton (Sedwick and

DiTullio 1997, Arrigo and van Dijken 2003, Raiswell et al. 2006, Smith et al. 2007, Lannuzel et al. 2010), respectively, parallel trends in open water and productivity are expected. In summary, high productivity and high $\delta^{15}N_{baseline}$ in the Ross Sea from about 6,000 to 800 YBP are likely driven by less sea ice cover and/or duration and increased melting during this period. Increased sea ice cover and/or duration and less melting probably cause a drop in productivity and $\delta^{15}N_{baseline}$ at about 800 YBP.

CONCLUSIONS

The Ross Sea has and will continue to experience considerable climate change due to anthropogenic emissions of greenhouse gases (Stammerjohn et al. 2012, Smith et al. 2014, Paolo et al. 2015). Since approximately the mid-20th century, the climate trends in the Ross Sea have been notably unlike that of other Antarctic regions. In the Ross Sea, sea ice extent has been increasing and the ice-free season has been shortening in recent times, sharply contrasting with the dramatic losses of sea ice coverage and duration in the WAP (Kwok and Comiso et al. 2002, Parkinson 2002, Ducklow et al. 2007, Smith et al. 2007, Stammerjohn et al. 2012). However, the sea ice trends in the Ross Sea are likely to reverse in the near future. Smith et al. (2014) predict that summer sea ice concentrations will decrease 56 % by 2050 and 78 % by 2100 as a result of expected changes in atmospheric temperatures (Bracegirdle and Stephenson 2012) and winds (Bracegirdle et al. 2008). These projected physical

changes in the Ross Sea will undoubtedly affect abundances and distributions of biota, particularly those with life cycles intricately tied to sea ice (Smith et al. 2014).

Trivelpiece et al. (2011) find that both climate conditions and reduced krill biomass impact predator populations in the rapidly warming region of West Antarctica. Although chinstrap penguins (*Pygoscelis antarctica*) prefer ice-free water in winter, their populations in the WAP and Scotia Sea – areas that have been experiencing considerable declines in seasonal sea ice extent and duration – have declined (Ducklow et al. 2007). Adélie penguin populations in the WAP and Scotia Sea have also declined, but this trend has not been surprising given that this species requires pack-ice in the winter (Ducklow et al. 2007). Trivelpiece et al. (2011) conclude that reduced krill availability is causing the unexpected declines in chinstrap penguin populations. The authors have determined that krill availability increased in the early 1800s in the WAP and Scotia Sea in response to severe depletion of krill-consuming marine mammals and favorable climate conditions, but it has decreased since approximately the 1970s as a result of significant warming, recovery of some marine mammal populations, and an expanding krill fishery (Trivelpiece et al. 2011). With continued warming in these areas (Vaughan et al. 2003, Meredith and King 2004) krill abundance is likely to decrease further (Loeb et al. 1997, Atkinson et al. 2004, Reiss et al. 2008, Trivelpiece et al. 2011).

Given observations in the WAP and Scotia Sea, the predicted reductions in sea ice extent and duration in the Ross Sea for later this century are likely to have considerable effects on krill and, consequently, top predator populations. Continued

recoveries of krill-consuming marine mammals, recent heavy consumption of krill by crabeater seals as suggested by our results, and changing climate conditions that are not favorable for krill recruitment and survival will likely result in lower krill biomass in the Ross Sea in the future (Smetacek and Nicol 2005, Trivelpiece et al. 2011, Smith et al. 2014). Potential responses by pinniped species in the Ross Sea are indicated by our findings. Although Weddell seals appear to have more diverse diets than crabeater seals today (Laws 1977, Chapter 2), trophic positions of Weddell seals have been relatively constant throughout the mid-to-late Holocene, despite a changing habitat during this time given the Weddell seal $\delta^{15}N_{baseline}$ trend, whereas crabeater seals have shown a wide range of foraging strategies in the past. Surprisingly, crabeater seals may be more capable generalists than Weddell seals, and thus may have higher adaptive capacities than the latter. In the rapidly changing Ross Sea environment expected for the coming century, crabeater seals may alter their foraging strategies to depend less on krill and thereby cope better with anthropogenic climate change. In contrast, our results have not revealed a Weddell seal response to environmental change and, consequently, this species may be less able to adapt to a warming, less icy Ross Sea.

Like crabeater seals, our results suggest that SES have a relatively high adaptive capacity. SES, which only rarely visit the Ross Sea today, have been able to utilize a spectrum of habitats, ranging from the productive coastal regions of the Ross Sea to the Antarctic Convergence region, throughout the Holocene. Given that these pinnipeds require rocky beaches with access to open water to breed and molt (Laws

1960, Gales and Burton 1989) and, as a species, use an array of environments for foraging, SES may benefit from reduced sea ice cover and duration and undergo a population expansion in the future Ross Sea, which is supported by the conclusions of Siniff et al. (2008). Since SES individuals and certain populations show high fidelity to foraging areas, while the species as a whole exhibits diversity in foraging migrations, effects of climate change on individual or population fitness are likely to vary (Biuw et al. 2007, McIntyre et al. 2011, New et al. 2014).

Lastly, our results suggest that the habitat of the Weddell seal has changed over approximately the last 5,000 years, possibly becoming less productive and having less nutrient drawdown after about 800 YBP. We believe that the habitat of the Weddell seal in the Holocene encompasses productive coastal polynyas and/or adjacent areas of landfast ice containing high phytoplankton biomass. A high $\delta^{15}N_{baseline}$ for the coastal polynyas and/or some landfast ice regions in the Ross Sea from about 800 YBP to 5,000 YBP is supported by the trend of MSA for Taylor Dome (Steig et al. 1998). For this period in the western Ross Sea, warmer temperatures than the LIA and less sea ice coverage and/or duration than the ME and LIA may have driven the high production, but the past sea ice conditions, in particular, are presently unclear for the mid-to-late Holocene. Regardless of the mechanism, our results suggest that the coastal region of the western Ross Sea likely experienced greater nutrient drawdown and productivity earlier in the Holocene than it does at present.

ACKNOWLEDGEMENTS

I am very grateful to Dr. Brenda Hall, Dr. Paul Koch, Scott Braddock, Jill Pelto, Rachel Reid, and Audra Norvaisa who spent many weeks in the Dry Valleys of Antarctica to sample hundreds of seal mummies for this project. I thank Dr. Rus Hoelzel, Dr. Andreanna Welch, and their laboratory group who completed the extensive ancient DNA analyses. Drs. Daniel Costa, Brenda Hall, Rus Hoelzel, Luis Hückstädt, Kimberly Goetz, and Kelton McMahon provided considerable insights into the planning of fieldwork, methodologies, and data interpretation. Dr. Laura Niven, Kwasi Gilbert, and Jonathan Nye also assisted in method development and data interpretation, as well as developed indices of carcass and bone weathering and a guide for species identification with subfossil bones. I thank Colin Carney, Dyke Andreasen, Elizabeth Gier, Aaron Rosenfield, Jonathan Nye, and Stephanie Christensen for laboratory assistance. We are grateful to the National Science Foundation for funding (NSF ANT-1142108).

REFERENCES

Abram NJ, Wolff EW, Curran MA (2013) A review of sea ice proxy information from polar ice cores. Quaternary Science Reviews 79:168-83

Ainley DG, Siniff DB (2009) The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. Antarct Sci 21:317-327

Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. J Archaeol Sci 17:431-451

Arrigo KR, Weiss AM, Smith WO (1998) Physical forcing of phytoplankton dynamics in the southwestern Ross Sea. J Geophys Res Oceans 103:1007-1021

Arrigo KR, van Dijken, GL (2003) Phytoplankton dynamics within 37 Antarctic coastal polynya systems. J Geophys Res Oceans 108:3271

Arrigo KR, van Dijken GL (2004) Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. Deep Sea Res II 51:117-138

Arrigo KR, van Dijken GL, Long M (2008a) Coastal Southern Ocean: A strong anthropogenic CO_2 sink. Geophys Res Lett 35:L21602

Arrigo KR, van Dijken GL, Bushinsky S (2008b) Primary production in the Southern Ocean, 1997–2006. J Geophys Res Oceans 113:C08004

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the southern ocean. Nature 432:100-103

Azzali M, Leonori I, De Felice A, Russo A (2006). Spatial–temporal relationships between two euphausiid species in the Ross Sea. Chem Ecol 22:S219-S233

Bamberg A (2007) Geologic and Biologic Indicators of Climate Change in the Ross Sea, Antarctica. M.S. thesis. The University of Maine, Orono, ME

Bertler NA, Mayewski PA, Carter L (2011) Cold conditions in Antarctica during the Little Ice Age—Implications for abrupt climate change mechanisms. Earth Planet Sci Lett. 308:41-51

Biuw M, Boehme L, Guinet C, Hindell M, Costa D, Charrassin JB, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proc Natl Acad Sci USA104:13705-13710

Box GE, Cox DR (1964) An analysis of transformations. J R Stat Soc Series B Stat Methodol 26:211-252

Bracegirdle TJ, Connolley WM, Turner J (2008) Antarctic climate change over the twenty first century. J Geophys Res Atmos 113:D03103

Bracegirdle TJ, Stephenson DB (2012) Higher precision estimates of regional polar warming by ensemble regression of climate model projections. Clim Dynam 39:2805-2821

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y, Suga H, Tomitani A, Miyashita H, Kitazato H, Ohkouchi N (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol Oceanogr Methods 7:740-750

Costa DP, Huckstadt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA (2010) Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. Integr Comp Biol 50:1018-1030

Curtis C, Stewart BS, Karl SA (2009) Pleistocene population expansions of Antarctic seals. Mol Ecol 18: 2112-2121

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest2: more models, new heuristics, and parallel computing. Nature Methods 9:772

Dasmahapatra KK, Hoffman JI, Amos W (2009) Pinniped phylogenetic relationships inferred using AFLP markers. Heredity 103:168-177

DeNiro MJ (1987) Stable isotopy and archaeology. Am Sci 75:182-191

de Bruyn M, Hall BL, Chauke LF, Baroni C, Koch PL, Hoelzel AR (2009) Rapid response of a marine mammal species to Holocene climate and habitat change. PLoS Genet 5:e1000554

de Bruyn M, Pinsky ML, Hall B, Koch P, Baroni C, Hoelzel AR (2014) Rapid increase in southern elephant seal genetic diversity after a founder event. Proc R Soc Lond B Biol Sci 281:20133078

DiFiore PJ, Sigman DM, Trull TW, Lourey MJ, Karsh K, Cane G, Ho R (2006) Nitrogen isotope constraints on subantarctic biogeochemistry. J Geophys Res Oceans 111:C08016

DiFiore PJ, Sigman DM, Dunbar RB (2009) Upper ocean nitrogen fluxes in the Polar Antarctic Zone: Constraints from the nitrogen and oxygen isotopes of nitrate. Geochem Geophys Geosyst 10:Q11016

Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W (2007) Marine pelagic ecosystems: the west Antarctic Peninsula. Philos Trans R Soc Lond B Biol Sci 362:67-94

Ducklow HW, Clarke A, Dickhut R, Doney SC, Geisz H, Huang K, Martinson DG, Meredith MP, Moeller HV, Montes-Hugo M, Schofield O, Stammerjohn SE, Steinberg D, Fraser W (2012) The marine system of the Western Antarctic Peninsula. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) Antarctic

ecosystems: an extreme environment in a changing world, Blackwell Publishing LTD, Hoboken, New Jersey, USA, p 121-159

Eder EB, Lewis MN, Campagna C, Koch PL (2010) Evidence of demersal foraging from stable isotope analysis of juvenile elephant seals from Patagonia. Mar Mamm Sci 26:430-442

Emslie SD, Patterson WP (2007) Abrupt recent shift in $\delta^{13}C$ and $\delta^{15}N$ values in Adélie penguin eggshell in Antarctica. Proc Natl Acad Sci USA.104:11666-11669

Ernest SK, Enquist BJ, Brown JH, Charnov EL, Gillooly JF, Savage VM, White EP, Smith FA, Hadly EA, Haskell JP, Lyons SK (2003) Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecol Lett 6:990-995

Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biol 11:525-531

Fry (2006) Stable isotope ecology. Springer+Business Media, LLC, New York, p 145

Fulton TL and Strobeck C (2010) Multiple markers and multiple individuals refine true seal phylogeny and bring molecules and morphology back in line. Proc R Soc Lond B Biol Sci 277:1065-1070

Gales NJ, Burton HR (1989) The past and present status of the southern elephant seal (*Mirounga leonina* Linn.) in Greater Antarctica. Mammalia 53:35-48

Goetz KT, Burns JM, Hückstädt LA, Shero MR, Costa DP (2017) Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. Deep Sea Res II 140:36-44

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes. Springer, Netherlands, p 299-318

Hall BL, Denton GH (2002) Holocene history of the Wilson Piedmont Glacier along the southern Scott Coast, Antarctica. The Holocene12:619-627

Hall BL, Hoelzel AR, Baroni C, Denton GH, Le Boeuf BJ, Overturf B, Töpf A (2006). Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. Proc Natl Acad Sci USA 103:10213-10217

Hall BL, Henderson GM, Baroni C, Kellogg TB (2010) Constant Holocene Southern-Ocean 14 C reservoir ages and ice-shelf flow rates. Earth Planet Sci Lett 296:115-123

Hall-Aspland SA, Rogers TL, Canfield RB (2005). Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. Mar Ecol Prog Ser 305:249-259

Hannides C, Popp BN, Landry MR, Graham BS (2009) Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. Limnol Oceanogr 54:50-61

Hayes, JM (2001) Fractionation of carbon and hydrogen isotopes in biosynthetic processes. Rev Mineral Geochem 43:225-277

Higgins DG, Sharp PM (1988) CLUSTAL: a package for performing multiple sequence alignment on a microcomputer Gene 73:237-244

Hoffman, R (2017) Sealing, whaling and krill fishing in the Southern Ocean: past and possible future effects on catch regulations. Polar Rec 53:88-99

Howland MR, Corr LT, Young SM, Jones V, Jim S, Van Der Merwe NJ, Mitchell AD, Evershed RP (2003) Expression of the dietary isotope signal in the compound-specific $\delta^{13}C$ values of pig bone lipids and amino acids. Int J Osteoarchaeol 13:54-65

Hückstädt LA, Burns JM, Koch PL, McDonald BI, Crocker DE, Costa DP (2012a) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287-301

Hückstädt LA, Koch PL, McDonald BI, Goebel ME, Crocker DE, Costa DP (2012b) Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. Oecologia 169:395-406

Hückstädt LA, McCarthy MD, Koch PL, Costa DP (2017) 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 284:20170927

Katoh K, Misawa K, Kuma KI, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res 29:4793-4799

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond

A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647-1649

Klunder MB, Laan P, Middag R, De Baar HJW, Van Ooijen JC (2011) Dissolved iron in the Southern Ocean (Atlantic sector). Deep Sea Res II 58:2678-2694

Koressaar T, Remm M (2007) Enhancements and modifications of primer design program Primer3. Bioinformatics 23:1289-1291

Kwok R, Comiso JC (2002) Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. J Clim 15:487-501

Lannuzel D, Schoemann V, De Jong J, Pasquer B, Van der Merwe P, Masson F, Tison JL, Bowie A (2010) Distribution of dissolved iron in Antarctic sea ice: Spatial, seasonal, and inter-annual variability. J Geophys Res Biogeosci115:G03022

Larsen T, Taylor DL, Leigh MB, O'Brien DM (2009) Stable isotope fingerprinting: a novel method for identifying plant, fungal, or bacterial origins of amino acids. Ecology 90:3526-3535

Laws R (1960) The southern elephant seal (*Mirounga leonine* Linn.) at South Georgia. Norsk Hvalfangst 49:466-476

Laws RM (1977) Seals and whales of the Southern Ocean. Philos Trans R Soc Lond B Biol Sci 279:81-96

Laws RM (1985) The ecology of the Southern Ocean: The Antarctic ecosystem, based on krill, appears to be moving toward a new balance of species in its recovery from the inroads of whaling. Am Sci 73:26-40

Le Boeuf BJ, Laws RM (1994) Elephant seals: An introduction to the genus. In: Le Boeuf BJ, Laws RM (eds) Elephant Seals: Population Ecology, Behavior, and Physiology. University of California Press, Berkley, CA, p 1-26

Leventer A, Dunbar RB (1988) Recent diatom record of McMurdo Sound, Antarctica: Implications for history of sea ice extent. Paleoceanography 3:259-274

Lewis R, O'Connell TC, Lewis M, Campagna C, Hoelzel AR (2006) Sex-specific foraging strategies and resource partitioning in the southern elephant seal (Mirounga leonina). Proc R Soc Lond B Biol Sci 273:2901-2907

Loeb VA, Puglise KI, Outram DA (1997) AMLR program: salps and other macrozooplankton collected from January to March 1997. Ant J US 32:131-134

Loeb VJ, Hofmann EE, Klinck JM, Holm-Hansen O (2009) White WB. ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. Antarct Sci 21:135-148

MacAvoy SE, Arneson LS, Bassett E (2006) Correlation of metabolism with tissue carbon and nitrogen turnover rate in small mammals. Oecologia 150:190-201

MacFadden BJ, Solounias N, Cerling TE (1999) Ancient Diets, Ecology, and Extinction of 5-Million-Year-Old Horses from Florida. Science 283:824-827

Martin C, Bentaleb I, Steelandt S, Guinet C (2011) Stable carbon and nitrogen isotope variations in canine dentine growth layers of Kerguelen southern elephant seals. Mar Ecol Prog Ser 439:295-305

Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. Nature 345:156-158

Masson V, Vimeux F, Jouzel J, Morgan V, Delmotte M, Ciais P, Hammer C, Johnsen S, Lipenkov VY, Mosley-Thompson E, Petit JR (2000) Holocene climate variability in Antarctica based on 11 ice-core isotopic records. Quaternary Res 54:348-358

Mayewski PA, Carleton AM, Birkel SD, Dixon D, Kurbatov AV, Korotkikh E, McConnell J, Curran M, Cole-Dai J, Jiang S, Plummer C (2017) Ice core and climate reanalysis analogs to predict Antarctic and Southern Hemisphere climate changes. Quaternary Sci Rev 155:50-66

McCarthy MD, Benner R, Lee C, Fogel ML (2007) Amino acid nitrogen isotopic fractionation patterns as indicators of heterotrophy in plankton, particulate, and dissolved organic matter. Geochim Cosmochim Ac 71:4727-4744

McCarthy MD, Lehman J, Kudela R (2013) Compound-specific amino acid $\delta^{15}N$ patterns in marine algae: Tracer potential for cyanobacterial vs. eukaryotic organic nitrogen sources in the ocean. Geochim Cosmochim Ac 103:104-120

McClelland JW, Montoya JP (2002) Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. Ecology 83:2173-2180

McIntyre T, Ansorge IJ, Bornemann H, Plötz J, Tosh CA, Bester MN (2011) Elephant seal dive behaviour is influenced by ocean temperature: implications for climate change impacts on an ocean predator. Mar Ecol Prog Ser 441:257-272

McMahon KW, Fogel ML, Elsdon TS, Thorrold SR (2010) Carbon isotope fractionation of amino acids in fish muscle reflects biosynthesis and isotopic routing from dietary protein. J Anim Ecol 79:1132-1141

McMahon KW, Hamady LL, Thorrold SR (2013) Ocean ecogeochemistry: a review. Oceanogr Mar Biol 51:327-374

McMahon KW, Polito MJ, Abel S, McCarthy MD, Thorrold SR (2015) Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (Pygoscelis papua). Ecol Evol 5:1278-1290

McMahon KW, McCarthy MD (2016) Embracing variability in amino acid δ15N fractionation: mechanisms, implications, and applications for trophic ecology. Ecosphere 7:e01511

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604

Mihlbachler MC, Rivals F, Solounias N, Semprebon GM (2011) Dietary change and evolution of horses in North America. Science 331:1178-1181

Minagawa M, Wada E (1984) Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. Geochim Cosmochim Ac 48:1135-1140

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western western Antarctic Peninsula. Science 323:1470-1473

New LF, Clark JS, Costa DP, Fleishman E, Hindell MA, Klanjšček T, Lusseau D, Kraus S, McMahon CR, Robinson PW, Schick RS (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. Mar Ecol Prog Ser 496:99-108

Newland C, Field IC, Cherel Y, Guinet C, Bradshaw CJ, McMahon CR, Hindell MA (2011) Diet of juvenile southern elephant seals reappraised by stable isotopes in whiskers. Mar Ecol Prog Ser 424:247-258

Nicol S (2006) Krill, currents, and sea ice: Euphausia superba and its changing environment. Bioscience 56:111-120

Paolo FS, Fricker HA, Padman L (2015) Volume loss from Antarctic ice shelves is accelerating. Science 348:327-331

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637-669

Parkinson CL (2002) Trends in the length of the Southern Ocean sea-ice season, 1979-99. Ann Glaciol 34:435-440

Peakall ROD and Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288-295

Peakall ROD and Smouse PE (2012) GENALEX 6.5: Genetic analysis in Excel. Population genetic software for teaching and research, an update. Bioinformatics 28:2537-2539

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293-320

Pinkerton MH, Forman J, Bury SJ, Brown J, Horn P, O'Driscoll RL (2013) Diet and trophic niche of Antarctic silverfish Pleuragramma antarcticum in the Ross Sea, Antarctica. J Fish Biol 82:141-164

Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott MJ, López-Ibarra GA, Galván-Magaña F, Fry B (2007) Insight into the trophic ecology of the yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of proteinaceous amino acids. In: Dawson T, Siegwolf R (eds) Stable Isotopes as Indicators of Ecological Change. Elsevier, New York, p 173-190

Quillfeldt P, Masello JF, McGill RA, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? Front Zool 7:1-11

R Core Team (2014). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria

Raiswell R, Tranter M, Benning LG, Siegert M, De'ath R, Huybrechts P, Payne T (2006) Contributions from glacially derived sediment to the global iron (oxyhydr) oxide cycle: implications for iron delivery to the oceans. Geochim Cosmochim Ac 70:2765-2780

Raiswell R, Benning LG, Tranter M, Tulaczyk S (2008) Bioavailable iron in the Southern Ocean: the significance of the iceberg conveyor belt. Geochem Trans 9:7

Raiswell R (2011) Iceberg-hosted nanoparticulate Fe in the Southern Ocean: Mineralogy, origin, dissolution kinetics and source of bioavailable Fe. Deep Sea Res II 58:1364-1375

Rankin AM, Wolff EW, Martin S (2002) Frost flowers: Implications for tropospheric chemistry and ice core interpretation. J Geophys Res Atmos 107:4683

Rankin, A.M., Wolff, E.W. and Mulvaney, R (2004) A reinterpretation of sea-salt records in Greenland and Antarctic ice cores? Ann Glaciol 39:276-282

Rau GH, Takahashi T, Des Marais DJ (1989) Latitudinal variations in plankton $\delta^{13}C$: implications for CO_2 and productivity in past oceans. Nature 341:516-518

Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar Ecol Prog Ser 84:1-8

Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Ramsey CB, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM (2013). IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1869-1887

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill (Euphausia superba) around the South Shetland Islands, 1996–2006. ICES J Mar Sci 65:497-508

Rhodes RH, Bertler NA, Baker JA, Steen-Larsen HC, Sneed SB, Morgenstern U, Johnsen SJ (2012) Little Ice Age climate and oceanic conditions of the Ross Sea, Antarctica from a coastal ice core record. Climat Past 8:1223-1238

Schell DM, Barnett BA, Vinette KA (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. Mar Ecol Prog Ser 162:11-23

Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How do polar marine ecosystems respond to rapid climate change? Science 328:1520-1523

Scott JH, O'Brien DM, Emerson D, Sun H, McDonald GD, Salgado A, Fogel ML (2006) An examination of the carbon isotope effects associated with amino acid biosynthesis. Astrobiology 6:867-880

Sedwick PN, DiTullio GR (1997) Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. Geophys Res Lett 24:2515-2518

Shaw TJ, Raiswell R, Hexel CR, Vu HP, Moore WS, Dudgeon R, Smith KL (2011) Input, composition, and potential impact of terrigenous material from free-drifting icebergs in the Weddell Sea. Deep Sea Res II 58:1376-1383

Siniff DB (1991) An overview of the ecology of Antarctic seals. Am Zool 31:143-149

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: Projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425-435

Silfer JA, Engel MH, Macko SA, Jumeau EJ (1991) Stable carbon isotope analysis of amino acid enantiomers by conventional isotope ratio mass spectrometry and combined gas chromatography/isotope ratio mass spectrometry. Anal Chem 63:370-374

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437:362-368

Smith WO, Ainley DG, Cattaneo-Vietti R (2007) Trophic interactions within the Ross Sea continental shelf ecosystem. Philos Trans R Soc Lond B Biol Sci 362:95-111

Smith WO, Dinniman MS, Hofmann EE, Klinck JM (2014) The effects of changing winds and temperatures on the oceanography of the Ross Sea in the 21st century. Geophys Res Lett 41:1624-1631

Sneed SB, Mayewski PA, Dixon DA (2011) An emerging technique: multi-ice-core multi-parameter correlations with Antarctic sea-ice extent. Ann Glaciol 52:347-354

Stammerjohn S, Massom R, Rind D, Martinson D (2012) Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophys Res Lett 39: L06501

Steig EJ, Hart CP, White JW, Cunningham WL, Davis MD, Saltzman ES (1998) Changes in climate, ocean and ice-sheet conditions in the Ross embayment, Antarctica, at 6 ka. Ann Glaciol 27:305-310

Steig EJ, Morse DL, Waddington ED, Stuiver M, Grootes PM, Mayewski PA, Twickler MS, Whitlow SI (2000) Wisconsinan and Holocene climate history from an ice core at Taylor Dome, western Ross Embayment, Antarctica. Geogr Ann A 82:213-235

Stenni B, Proposito M, Gragnani R, Flora O, Jouzel J, Falourd S, Frezzotti M (2002) Eight centuries of volcanic signal and climate change at Talos Dome (East Antarctica). J Geophys Res Atmos 107:4076

Surma S, Pakhomov EA, Pitcher TJ (2014) Effects of whaling on the structure of the southern ocean food web: insights on the "Krill Surplus" from ecosystem modelling. PLoS One 9:e114978

Swofford DL (1998) PAUP 4.0: Phylogenic analysis using parsimony (and other methods). 4.0b10 ed. Sinauer Associates, Inc., Sunderland, MA

Trathan PN, Ratcliffe N, Masden EA (2012) Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35:983-993

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011)Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci USA 108:7625-7628

Untergasser A, Cutcutache I, Koressaar T, Ye J, Faircloth BC, Remm M, Rozen SG (2012) Primer3--new capabilities and interfaces. Nucleic Acids Res 40:e115

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243-274

Walker MJC, Berkelhammer M, Björck S, Cwynar LC, Fisher DA, Long AJ, Lowe JJ, Newnham RM, Rasmussen SO, Weiss H (2012), Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). J Quaternary Sci 27:649-659

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389-395

Zhao L, Castellini MA, Mau TL, Trumble SJ (2004) Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biol 27:368-373

FIGURES

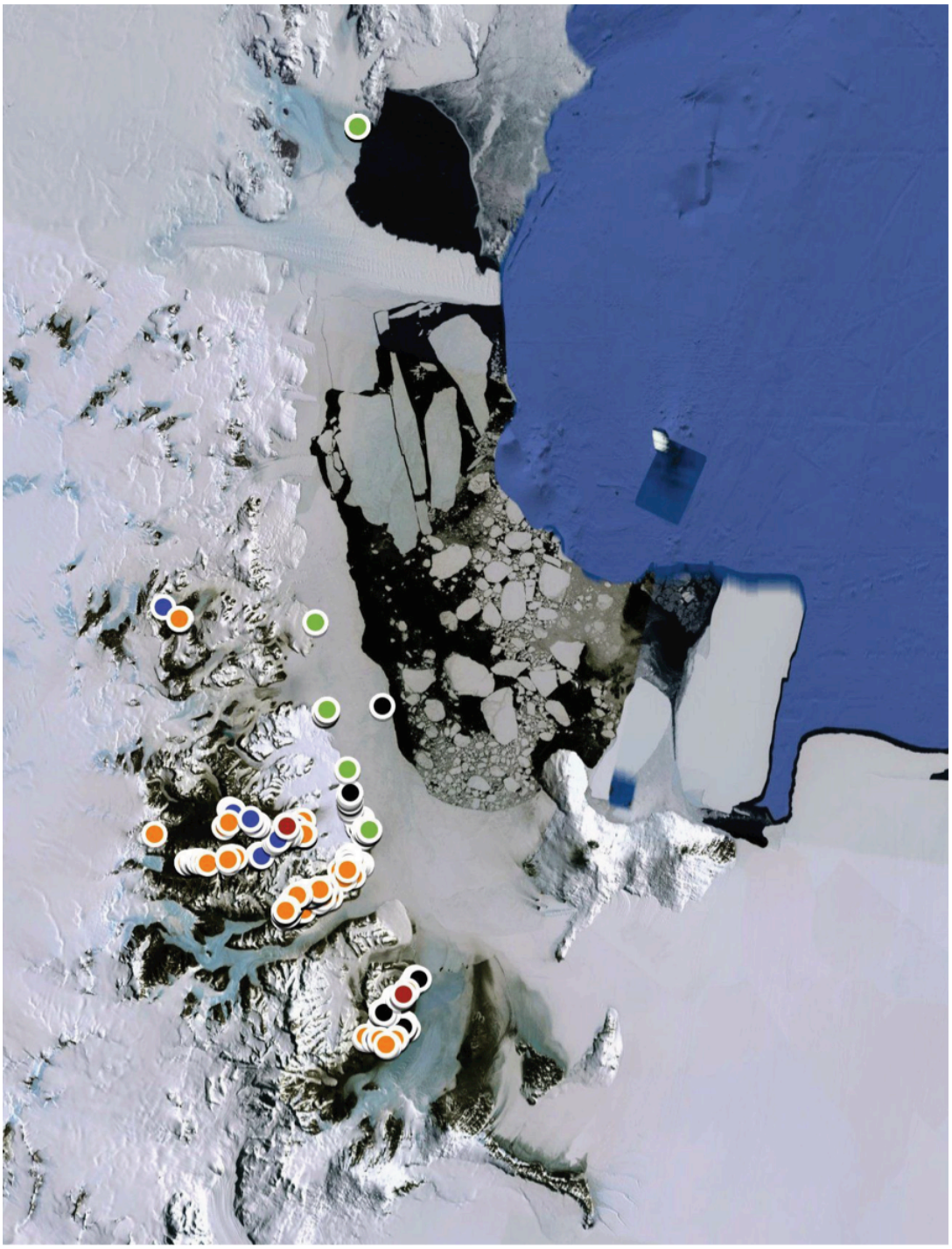

Figure 3.1. Locations of subfossil seal specimens. Blue, orange, green, red, and black circles indicate the locations where Weddell, crabeater, southern elephant, leopard, and unknown seals were obtained.

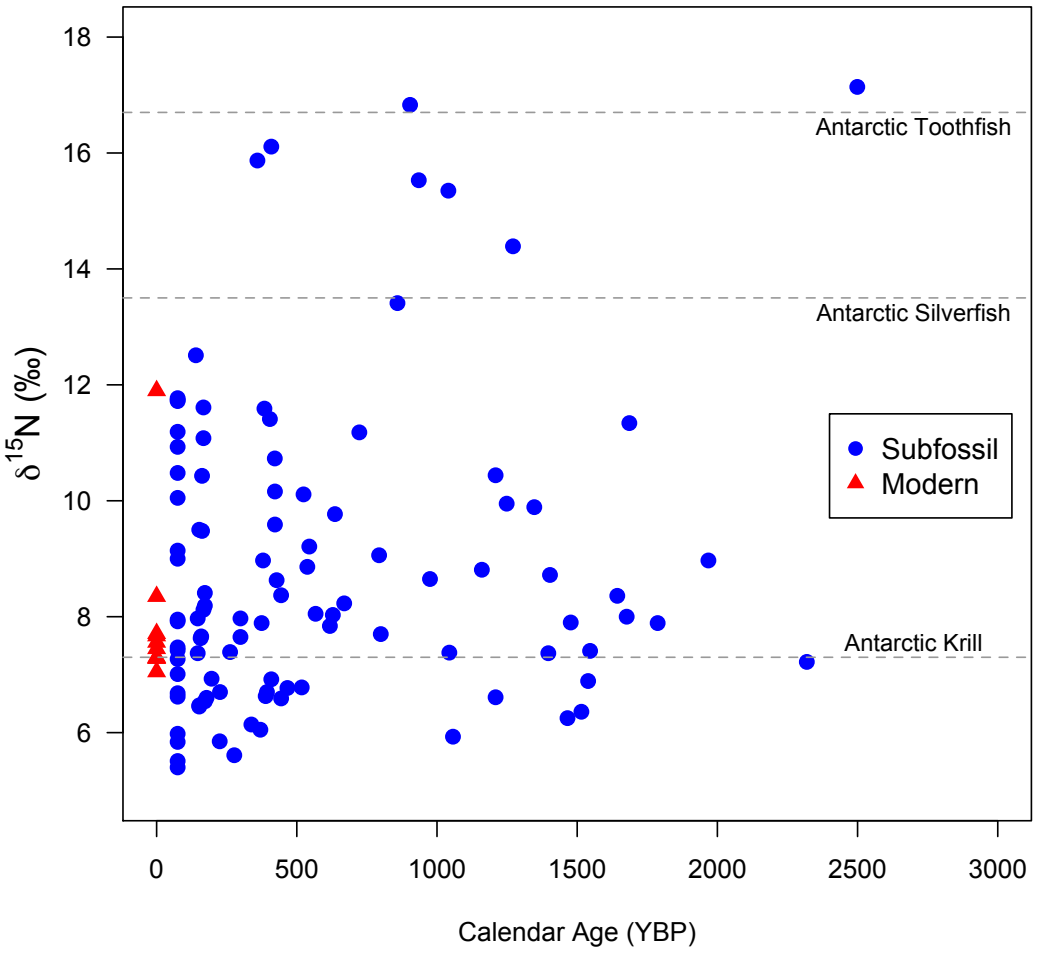

Figure 3.2. $\delta^{15}N$ values of crabeater seals over the mid-to-late Holocene. Blue circles and red triangles represent subfossil and modern specimens from the Ross Sea, respectively. Dashed lines indicate the approximate $\delta^{15}N$ value of a predator consuming entirely Antarctic toothfish, Antarctic silverfish, or Antarctic krill.

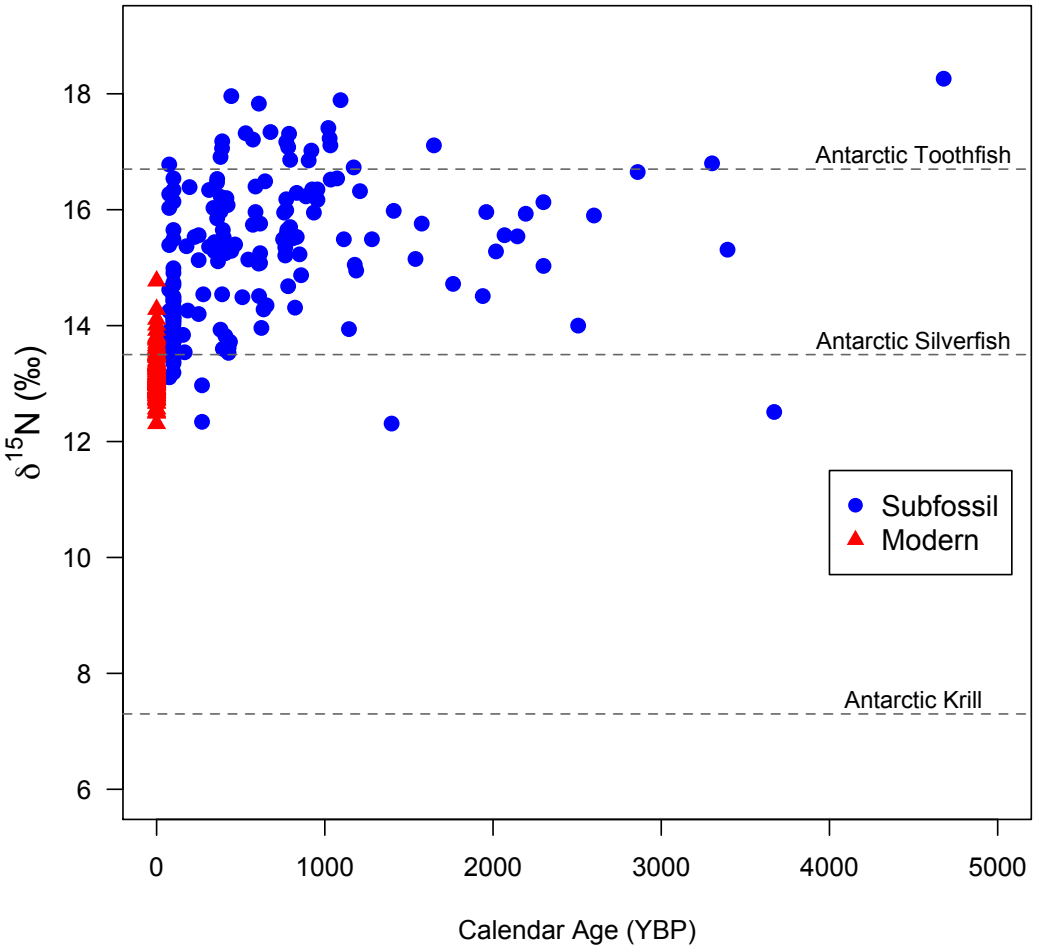

Figure 3.3. $\delta^{15}N$ values of Weddell seals over the mid-to-late Holocene. Blue circles and red triangles represent subfossil and modern specimens from the Ross Sea, respectively. Dashed lines indicate the approximate $\delta^{15}N$ value of a predator consuming entirely Antarctic toothfish, Antarctic silverfish, or Antarctic krill.

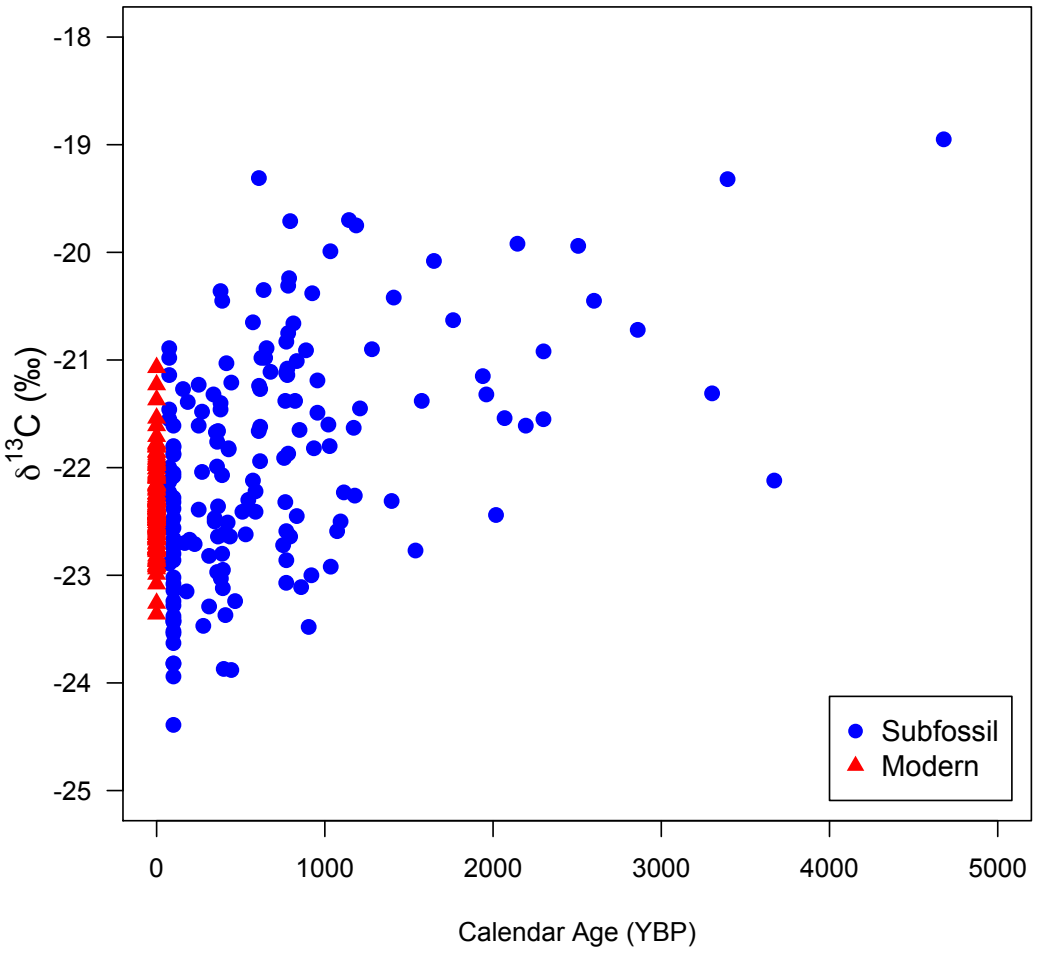

Figure 3.4. $\delta^{13}C$ values of Weddell seals over the mid-to-late Holocene. Blue circles and red triangles represent subfossil and modern specimens from the Ross Sea, respectively.

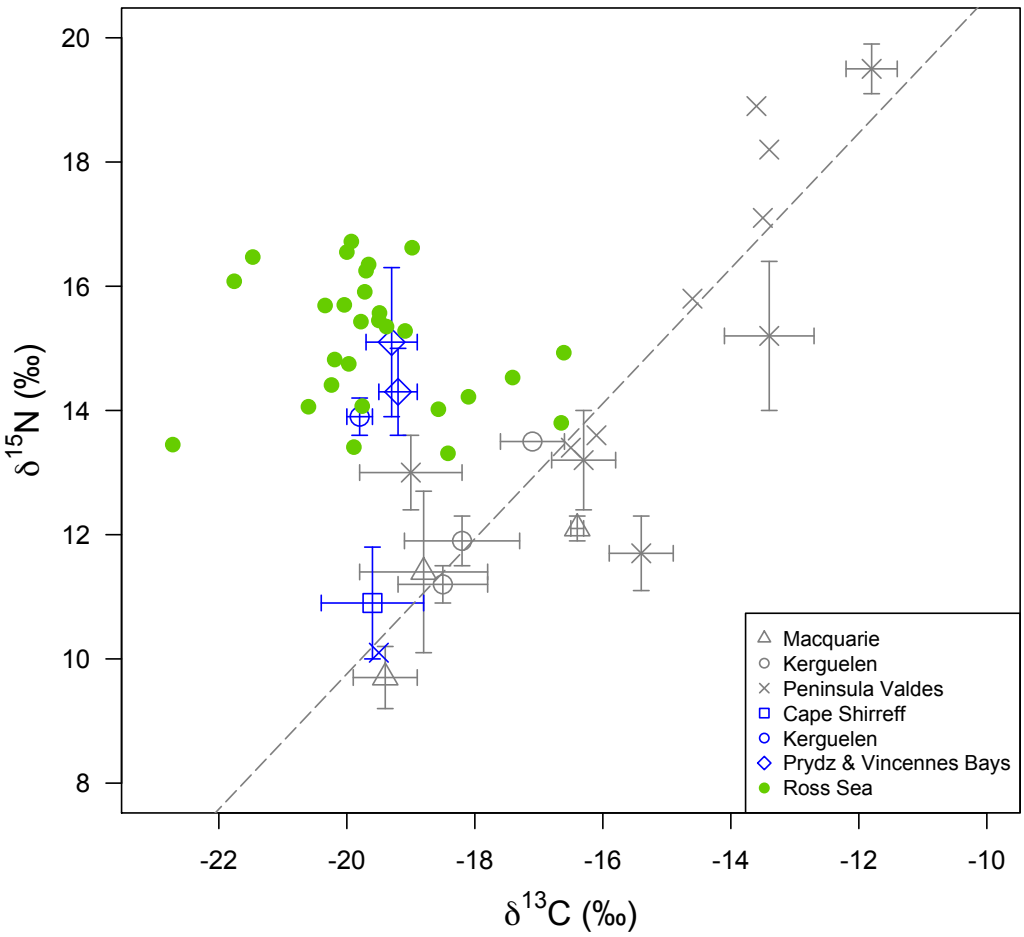

Figure 3.5. $\delta^{15}N$ and $\delta^{13}C$ values of southern elephant seals over the mid-to-late Holocene. Blue circles represent modern individuals that are known to have visited Antarctic continental waters, while green circles represent subfossil specimens. Gray symbols represent modern individuals with unknown movement patterns. For all modern animals, each symbol type corresponds to a different location or colony.

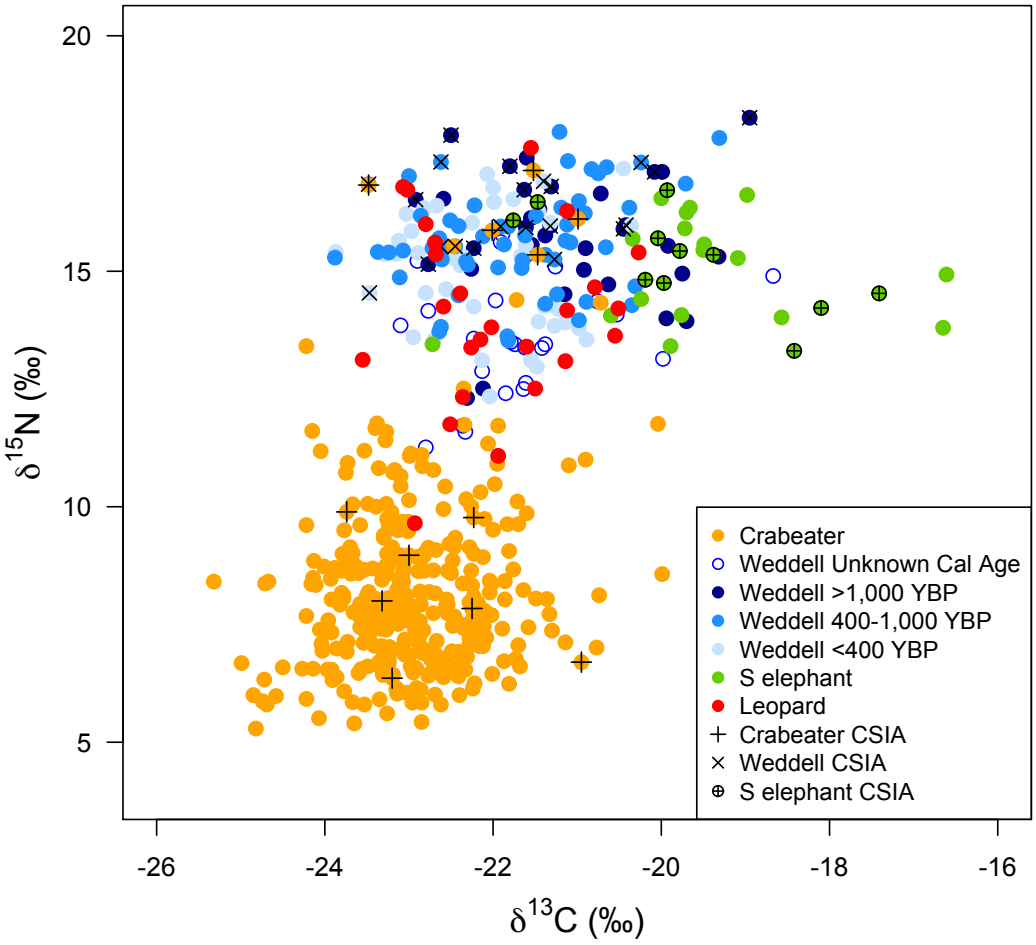

Figure 3.6. Bulk $\delta^{15}N$ versus $\delta^{13}C$ isotope values for all subfossil seal specimens. "Calendar Age" is abbreviated as "Cal Age" on this figure. Weddell seals of unknown calendar age, > 1,000 YBP, 400-1,000 YBP, and < 400 YBP are represented by open blue, filled dark blue, filled medium blue, and filled light blue circles, correspondingly. Crabeater, southern elephant, and leopard seals are shown with orange, green, and red filled circles, respectively. A plus sign, x, and circle containing a plus sign indicate crabeater, Weddell, and southern elephant seal samples used for amino acid $\delta^{15}N$ analyses.

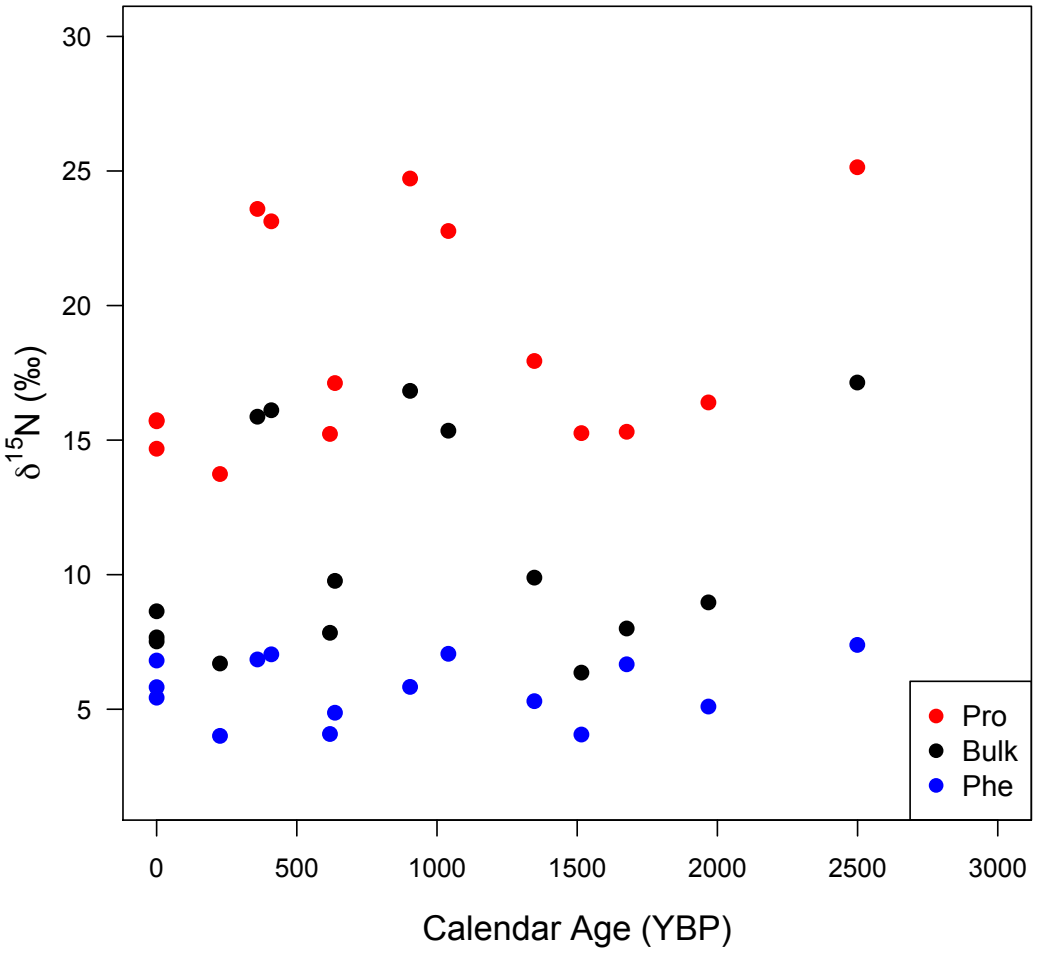

Figure 3.7. $\delta^{15}N$ values of Pro, bulk material, and Phe for crabeater seals over the late Holocene. Isotopic data for Pro, bulk material, and Phe are represented by red, black, and blue circles, respectively.

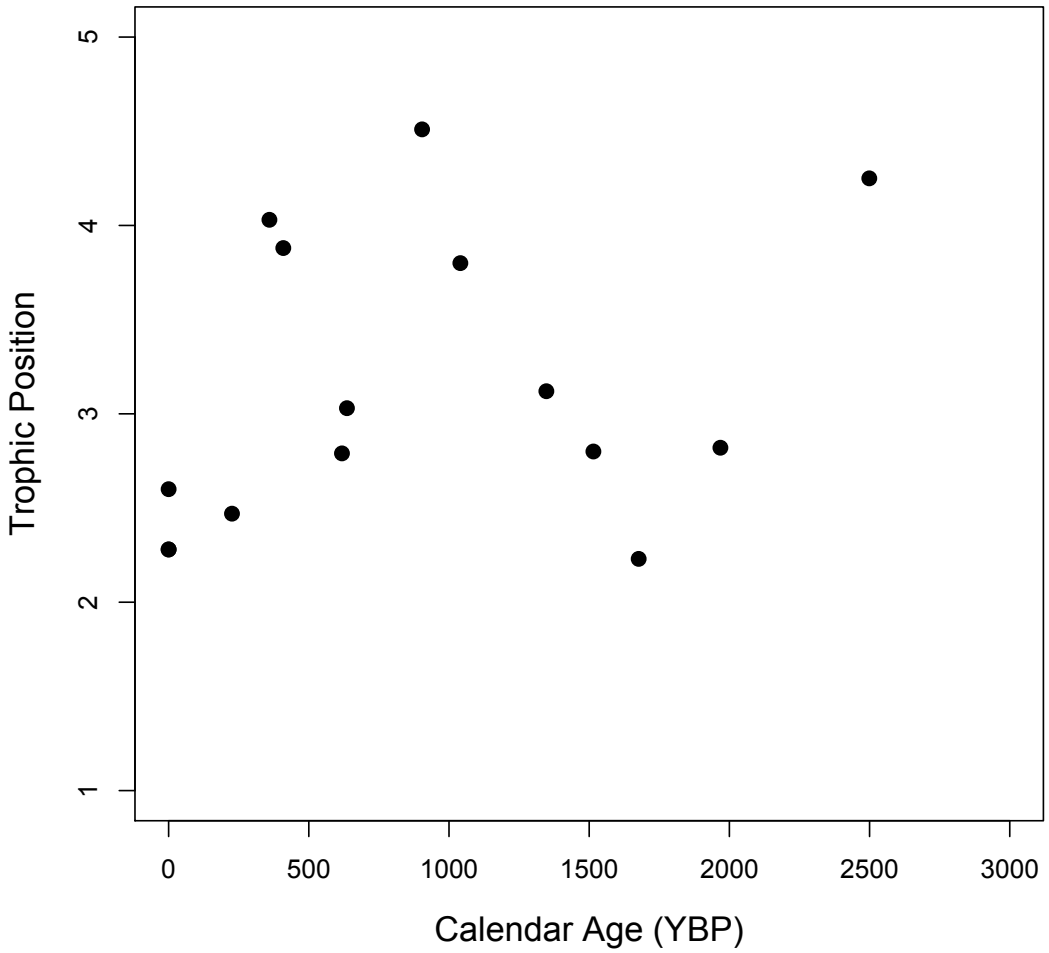

Figure 3.8. Trophic positions for crabeater seals during the Holocene. Trophic positions are caculated based on Pro and Phe $\delta^{15}N$ values, see text.

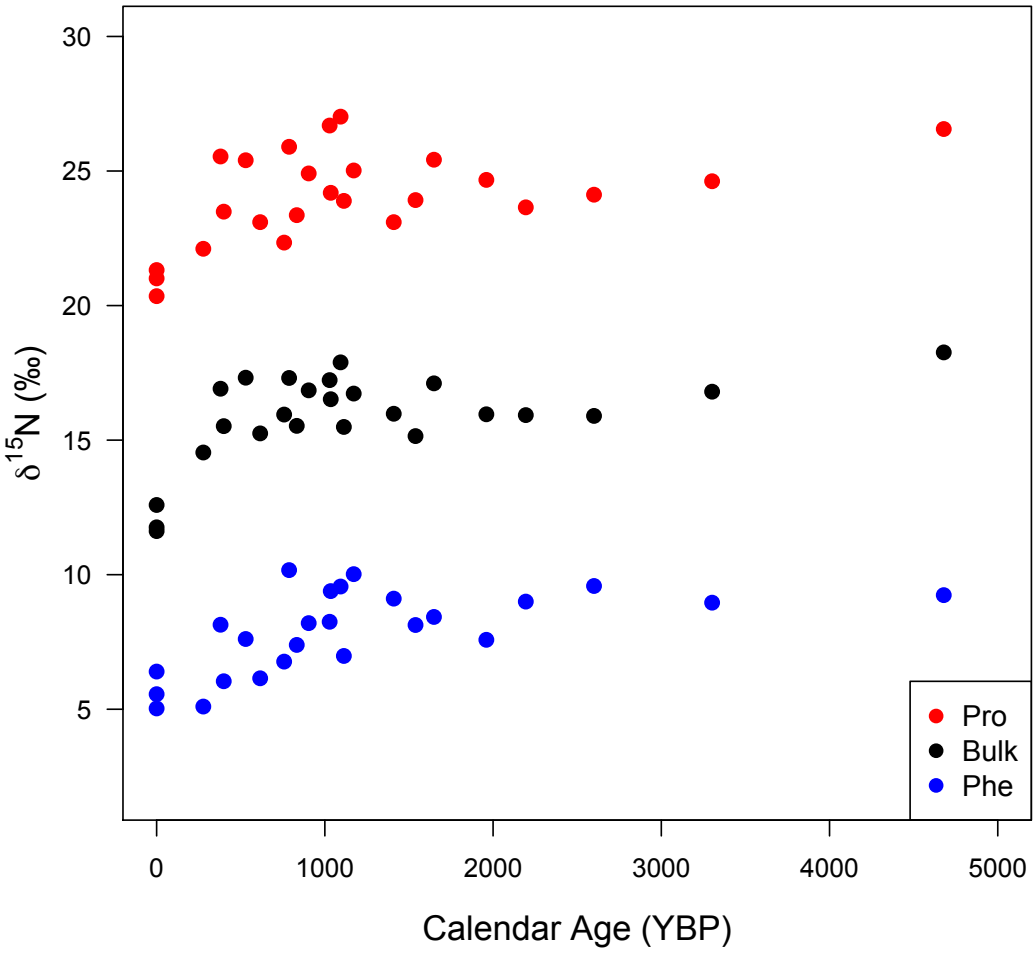

Figure 3.9. $\delta^{15}N$ values of Pro, bulk material, and Phe for Weddell seals over the mid-to-late Holocene. Isotopic data for Pro, bulk material, and Phe are represented by red, black, and blue circles, respectively.

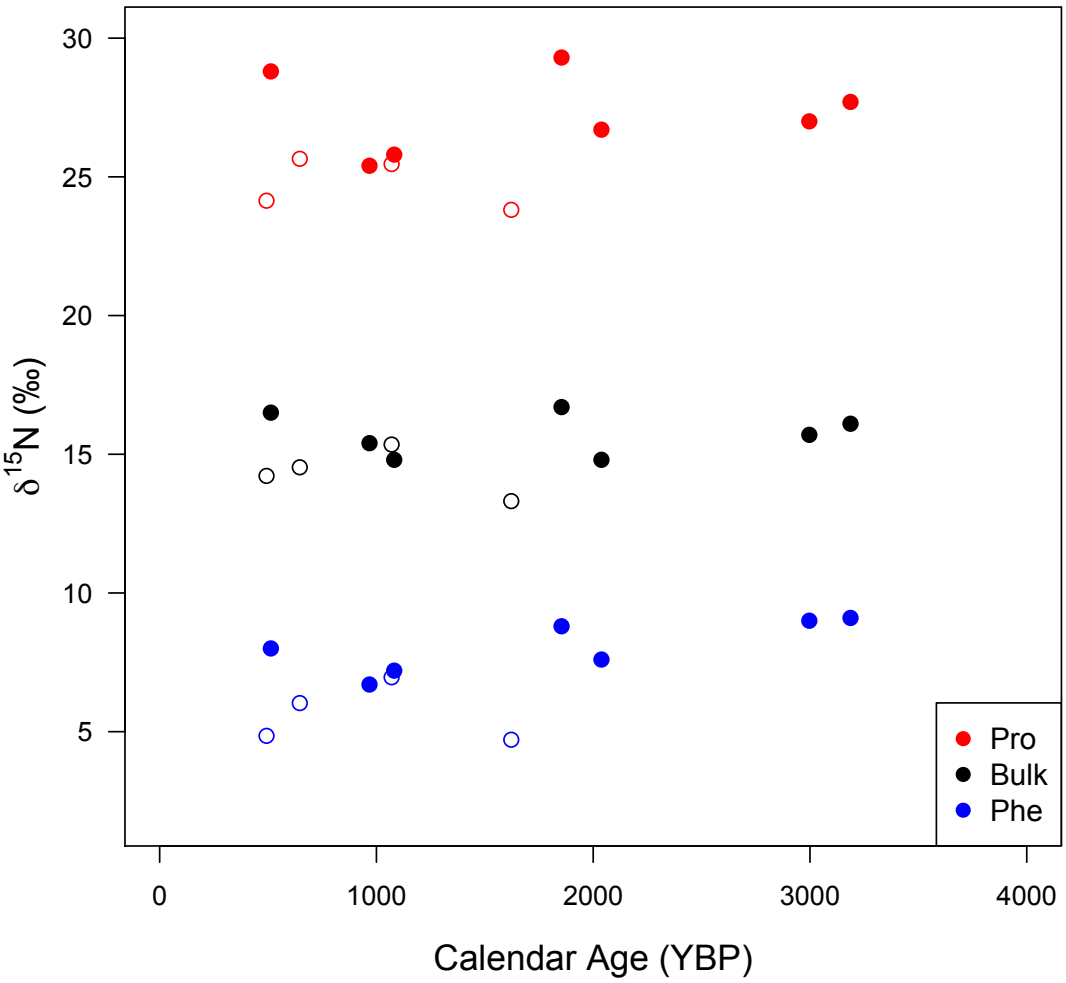

Figure 3.10. $\delta^{15}N$ values of Pro, bulk material, and Phe for southern elephant seals over the late Holocene. Isotopic data for Pro, bulk material, and Phe are represented by red, black, and blue circles, respectively. Solid circles indicate animals with bulk $\delta^{13}C$ values < -19.7 ‰, overlapping with the bulk $\delta^{13}C$ values of other true Antarctic seal species, and open circles represent animals with bulk $\delta^{13}C$ values ≥ -19.7 ‰.

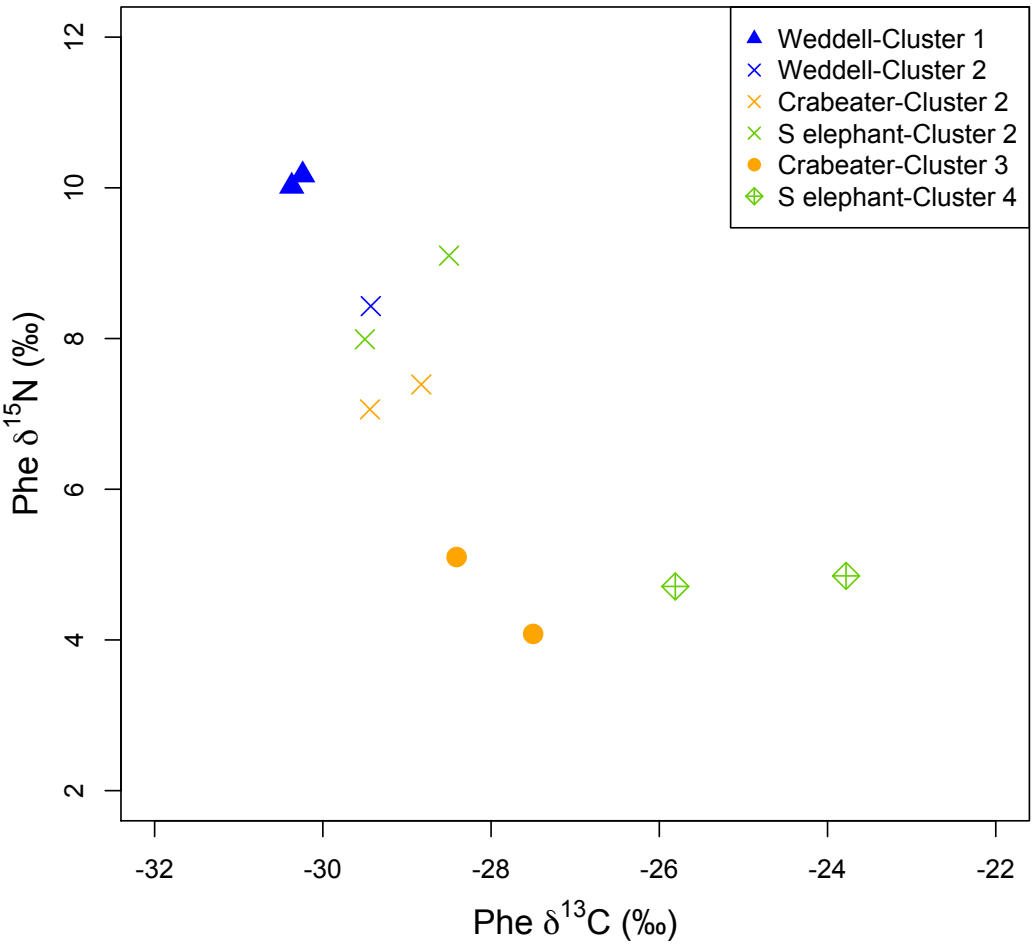

Figure 3.11. $\delta^{15}N$ versus $\delta^{13}C$ values of Phe for subfossil seals. Weddell, crabeater, and southern elephant seals are indicated with blue, orange, and green symbols, respectively. Each symbol type represents a unique cluster determined in a k-means cluster analysis.

SUPPLEMENTAL MATERIAL

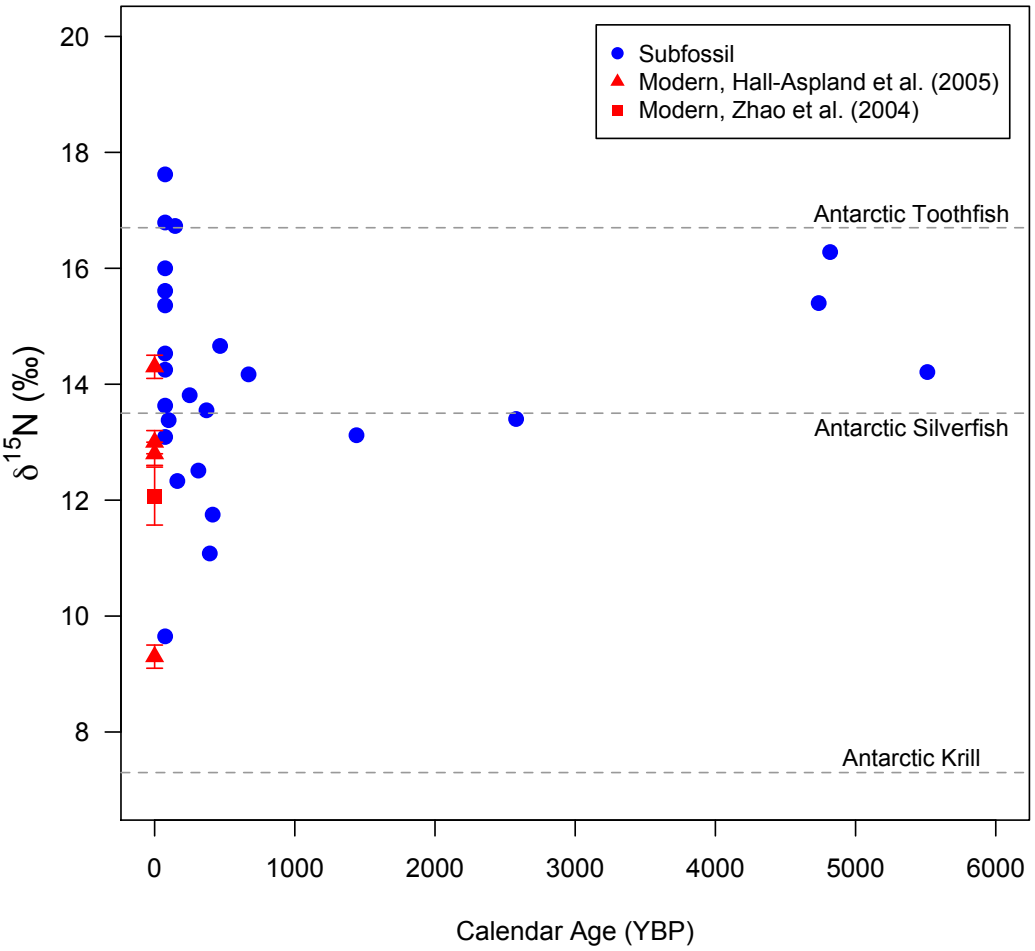

Figure 3.S1. $\delta^{15}N$ values of leopard seals over the mid-to-late Holocene. Blue circles and red triangles represent subfossil and modern specimens from the Ross Sea, respectively. Modern data are from Zhao et al. (2004) and Hall-Aspland et al. (2005). Data from Zhao et al. (2004) are the mean ± standard deviation for two adult male leopard seals. Data from Hall-Aspland et al. (2005) are the mean ± standard error for a whisker from an individual leopard seal. Dashed lines indicate the approximate $\delta^{15}N$ value of a predator consuming entirely Antarctic toothfish, Antarctic silverfish, or Antarctic krill.

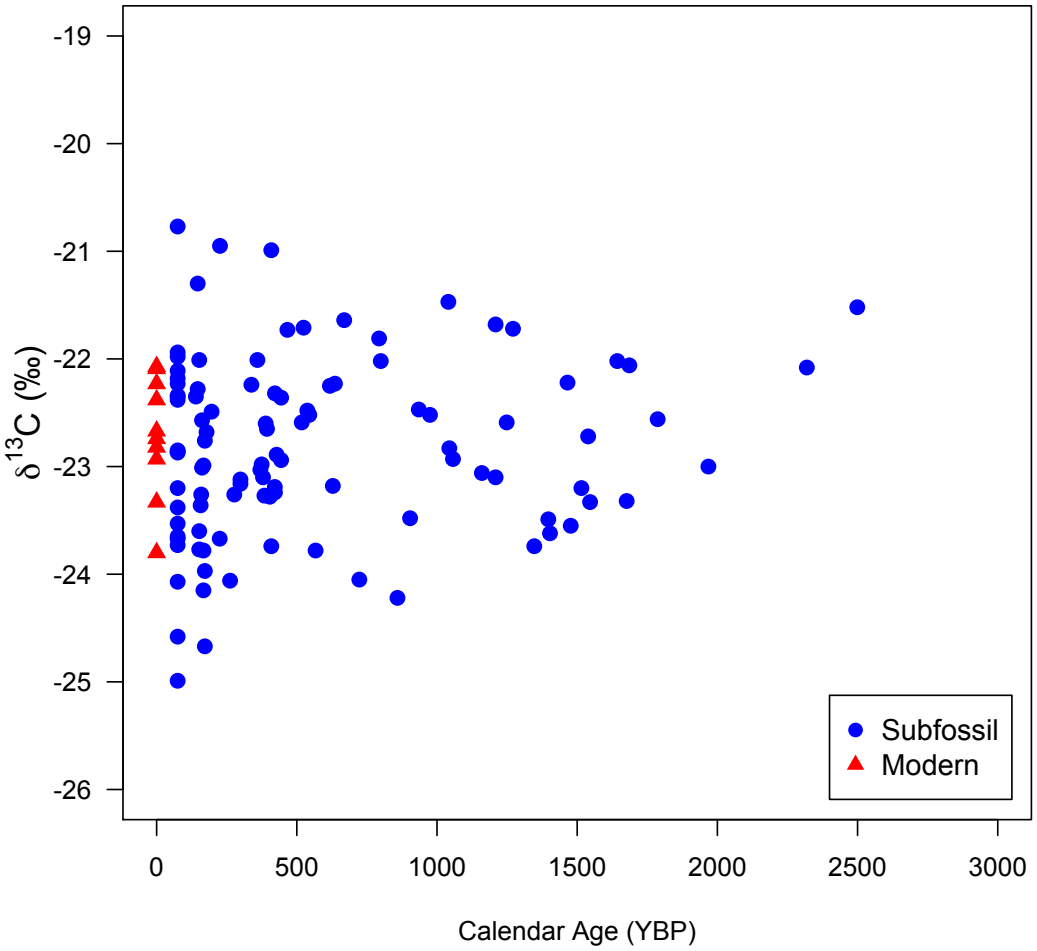

Figure 3.S2. $\delta^{13}C$ values of crabeater seals over the mid-to-late Holocene. Blue circles and red triangles represent subfossil and modern specimens from the Ross Sea, respectively.

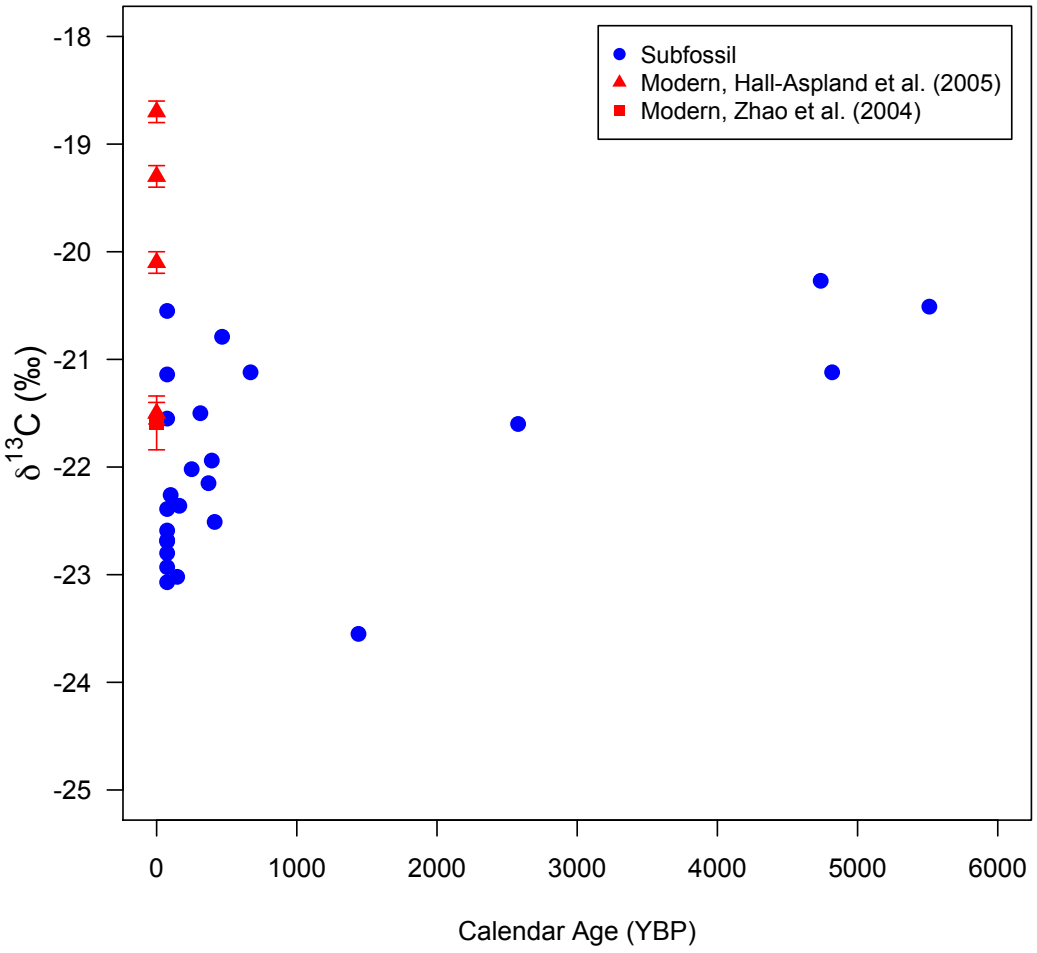

Figure 3.S3. $\delta^{13}C$ values of leopard seals over the mid-to-late Holocene. Blue circles and red triangles represent subfossil and modern specimens from the Ross Sea, respectively. Modern data are from Zhao et al. (2004) and Hall-Aspland et al. (2005). Data from Zhao et al. (2004) are the mean ± standard deviation for two adult male leopard seals. Data from Hall-Aspland et al. (2005) are the mean ± standard error for a whisker from an individual leopard seal.

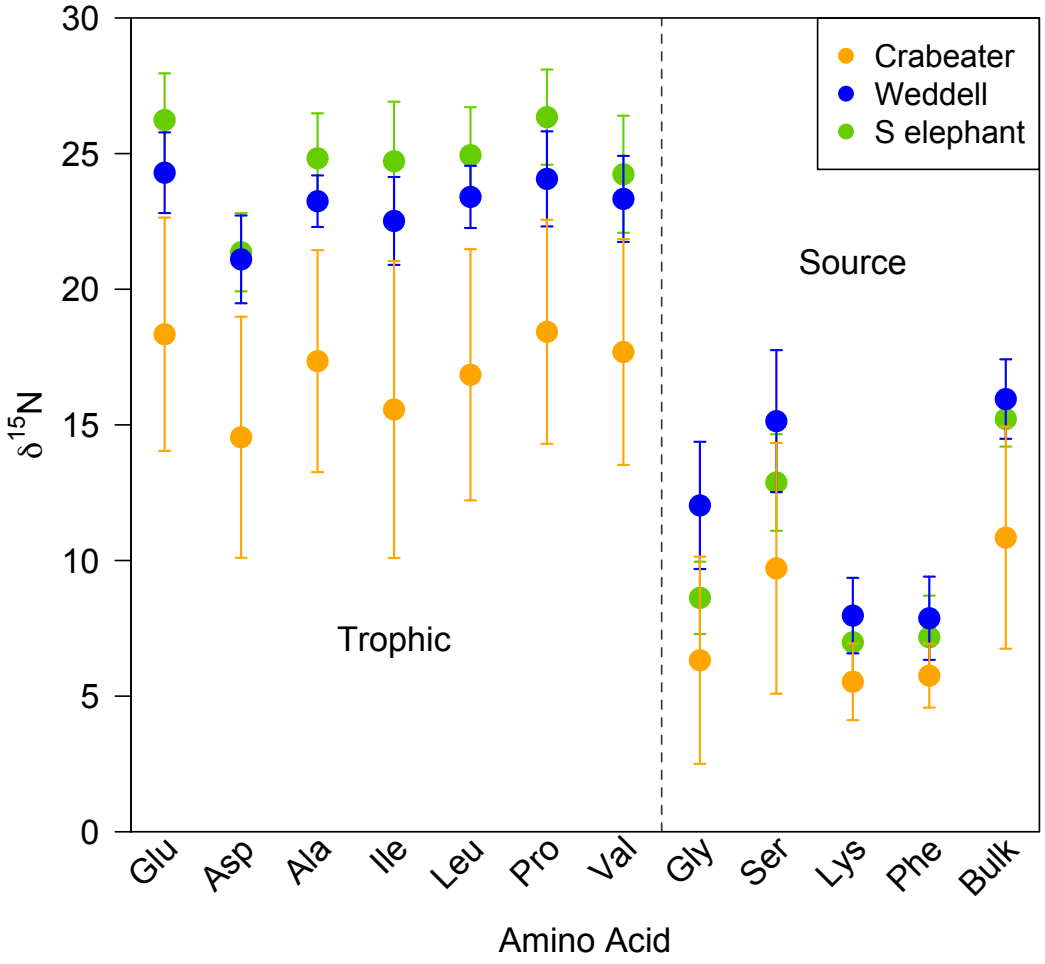

Figure 3.S4. Amino acid $\delta^{15}N$ values for subfossil specimens. Orange, blue, and green circles represent crabeater, Weddell, and southern elephant seals, respectively. Sample sizes are 12, 22, and 11 for crabeater, Weddell, and southern elephant seals, correspondingly.

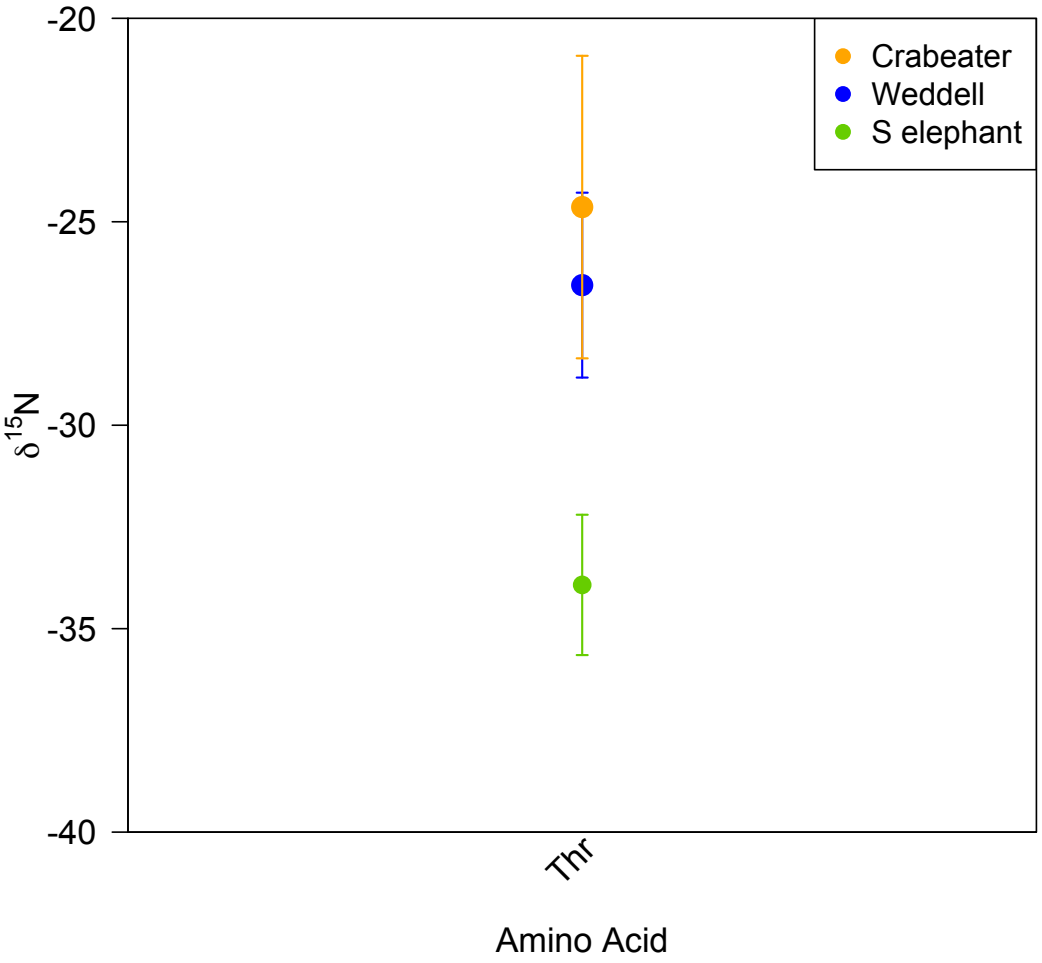

Figure 3.S5. Threonine $\delta^{15}N$ values for subfossil specimens. Orange, blue, and green circles represent crabeater, Weddell, and southern elephant seals, respectively. Sample sizes are 12, 22, and 11 for crabeater, Weddell, and southern elephant seals, correspondingly.

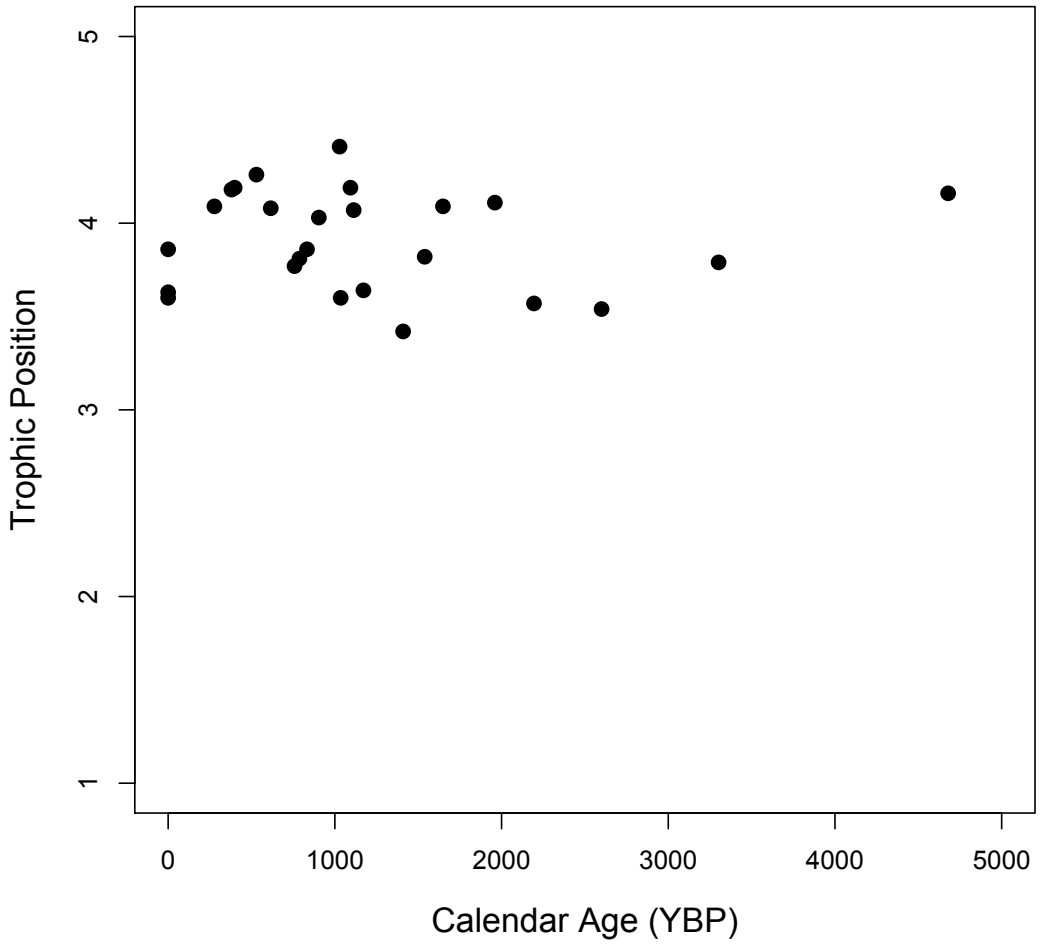

Figure 3.S6. Trophic positions for Weddell seals during the Holocene. Trophic positions are caculated based on Pro and Phe $\delta^{15}N$ values, see text.

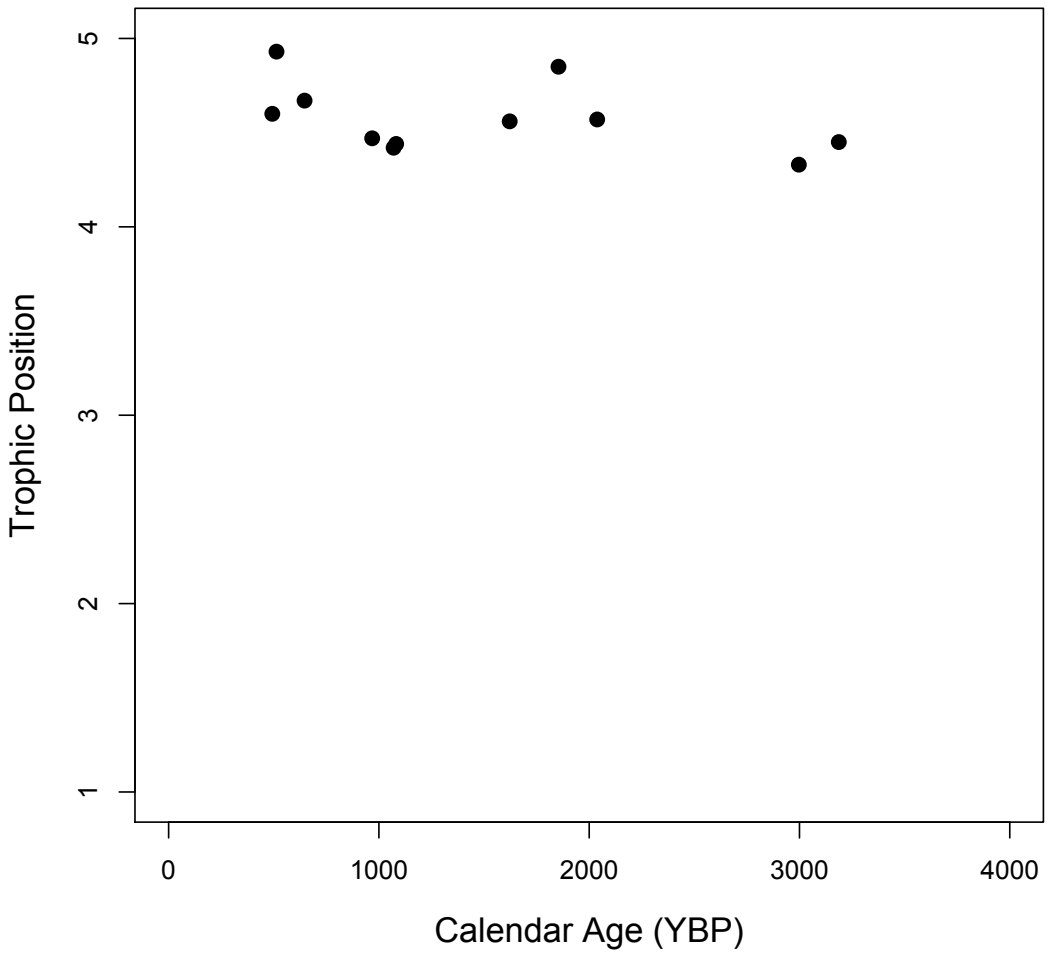

Figure 3.S7. Trophic positions for southern elephant seals during the Holocene. Trophic positions are caculated based on Pro and Phe $\delta^{15}N$ values, see text.

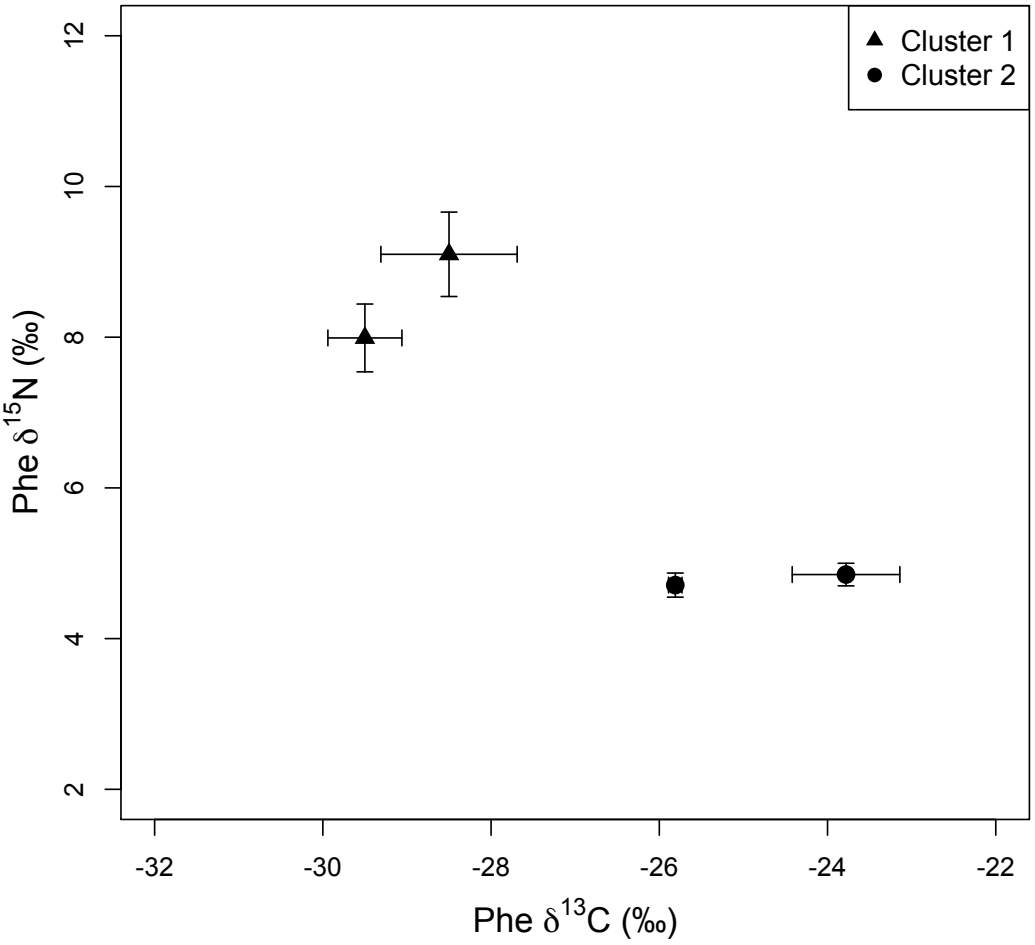

Figure 3.S8. $\delta^{15}N$ versus $\delta^{13}C$ values of Phe for subfossil southern elephant seals. Each symbol type represents a unique cluster from a k-means cluster analysis.

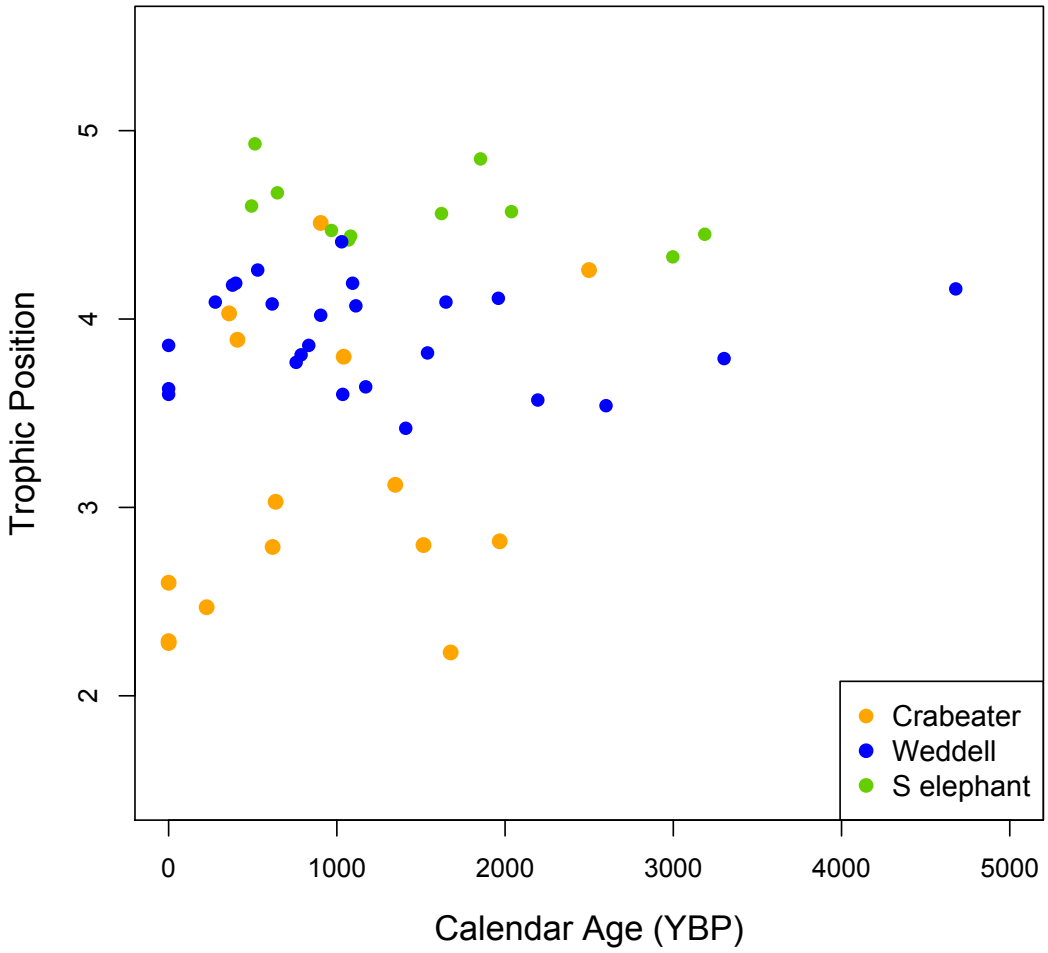

Figure 3.S9. Trophic positions of all subfossil seals. Trophic positions are caculated based on Pro and Phe $\delta^{15}N$ values, see text. Orange, blue, and green circles represent crabeater, Weddell, and southern elephant seals, respectively.

Table 3.S1. Isotope values of subfossil Weddell and crabeater specimens for multiple tissue types. These isotopic values are used to calculate the isotopic offsets between different tissue types, see Table 2 below.

Species	ID	Bone		Hair	
		$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Crabeater	HGA-12-21	-24.1	8.5	-25.1	8.5
	HGC-12-04	-22.2	9.0	-24.6	9.5
	LBA-13-40	-23.1	8.8	-25.1	8.2
	LBA-13-41	-23.4	10.8	-25.2	10.9
	LBA-13-44	-23.8	8.8	-25.3	8.4
	LBA-13-46	-23.2	9.9	-24.9	10.0
	LBB-13-38	-22.8	9.1	-24.6	9.0
	LBC-13-24	-21.5	17.1	-22.8	16.2
Weddell	LBC-13-44	-22.5	15.5	-22.8	14.4
	LBA-13-29	-23.2	15.4	-24.6	14.6
	LBA-13-34	-21.8	13.6	-24.4	14.6
	HGC-12-46	-22.6	13.7	-25.1	14.3
	LBC-13-32	-21.3	15.3	-23.2	14.6
	LBA-13-48	-22.4	15.1	-24.3	14.3
	HGC-12-14	-23.9	15.4	-23.9	14.5

Table 3.S2. Calculated isotope offsets between bone and hair (bone minus hair isotopic values) for crabeater and Weddell seals. If a calculated mean offset is ≤0.2‰, then the offset between the two tissue types is considered insignificant since ≤0.2‰ is within the instrument error.

Species	ID	$\delta^{13}C$ Offset (‰)	$\delta^{15}N$ Offset (‰)	Mean $\delta^{13}C$ Offset (‰)	Mean $\delta^{15}N$ Offset (‰)
Crabeater	HGA-12-21	0.9	0.0	1.7	0.2
	HGC-12-04	2.4	-0.5		
	LBA-13-40	2.0	0.6		
	LBA-13-41	1.8	0.0		
	LBA-13-44	1.6	0.4		
	LBA-13-46	1.7	-0.1		
	LBB-13-38	1.8	0.2		
	LBC-13-24	1.2	0.9		
Weddell	LBC-13-44	0.4	1.1	1.5	0.4
	LBA-13-29	1.3	0.8		
	LBA-13-34	2.6	-1.0		
	HGC-12-46	2.5	-0.6		
	LBC-13-32	1.9	0.6		
	LBA-13-48	1.9	0.8		
	HGC-12-14	0.0	0.9		

Table 3.S3. Isotopic values of all subfossil specimens. Type (of tissue) is abbreviated as *B*, *H*, and *S* for *bone*, *hair*, and *skin* sample, respectively. Age class is abbreviated as *Sub*, *U*, and *Ad* for *subadult/yearling*, *unknown*, and *adult*, correspondingly.

Sample ID	Species ID	Calendar Age (YBP)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	Atomic C:N	Type	Age Class
Salmon Seal 2012	Cr		-24.2	5.9	3.2	B	Sub
LBA-13-01	Lp	75	-21.1	13.1	3.2	B	Sub
LBA-13-02	Cr	1477	-23.6	7.9	3.1	B	Sub
LBA-13-03	Cr		-23.9	7.3	3.3	B	Sub
LBA-13-04	Unknown		-23.7	6.9	3.2	B	Sub
LBA-13-05	Cr	262	-24.1	7.4	3.1	B	Sub
LBA-13-06	Cr		-21.8	9.6	3.2	B	Sub
LBA-13-07	Cr		-22.9	5.4	3.2	B	Sub
LBA-13-08	Cr	1643	-22.0	8.4	3.2	B	U
LBA-13-09	Cr		-23.7	8.9	3.2	B	Sub
LBA-13-10	Wd	615	-21.9	15.1	3.1	B	Pup
LBA-13-11A	Wd	813	-20.7	15.5	3.2	B	Pup
LBA-13-11B	Wd	888	-20.9	16.2	3.3	B	Pup
LBA-13-12	Cr		-23.0	7.8	3.1	B	Sub
LBA-13-13	Unknown		-22.5	10.6	3.2	B	Sub
LBA-13-13 Af. Sp.	Cr		-22.6	6.4	3.2	B	U
LBA-13-14	Cr		-24.1	8.9	3.2	B	Sub
LBA-13-14 Af. Sp.	Cr		-22.5	8.6	3.2	B	U
LBA-13-15	Cr	389	-22.6	6.6	3.2	B	U
LBA-13-16	Cr	385	-23.3	11.6	3.2	B	Sub
LBA-13-17	Cr		-22.9	6.6	3.3	B	Sub
LBA-13-18	Cr		-23.3	8.8	3.2	B	Sub
LBA-13-19	Cr	1249	-22.6	10.0	3.2	B	Sub
LBA-13-20	Cr		-23.1	7.5	3.2	B	Sub
LBA-13-21	Cr	538	-22.5	8.9	3.2	B	U
LBA-13-22	Cr	1403	-23.6	8.7	3.2	B	Sub
LBA-13-22B	Unknown		-25.0	7.0	3.2	B	U
LBA-13-23	Cr	975	-22.5	8.7	3.2	B	Sub
LBA-13-24	Wd	178	-23.2	15.4	3.3	B	Sub
LBA-13-24A	Cr		-20.9	11.0	3.1	B	U
LBA-13-24B	Cr		-21.9	8.0	3.1	B	U
LBA-13-24C	Cr		-24.7	5.9	3.2	B	U
LBA-13-24D	Cr		-24.7	5.8	3.2	B	U
LBA-13-24E	Cr		-24.7	6.3	3.2	B	U
LBA-13-24F	Cr		-21.7	7.1	3.3	B	U
LBA-13-24G	Cr		-24.8	5.3	3.1	B	U
LBA-13-24H	Cr		-22.3	6.8	3.3	B	U
LBA-13-24I	Cr		-23.2	6.8	3.1	B	
LBA-13-25	Lp	5512	-20.5	14.2	3.2	B	U
LBA-13-26	Cr	1397	-23.5	7.4	3.2	B	Sub
LBA-13-27	Wd	904	-23.5	16.9	3.4	B	Sub
LBA-13-28	Wd	444	-21.2	18.0	3.3	B	Sub
LBA-13-29	Wd	467	-23.2	15.4	3.3	B	Sub
LBA-13-30	Wd	2600	-20.5	15.9	3.2	B	U
LBA-13-32	Wd	2018	-22.4	15.3	3.2	B	Sub
LBA-13-33A	Wd	833	-21.0	16.3	3.2	B	U
LBA-13-33B	Wd	409	-23.4	15.4	3.2	B	U

LBA-13-33C	Wd	956	-21.2	16.4	3.2	B	U
LBA-13-34	Wd	428	-21.8	13.6	3.1	B	Sub
LBA-13-34 Af. Sp.	Cr		-23.4	8.0	3.2	B	U
LBA-13-35	Wd	771	-22.9	16.2	3.1	B	U
LBA-13-35 Af. Sp.	Cr		-23.3	8.6	3.2	B	U
LBA-13-36	Wd	1280	-20.9	15.5	3.3	B	U
LBA-13-37	Unknown		-21.3	16.3	3.2	B	Sub
LBA-13-37 Af. Sp.	Wd		-20.0	13.1	3.2	B	U
LBA-13-38	Cr		-24.3	10.6	3.4	H	Sub
LBA-13-40	Cr	1160	-23.1	8.8	3.2	B	U
LBA-13-40	Cr	1160	-25.1	8.2	3.4	H	U
LBA-13-40	Cr	1160	-24.3	10.2	3.3	S	U
LBA-13-41	Cr		-23.4	10.8	3.1	B	Sub
LBA-13-41	Cr		-25.2	10.9	3.4	H	Sub
LBA-13-42	Cr		-21.9	7.4	3.2	B	U
LBA-13-43	Cr		-22.9	6.1	3.1	B	Sub
LBA-13-44	Cr		-23.8	8.8	3.2	B	Sub
LBA-13-44	Cr		-25.3	8.4	3.5	H	Sub
LBA-13-45	Cr		-22.9	7.6	3.2	B	Sub
LBA-13-46	Cr		-23.2	9.9	3.1	B	Sub
LBA-13-46	Cr		-24.2	12.1	3.3	S	Sub
LBA-13-46	Cr		-24.9	10.0	3.2	H	Sub
LBA-13-47	Wd	607	-21.7	15.1	3.1	B	Sub
LBA-13-48	Wd	250	-22.4	15.1	3.2	B	Sub
LBB-13-01	Cr	1968	-23.0	9.0	3.1	B	Sub
LBB-13-03	Cr		-23.5	8.7	3.2	B	Sub
LBB-13-03 Af. Sp.	Cr		-22.9	6.2	3.2	B	U
LBB-13-05	Cr		-22.1	9.7	3.2	B	U
LBB-13-06B	Cr		-22.7	7.0	3.1	B	U
LBB-13-06C	Cr		-22.7	7.2	3.1	B	U
LBB-13-07	Cr		-23.5	8.1	3.3	B	U
LBB-13-08	Cr		-23.9	8.0	3.3	B	Sub
LBB-13-10	Cr		-24.1	8.3	3.2	B	Sub
LBB-13-11	Wd	765	-22.3	15.2	3.3	B	Pup
LBB-13-12	Wd	2195	-21.6	15.9	3.3	B	Pup
LBB-13-13	Cr		-25.2	7.9	3.4	H	Sub
LBB-13-14	Wd	823	-21.4	14.3	3.2	B	Pup
LBB-13-15	Wd	616	-21.6	15.8	3.1	B	Sub
LBB-13-15 Af. Sp.	Cr		-23.4	6.7	3.2	B	U
LBB-13-16	Cr		-21.7	9.6	3.2	B	Sub
LBB-13-17	Cr	467	-21.7	6.8	3.2	B	Ad
LBB-13-18	Lp	1440	-23.6	13.1	3.3	B	U
LBB-13-19	Cr	375	-23.0	7.9	3.2	B	Sub
LBB-13-20	Unknown		-21.5	8.8	3.2	B	U
LBB-13-21	Wd	771	-21.1	16.0	3.3	B	Sub
LBB-13-22	Cr		-22.5	7.7	3.3	B	Sub
LBB-13-23	Cr	636	-22.2	9.8	3.2	B	Sub
LBB-13-24	Cr	794	-21.8	9.1	3.2	B	Sub
LBB-13-25	Cr		-23.1	7.2	3.2	B	Sub
LBB-13-25 Af. Sp.	Cr		-23.1	8.6	3.2	B	U
LBB-13-26	Cr	380	-23.1	9.0	3.3	B	Sub
LBB-13-27	Cr	422	-23.2	10.7	3.1	B	Sub
LBB-13-28	Cr		-23.8	9.2	3.5	H	Sub

LBB-13-29A	Cr	1686	-22.1	11.3	3.2	B	U
LBB-13-29B	Cr	1677	-23.3	8.0	3.1	B	Pup
LBB-13-30	Cr		-22.7	8.2	3.3	B	Sub
LBB-13-31	Cr	172	-22.8	8.2	3.2	B	Sub
LBB-13-32	Cr		-24.5	7.8	3.2	H	Sub
LBB-13-33	Cr		-22.5	7.7	3.2	B	Sub
LBB-13-34A	Cr	1271	-21.7	14.4	3.2	B	Sub
LBB-13-34B	Cr	75	-22.1	7.5	3.2	B	U
LBB-13-35	Wd	2069	-21.5	15.6	3.4	B	Sub
LBB-13-35 Af. Sp.	Cr		-23.3	9.3	3.2	B	U
LBB-13-36	Cr		-24.0	10.7	3.4	H	Sub
LBB-13-37	Cr	1209	-23.1	10.4	3.2	B	Sub
LBB-13-38	Cr		-22.8	9.1	3.2	B	Sub
LBB-13-38	Cr		-23.7	11.1	3.3	S	Sub
LBB-13-38	Cr		-24.6	9.0	3.4	H	Sub
LBB-13-39	Cr	518	-22.6	6.8	3.2	B	Sub
LBB-13-40	Cr	629	-23.2	8.0	3.2	B	Sub
LBB-13-41	Unknown		-23.5	7.4	3.2	B	Sub
LBB-13-41	Unknown		-24.4	8.5	3.4	S	Sub
LBB-13-42	Cr		-24.4	7.5	3.4	H	Sub
LBB-13-43	Cr		-23.4	9.0	3.5	H	Sub
LBB-13-44	Cr	75	-22.9	7.9	3.2	B	U
LBB-13-44 Af. Sp.	Unknown		-22.6	7.5	3.1	B	U
LBB-13-45	Cr	75	-23.4	11.8	3.3	B	Sub
LBB-13-46	Cr		-22.3	8.6	3.4	B	Sub
LBB-13-47	Cr		-23.1	9.5	3.2	B	Sub
LBB-13-48	Lp	2579	-21.6	13.4	3.2	B	U
LBB-13-48 Af. Sp.	Cr		-23.5	5.8	3.2	B	U
LBB-13-49	Cr	1466	-22.2	6.3	3.2	B	Sub
LBB-13-49 Af. Sp.	Cr		-22.3	6.5	3.1	B	U
LBB-13-50	Cr		-22.1	7.8	3.2	B	U
LBB-13-51	Cr		-23.2	8.0	3.2	B	Sub
LBB-13-52	Cr		-23.2	10.8	3.3	B	Sub
LBB-13-53	Lp	147	-23.0	16.7	3.4	B	Sub
LBB-13-55	Cr		-23.6	7.7	3.3	B	Sub
LBB-13-56	Wd	2300	-21.6	16.1	3.2	B	U
LBB-13-57	Cr		-23.3	7.8	3.2	B	Sub
LBB-13-58	Cr	338	-22.2	6.1	3.2	B	Sub
LBB-13-59	Wd	1172	-21.6	16.7	3.2	B	U
LBB-13-60	Wd	782	-20.8	17.1	3.2	B	U
LBB-13-61	Cr		-23.0	10.1	3.3	B	Sub
LBB-13-62	Cr		-24.8	9.6	3.4	H	Sub
LBB-13-62 Af. Sp.	Cr		-22.8	8.6	3.1	B	U
LBC-13-01	Cr		-25.3	7.6	3.4	H	Sub
LBC-13-02	Cr		-22.2	10.3	3.1	B	Sub
LBC-13-05	Cr		-21.9	6.7	3.2	B	Sub
LBC-13-06	Cr		-25.3	7.8	3.4	H	Sub
LBC-13-07	Cr	172	-24.7	8.4	3.2	B	Sub
LBC-13-08	Cr	147	-22.3	8.0	3.2	B	Sub
LBC-13-10A	Wd	415	-21.0	16.2	3.3	B	Sub
LBC-13-10B	Cr	370	-23.0	6.1	3.1	B	U
LBC-13-10C	Cr		-23.1	6.0	3.2	B	U
LBC-13-11A	Wd		-21.9	15.8	3.4	B	Sub

LBC-13-11B	Cr		-23.9	6.5	3.2	B	Sub
LBC-13-11C	Cr		-23.4	7.1	3.3	B	Sub
LBC-13-11D	Wd	359	-22.0	16.5	3.3	B	Sub
LBC-13-11E	Wd	1021	-21.6	17.4	3.3	B	U
LBC-13-11F	Wd	1029	-21.8	17.2	3.3	B	U
LBC-13-11G	Wd	1094	-22.5	17.9	3.4	B	U
LBC-13-12	Cr	147	-21.3	7.4	3.2	B	Sub
LBC-13-13	Cr	1539	-22.7	6.9	3.2	B	U
LBC-13-14	Lp	4819	-21.1	16.3	3.4	B	U
LBC-13-15	Wd	1960	-21.3	16.0	3.2	B	Sub
LBC-13-16	Wd	782	-20.3	14.7	3.3	B	U
LBC-13-17	Cr	1515	-23.2	6.4	3.1	B	U
LBC-13-18	Wd	345	-22.5	15.4	3.3	B	Sub
LBC-13-19	Wd	956	-21.5	16.2	3.3	B	Sub
LBC-13-20	Cr	800	-22.0	7.7	3.2	B	Sub
LBC-13-21	Wd	278	-23.5	14.5	3.4	B	Sub
LBC-13-24	Cr	2499	-22.8	16.2	3.5	H	U
LBC-13-24	Cr	2499	-21.5	17.1	3.2	B	U
LBC-13-25	Wd	1763	-20.6	14.7	3.1	B	U
LBC-13-26	Cr	444	-22.4	8.4	3.3	B	Sub
LBC-13-27	Wd	850	-21.7	15.2	3.1	B	U
LBC-13-28	Wd		-23.1	14.5	3.4	H	Sub
LBC-13-29	Wd	1410	-20.4	16.0	3.2	B	Sub
LBC-13-30	Cr	75	-20.8	7.0	3.1	B	Sub
LBC-13-30 Af. Sp.	Lp	4737	-20.3	15.4	3.2	B	U
LBC-13-31	Cr		-25.1	8.2	3.4	H	Sub
LBC-13-32	Wd	616	-21.3	15.3	3.2	B	Sub
LBC-13-33	Cr		-22.2	7.7	3.2	B	Sub
LBC-13-34	Cr		-23.0	6.6	3.1	B	U
LBC-13-35	Wd	1187	-19.8	15.0	3.2	B	Sub
LBC-13-36	Cr	75	-25.2	8.5	3.4	H	Sub
LBC-13-37	Cr	196	-22.5	6.9	3.2	B	Sub
LBC-13-38A	Cr	75	-22.3	11.7	3.1	B	U
LBC-13-39A	Wd	428	-21.8	13.5	3.1	B	U
LBC-13-39B	Cr		-22.6	5.8	3.1	B	U
LBC-13-39C	Wd	75	-22.6	14.6	3.3	B	U
LBC-13-39D	Cr		-23.1	6.1	3.1	B	U
LBC-13-39E	Cr		-23.7	8.6	3.1	B	U
LBC-13-40A	Lp	162	-22.4	12.3	3.3	B	U
LBC-13-40B	Cr		-23.5	8.1	3.2	B	U
LBC-13-40C	Cr		-23.1	8.1	3.1	B	U
LBC-13-40D	Cr	75	-21.9	11.7	3.2	B	U
LBC-13-40E	Lp	75	-22.9	9.7	3.2	B	U
LBC-13-40F	Cr		-22.4	6.4	3.2	B	U
LBC-13-40G	Cr		-21.8	8.7	3.1	B	U
LBC-13-40H	Unknown		-23.1	10.3	3.1	B	U
LBC-13-41	Wd	75	-21.5	16.3	3.2	B	Sub
LBC-13-42	Cr		-23.7	9.0	3.2	B	Sub
LBC-13-43	Cr		-23.6	8.6	3.2	B	Sub
LBC-13-44	Wd	833	-22.5	15.5	3.2	B	Pup
LBC-13-45	Cr		-23.0	7.6	3.2	B	Sub
LBC-13-46	Cr		-22.3	7.4	3.2	B	Sub
LBC-13-47	Cr	545	-22.5	9.2	3.2	B	Sub

LBC-13-48	Lp	75	-21.6	17.6	3.2	B	Sub
LBC-13-49	Cr	75	-23.7	10.1	3.2	B	U
LBC-13-49 Af. Sp.	Unknown		-23.2	7.1	3.2	B	U
LBC-13-50	Lp	250	-22.0	13.8	3.3	B	Sub
LBC-13-51	Wd	935	-21.8	16.0	3.3	B	Pup
LBC-13-52	Cr	226	-21.0	6.7	3.3	B	U
LBC-13-53	Cr		-23.3	7.4	3.2	B	Sub
LBC-13-54	Cr		-23.7	7.8	3.2	B	Sub
LBC-13-55	Wd	765	-21.4	15.4	3.2	B	Pup
LBC-13-55 Af. Sp.	Cr		-22.1	7.1	3.1	B	U
LBC-13-56	Cr		-22.9	11.1	3.2	B	Sub
LBC-13-57	Cr		-23.1	7.0	3.2	B	Sub
LBC-13-58	Cr	152	-23.6	6.5	3.2	B	Sub
MVA-13-01	Cr		-23.1	8.4	3.2	B	Sub
MVA-13-01 Af. Sp.	Cr		-23.4	7.4	3.1	B	U
MVA-13-02	Cr		-22.7	9.1	3.2	B	Sub
MVA-13-02 Af. Sp. 1	Wd		-22.8	14.2	3.2	B	U
MVA-13-03	Wd	1144	-19.7	13.9	3.2	B	U
MVA-13-03 Af. Sp.	Wd	380	-21.4	16.9	3.2	B	U
MVA-13-04	Cr		-22.6	8.0	3.1	B	U
MVA-13-05	Cr	409	-21.0	16.1	3.2	B	Sub
MVA-13-06	Wd	758	-21.9	16.0	3.1	B	Pup
MVA-13-07	Cr	162	-22.6	10.4	3.2	B	Sub
MVA-13-08	Cr		-22.5	8.6	3.2	B	Sub
MVA-13-09	Cr		-23.1	8.2	3.2	B	Sub
MVA-13-10	Wd	530	-22.6	17.3	3.1	B	Sub
MVA-13-11	Cr		-22.6	6.5	3.2	B	Sub
MVA-13-12	Cr		-23.1	8.7	3.2	B	Sub
MVA-13-13	Lp	394	-21.9	11.1	3.2	B	Sub
MVA-13-14	Wd	794	-22.6	15.7	3.3	B	Sub
MVA-13-15	Wd	573	-20.7	17.2	3.2	B	Sub
MVA-13-15 Af. Sp.	Cr		-23.3	6.5	3.2	B	U
MVA-13-16	Cr		-23.0	8.1	3.2	B	Sub
MVA-13-18 Af. Sp.	Unknown		-22.5	9.1	3.3	B	U
MVA-13-19 Af. Sp.	Lp	100	-22.3	13.4	3.2	B	U
MVA-13-21	Cr		-24.2	9.6	3.4	B	Sub
MVA-13-22	Cr		-21.6	7.4	3.2	B	Sub
MVA-13-23	Cr		-23.8	7.8	3.4	H	Sub
MVA-13-24	Cr	1041	-21.5	15.4	3.4	B	U
MVA-13-26	Cr		-22.7	10.8	3.2	B	U
MVA-13-26 Af. Sp.	Lp	75	-22.6	14.3	3.2	B	U
MVA-13-28A	Wd	2506	-19.9	14.0	3.2	B	Sub
MVA-13-28B	Unknown		-21.6	14.5	3.2	B	U
MVA-13-28C	Wd	510	-22.4	14.5	3.2	B	U
MVA-13-29	Wd	167	-22.7	13.5	3.2	B	Sub
MVA-13-31	Wd	782	-21.9	15.6	3.1	B	Pup
MVA-13-32	Cr		-24.0	9.1	3.3	S	Sub
MVA-13-33	Cr		-23.3	6.6	3.2	B	U
MVA-13-33 Af. Sp.	Cr		-23.5	7.6	3.2	B	U
MVA-13-34	Cr	360	-22.0	15.9	3.3	B	U
MVA-13-35	Cr		-22.7	6.5	3.3	B	Sub
MVA-13-37	Unknown		-23.5	9.7	3.3	S	U
MVA-13-37 Af. Sp.	Wd	380	-20.4	16.0	3.2	B	U

MVA-13-38	Cr		-25.1	8.7	3.4	H	Pup
MVA-13-39	Cr		-22.0	10.9	3.3	B	U
MVA-13-40	Wd	3302	-21.3	16.8	3.2	B	Sub
MVA-13-41	Cr		-22.2	8.1	3.2	B	Sub
MVA-13-42	Wd	771	-22.6	15.6	3.1	B	Pup
MVA-13-43A	Wd	3672	-22.1	12.5	3.2	B	U
MVA-13-43B	Unknown		-22.4	8.9	3.2	B	U
MVA-13-43C	Cr		-23.2	6.4	3.2	B	U
MVA-13-45	Cr		-23.3	10.1	3.4	B	Sub
MVA-13-45 Af. Sp.	Cr		-23.5	7.6	3.2	B	U
MVA-13-47	Cr		-23.4	10.0	3.2	B	Sub
MVA-13-49	Wd	75	-22.3	16.0	3.2	B	Sub
MVA-13-50	Unknown		-22.0	8.3	3.3	B	U
MVA-13-50 Af. Sp.	Unknown		-21.9	8.0	3.2	B	U
MVA-13-51	Wd	654	-20.9	14.4	3.1	B	Sub
MVA-13-51 Af. Sp.	Unknown		-21.8	10.3	3.2	B	U
MVA-13-52	Wd	389	-22.1	17.1	3.2	B	U
MVA-13-53A	Wd	394	-23.0	13.6	3.2	B	U
MVA-13-53B	Wd	677	-21.1	17.3	3.3	B	U
MVA-13-53C	Wd		-21.6	15.4	3.2	B	U
MVB-13-01	Cr		-22.0	8.4	3.2	B	Sub
MVB-13-02	Cr		-21.9	8.4	3.1	B	Sub
MVB-13-03	Wd	859	-23.1	14.9	3.1	B	Pup
MVB-13-04	Wd	1576	-21.4	15.8	3.1	B	Sub
MVB-13-05	Cr	394	-22.7	6.7	3.2	B	Sub
MVB-13-06	Cr	152	-22.0	6.5	3.3	B	Sub
MVB-13-07	Wd	1178	-22.3	15.1	3.3	B	Pup
MVB-13-08	Cr		-23.0	9.7	3.3	B	Sub
MVB-13-09	Wd	75	-22.2	14.3	3.2	B	U
MVB-13-10A	Cr		-23.5	6.6	3.2	B	U
MVB-13-10B	Unknown		-22.1	8.6	3.2	B	U
MVB-13-10D	Unknown		-23.8	7.6	3.1	B	U
MVB-13-10F	Unknown		-22.4	7.4	3.2	B	U
MVB-13-10H	Unknown		-21.8	6.3	3.2	B	U
MVB-13-11A	Unknown		-22.9	6.1	3.3	B	U
MVB-13-11B	Unknown		-22.4	12.0	3.1	B	U
MVB-13-12A	Unknown		-23.5	6.5	3.2	B	U
MVB-13-12D	Unknown		-22.3	13.5	3.2	B	U
MVB-13-12E	Unknown		-23.2	8.1	3.2	B	U
MVB-13-13A	Unknown		-21.7	8.3	3.2	B	U
MVB-13-13B	Unknown		-22.8	8.3	3.2	B	U
MVB-13-13D	Unknown		-21.3	14.0	3.2	B	U
MVB-13-14	Wd	353	-21.7	15.3	3.2	B	Sub
MVB-13-15	Cr		-23.1	8.5	3.3	B	Sub
MVB-13-16	Lp	370	-22.2	13.6	3.2	B	Sub
MVB-13-17	Wd	1209	-21.5	16.3	3.4	B	Sub
MVB-13-18	Unknown		-24.0	7.8	3.5	H	Sub
MVB-13-19	Wd	394	-23.1	15.7	3.3	B	Sub
MVB-13-19 Af. Sp.	Wd	312	-23.3	15.4	3.2	B	U
MVB-13-20A	Cr		-23.1	10.7	3.2	B	U
MVB-13-20B	Cr		-22.5	9.3	3.3	B	U
MVB-13-20C	Unknown		-23.1	11.2	3.2	B	U
MVB-13-20D	Cr		-23.3	9.4	3.2	B	U

MVB-13-21	Cr		-23.3	7.6	3.3	B	Sub
MVB-13-22	Unknown		-22.2	7.0	3.2	B	U
MVB-13-23	Cr		-22.3	7.2	3.3	B	Sub
MVB-13-24	Cr		-22.3	10.0	3.2	B	Sub
MVB-13-25	Cr		-23.8	10.7	3.3	B	Sub
MVB-13-26	Cr		-22.0	8.2	3.2	B	Sub
MVB-13-26 Af. Sp.	Unknown		-22.3	7.3	3.2	B	U
MVB-13-28	Wd		-20.8	14.4	3.1	B	Sub
MVB-13-29	Unknown		-24.6	11.7	3.4	H	Sub
MVB-13-30	Wd		-23.4	16.2	3.4	S	Sub
MVB-13-32	Unknown		-10.4	5.8	3.2	B	U
MVB-13-33	Unknown		-22.8	6.6	3.2	B	U
MVB-13-34	Wd		-21.4	13.5	3.1	B	U
MVB-13-35	Unknown		-21.1	15.1	3.2	B	U
MVB-13-36	Wd	409	-22.6	15.3	3.2	B	U
MVC-13-03	Cr		-24.5	9.2	3.5	H	Sub
MVC-13-04	Cr		-22.4	7.6	3.2	B	Sub
MVC-13-05	Cr		-23.7	8.6	3.3	B	Sub
MVC-13-05 Af. Sp. A	Unknown		-23.2	8.9	3.3	B	U
MVC-13-05 Af. Sp. B	Unknown		-21.5	15.5	3.3	B	U
MVC-13-05 Af. Sp. C	Unknown		-23.3	6.2	3.1	B	U
MVC-13-05 Af. Sp. D	Unknown		-23.5	6.2	3.3	B	U
MVC-13-05 Af. Sp. E	Unknown		-23.6	6.5	3.3	B	U
MVC-13-06	Wd	788	-20.2	17.3	3.2	B	Sub
MVC-13-07	Unknown	2674	-21.9	14.1	3.4	B	Sub
MVC-13-08	Wd		-22.9	15.5	3.5	H	Sub
MVC-13-09	Unknown		-25.1	10.2	3.4	H	Sub
MVC-13-10	Unknown		-23.0	7.8	3.4	B	U
MVC-13-11	Wd	365	-22.6	15.4	3.1	B	Sub
MVC-13-12	Cr	1209	-21.7	6.6	3.3	B	Sub
MVC-13-13	Cr		-24.0	8.0	3.4	H	Sub
MVC-13-14	Wd	1539	-22.8	15.2	3.3	B	Sub
MVC-13-15	Wd	390	-22.8	14.5	3.1	B	Sub
MVC-13-16	Unknown		-22.1	15.3	3.2	B	U
MVC-13-17	Unknown		-21.9	10.8	3.2	B	U
MVC-13-18	Unknown		-22.1	17.3	3.2	B	U
MVC-13-19	Unknown		-21.7	16.2	3.2	B	U
MVC-13-20	Unknown		-21.1	13.5	3.2	B	U
MVC-13-23	Unknown		-21.0	12.3	3.2	B	U
MVC-13-24	SES	1886	-19.5	15.5	3.1	B	Sub
MVC-13-25	Unknown		-20.0	15.8	3.2	B	U
MVC-13-26	Wd	3394	-19.3	15.3	3.2	B	U
MVC-13-27	Wd	1649	-20.1	17.1	3.3	B	U
MVC-13-28	Wd	409	-22.6	13.8	3.2	B	U
MVC-13-29A	Unknown		-21.5	9.0	3.2	B	U
MVC-13-29B	Unknown		-23.4	7.9	3.2	B	U
MVC-13-29C	Unknown		-22.6	13.4	3.2	B	U
MVC-13-29D	Unknown		-22.4	11.4	3.2	B	U
MVC-13-29E	Unknown		-22.7	7.1	3.2	B	U
MVC-13-30A	Unknown		-22.2	6.2	3.2	B	U
MVC-13-31A	Unknown		-23.3	7.7	3.1	B	U
MVC-13-31B	Cr		-22.5	9.2	3.2	B	U
MVC-13-31C	Unknown		-23.4	7.5	3.4	H	U

MVC-13-31D	Unknown		-21.7	7.3	3.2	B	U
MVC-13-32	Cr		-20.7	8.1	3.2	B	Sub
MVC-13-33	Unknown	75	-24.2	9.3	3.3	B	Sub
MVC-13-34	Unknown		-22.6	14.7	3.5	H	Sub
MVC-13-35	Cr		-22.3	7.5	3.3	B	Sub
MVC-13-35A	Cr		-20.7	14.3	3.3	B	Sub
MVC-13-36 AF. SP. 2	Unknown		-21.7	15.7	3.3	B	U
MVC-13-36 AF. SP. 3	Unknown		-23.0	9.7	3.2	B	U
MVC-13-36 AF. SP. 5	Unknown		-21.2	11.1	3.2	B	U
MVC-13-38A	Cr		-23.4	11.7	3.3	B	U
MVC-13-38B	Unknown		-23.4	11.8	3.2	B	U
MVC-13-39	Wd	1113	-22.2	15.5	3.2	B	Pup
MVC-13-40	Wd	771	-23.1	15.4	3.2	B	Pup
MVC-13-41	Unknown		-22.8	9.3	3.2	S	U
MVC-13-42	Cr		-22.9	7.3	3.2	B	Sub
MVC-13-43A	Unknown		-23.3	6.5	3.1	B	U
MVC-13-45A	Unknown		-21.3	6.2	3.2	B	U
MVC-13-45B	Unknown		-22.2	8.0	3.2	B	U
MVC-13-45C	Unknown		-23.0	15.5	3.3	B	U
MVC-13-46	Cr	178	-22.7	6.6	3.2	B	Sub
MVC-13-47	Cr		-25.1	8.9	3.5	H	Sub
MVC-13-48	Unknown		-24.2	7.1	3.4	H	Sub
MVC-13-49	Unknown	75	-23.9	7.6	3.5	H	U
MVC-13-51	Unknown		-12.8	5.0	3.4	B	U
MVC-13-52	Unknown		-21.1	13.0	3.2	B	U
MVC-13-53	Unknown	415	-21.9	12.7	3.4	B	U
MVC-13-54	Unknown		-21.9	13.7	3.2	B	U
MVC-13-55A	Unknown		-21.0	14.4	3.2	B	U
MVC-13-55B	Unknown		-22.3	12.5	3.2	B	U
ECA-12-01	Cr	167	-23.8	8.1	3.3	B	Sub
ECA-12-02	Cr		-23.1	7.1	3.2	B	Sub
ECA-12-03	Cr	299	-23.1	7.7	3.4	B	Ad
ECA-12-04	Cr	75	-23.2	9.4	3.4	S	Sub
ECA-12-05	Cr	422	-23.2	9.6	3.2	B	Sub
ECA-12-06	Cr	299	-23.2	8.0	3.2	B	Sub
ECA-12-07	Cr	404	-23.3	11.4	3.2	B	U
ECA-12-10	Wd	360	-21.8	16.5	3.3	B	Sub
ECA-12-11	Cr	444	-22.9	6.6	3.3	B	U
ECA-12-12	Wd	75	-22.0	16.8	3.2	B	U
ECA-12-13	Cr		-23.3	7.0	3.2	B	U
ECA-12-14	Lp	312	-21.5	12.5	3.4	B	U
ECA-12-15	SES	2205	-19.8	14.1	3.4	B	U
ECA-12-16	Cr		-22.0	9.5	3.3	B	U
ECA-12-17	Unknown		-22.4	7.1	3.3	B	U
ECA-12-18	Cr		-23.3	8.5	3.1	B	U
ECA-12-19	Cr		-23.5	7.3	3.3	B	U
ECA-12-20	Wd		-23.1	13.9	3.3	B	U
ECA-12-21	Wd		-22.8	11.3	3.3	B	U
ECA-12-22	Wd	422	-22.5	16.1	3.1	B	U
ECA-12-23	Wd		-22.0	14.4	3.2	B	U
ECA-12-24	Wd	382	-23.0	16.2	3.4	B	U
ECB-12-04	Wd	75	-23.0	15.4	3.4	S	Sub
ECB-12-05	Wd	75	-23.4	15.9	3.4	S	Sub

ECB-12-05	Wd	75	-24.1	14.3	3.5	H	Sub
ECB-12-06	Wd	157	-21.3	13.8	3.2	B	Ad
ECB-12-07	Wd	185	-21.4	14.3	3.3	B	U
ECB-12-09	Cr	140	-22.4	12.5	3.2	B	Sub
ECB-12-10	Wd		-21.6	13.4	3.2	B	U
ECB-12-11	SES		-18.6	14.0	3.3	B	U
ECB-12-12	Wd	399	-22.6	15.5	3.1	B	U
ECB-12-13	Cr	75	-22.9	5.8	3.1	B	U
ECB-12-14	Wd		-21.6	12.6	3.2	B	U
ECB-12-15	Wd	270	-22.0	12.3	3.2	B	U
ECB-12-16	Wd		-21.6	12.5	2.9	B	U
ECB-12-18	Lp	414	-22.5	11.8	3.2	B	Sub
ECB-12-19	Wd	196	-22.7	16.4	3.3	B	U
ECB-12-20	Wd		-21.3	15.1	3.2	B	U
ECB-12-21A	Cr		-23.0	11.1	3.3	B	U
ECB-12-22	Cr		-24.0	7.6	3.1	B	U
ECB-12-23	Cr		-24.3	6.6	3.2	B	U
ECB-12-24	Wd		-22.9	15.2	3.1	B	U
ECB-12-25	Wd		-22.1	12.9	2.9	B	U
ECB-12-27	Wd		-21.9	12.4	2.9	B	U
ECB-12-28	Cr		-23.3	9.7	3.4	B	Sub
ECB-12-29	Cr	75	-23.2	9.1	3.2	B	Sub
ECB-12-30	Cr		-23.8	7.9	3.3	B	Sub
ECB-12-31	Cr		-23.9	8.7	3.3	B	Sub
ECB-12-34	Wd	380	-21.5	13.9	3.2	B	Sub
ECB-12-36	Cr		-21.5	8.1	3.0	B	U
ECB-12-37	Unknown		-22.3	6.4	3.3	B	U
ECB-12-38	Cr	75	-22.9	7.3	3.2	B	U
ECB-12-39	Cr	159	-23.3	7.7	3.2	B	Sub
ECB-12-40	Cr	428	-22.9	8.6	3.2	B	Sub
ECB-12-41	Unknown		-12.5	3.7	3.4	B	U
ECB-12-42	Wd	75	-22.1	13.1	3.2	B	Sub
ECB-12-43	Wd	771	-20.8	17.2	3.3	B	U
ECB-12-44	Wd		-18.7	14.9	3.0	B	U
ECB-12-45	Wd		-20.5	14.1	3.2	B	U
ECB-12-47	Wd	608	-19.3	17.8	3.1	B	U
ECB-12-48	Wd	226	-22.7	15.5	3.0	B	U
ECB-12-50	Wd		-21.4	13.4	3.0	B	U
ECB-12-51	Cr	75	-22.2	8.0	2.9	B	U
ECB-12-52	Wd	75	-22.9	15.4	3.3	B	Sub
ECB-12-53	Cr		-24.2	7.7	3.4	B	Sub
ECB-12-54	Wd	75	-21.1	13.9	3.2	B	U
ECB-12-55	Cr		-22.1	7.0	3.2	B	U
ECB-12-56	Wd	338	-21.3	16.0	3.2	B	Sub
ECB-12-58	Cr	157	-23.4	7.6	3.2	B	Sub
ECB-12-59	Wd	4679	-19.0	18.3	3.2	B	U
ECB-12-62	Unknown		-20.8	16.8	3.3	B	U
ECB-12-63	Cr		-23.8	11.2	3.5	S	Sub
ECB-12-64	Cr		-23.7	7.1	3.4	B	U
ECB-12-65	Cr		-22.2	7.0	3.1	B	U
ECB-12-66	Cr		-23.6	9.6	3.3	B	U
ECB-12-67	Cr		-23.0	6.5	3.2	B	U
ECB-12-68	Cr	75	-22.4	6.6	2.9	B	U

ECB-12-69	Cr		-23.3	8.6	3.2	B	Sub
ECB-12-70	Cr	75	-23.7	5.4	3.2	B	Sub
ECB-12-71	Wd	1397	-22.3	12.3	3.2	B	U
ECC-12-01	Cr		-23.4	7.9	3.1	B	U
ECC-12-02	Cr		-24.5	6.6	3.2	B	Sub
ECC-12-03	Cr		-23.5	7.3	3.3	B	Sub
ECC-12-04	Cr		-23.0	7.7	3.2	B	Sub
ECC-12-05	Cr		-23.3	9.0	3.2	B	U
ECC-12-06	Wd	573	-22.1	15.7	3.2	B	U
ECC-12-07	Wd	588	-22.4	16.0	3.3	B	U
ECC-12-09	Wd	390	-20.5	17.2	2.9	B	U
ECC-12-10	Cr		-22.7	6.0	3.2	B	U
ECC-12-11	Wd	925	-20.4	16.4	3.1	B	Sub
ECC-12-12	Cr	669	-21.6	8.2	3.2	B	Sub
ECC-12-14	Cr		-22.9	6.9	3.2	B	Sub
ECC-12-15	Wd	345	-22.5	15.3	3.2	B	Sub
ECC-12-17	Cr	904	-23.5	16.8	3.3	B	Sub
ECC-12-18	Cr		-23.9	9.3	3.4	H	Sub
ECC-12-19	Cr	1546	-23.3	7.4	3.2	B	U
ECC-12-20	Cr		-24.0	8.7	3.2	B	Sub
ECC-12-21	Unknown		-23.8	6.2	3.1	B	Sub
ECC-12-22	Cr		-22.8	6.4	3.1	B	Sub
ECC-12-23	Cr		-23.7	9.1	3.2	B	Sub
ECC-12-24	Cr		-23.3	7.6	3.2	B	Sub
ECC-12-25	Cr	75	-25.0	6.7	3.2	B	Sub
ECC-12-26	Lp	75	-20.6	13.6	3.2	B	U
ECC-12-27	Wd	250	-21.2	14.2	3.0	B	U
ECC-12-28	Wd		-22.3	11.6	3.2	B	U
ECC-12-29	Unknown		-24.5	6.0	3.2	B	U
ECC-12-30	Wd		-22.4	11.7	3.2	B	U
ECC-12-31	Wd	185	-18.3	16.5	3.3	S	Sub
ECC-12-32	Wd	312	-22.8	16.3	3.2	B	U
ECC-12-33	Wd	636	-20.4	14.3	3.4	B	U
ECC-12-34	SES	500	-19.9	13.4	3.2	B	U
ECC-12-35	Wd	2860	-20.7	16.7	3.4	B	U
ECC-12-36	Wd		-22.2	13.6	3.2	B	U
ECC-12-37	Cr		-25.2	9.0	3.5	H	Sub
ECC-12-38	Wd	623	-21.0	14.0	3.2	B	U
ECC-12-39	Wd		-21.7	13.5	3.3	B	U
ECC-12-40	Unknown		-22.4	8.0	3.2	B	U
ECC-12-41	Wd	75	-21.0	13.8	3.2	B	U
ECC-12-42	Cr		-20.0	11.8	3.2	B	U
ECC-12-43	Wd	75	-21.6	13.1	3.1	B	U
ECC-12-44	Wd	1939	-21.2	14.5	3.2	B	U
ECC-12-45	Wd	270	-21.5	13.0	3.2	B	Sub
ECC-12-46	Wd		-21.8	13.5	3.3	B	U
ECC-12-47	Wd	250	-21.6	15.6	3.2	B	U
ECC-12-49	Cr		-23.3	6.4	3.1	B	U
ECC-12-52	SES	1959	-19.7	16.4	3.2	B	U
ECC-12-53	SES	1996	-19.7	16.3	3.2	B	U
ECC-12-56E	SES	1380	-20.0	16.6	3.3	B	U
ECC-12-56I	Unknown	1966	-19.8	16.5	3.2	B	U
ECC-12-57A	Wd	360	-23.0	15.9	3.4	B	U

ECC-12-58	Cr		-22.9	7.4	3.4	B	Sub
ECC-12-59	Cr		-22.1	8.9	3.2	B	Sub
ECC-12-62	Unknown	501	-23.5	16.1	3.4	B	Sub
HGA-12-01	Cr		-22.5	7.9	3.3	B	U
HGA-12-02A	Unknown		-21.8	16.1	3.1	B	U
HGA-12-02B	Wd		-21.9	15.6	3.2	B	U
HGA-12-03	Lp	467	-20.8	14.7	3.2	B	Sub
HGA-12-04	Cr	859	-24.2	13.4	3.4	B	Sub
HGA-12-05	Cr		-23.8	8.2	3.3	B	Sub
HGA-12-06	Unknown		-24.1	7.0	3.0	B	U
HGA-12-07	Cr		-23.4	9.4	3.4	H	Sub
HGA-12-08	Wd	777	-21.1	15.7	3.3	B	Pup
HGA-12-09	Wd	75	-20.9	13.6	3.3	B	Sub
HGA-12-10	Cr		-22.8	10.9	3.1	B	U
HGA-12-11	Wd	545	-22.3	15.1	3.3	B	Pup
HGA-12-13	Cr		-22.3	9.1	3.1	B	Sub
HGA-12-14	Cr		-24.8	9.0	3.4	H	Sub
HGA-12-15	Cr		-23.1	6.9	3.3	B	U
HGA-12-16	Cr		-22.9	7.2	3.2	B	U
HGA-12-17	Cr		-22.5	6.6	3.1	B	Sub
HGA-12-18	Cr	75	-24.6	6.0	3.3	B	Sub
HGA-12-19	Cr		-23.2	6.1	3.3	B	Sub
HGA-12-20	Cr	1057	-22.9	5.9	3.1	B	U
HGA-12-21	Cr		-24.1	8.5	3.3	B	Sub
HGA-12-21	Cr		-24.6	9.5	3.4	S	Sub
HGA-12-21	Cr		-25.1	8.5	3.4	H	Sub
HGA-12-22	Cr		-23.4	8.0	3.3	B	Sub
HGA-12-23	Unknown		-22.2	9.2	3.2	B	Sub
HGA-12-24	Cr		-21.4	8.0	3.3	B	Sub
HGA-12-25	Cr	167	-24.2	11.6	3.4	B	Sub
HGA-12-26	Cr	75	-23.5	11.2	3.3	B	Sub
HGA-12-27	Cr	1044	-22.8	7.4	3.1	B	U
HGA-12-28	Lp	75	-23.1	16.8	3.4	B	Sub
HGA-12-29	Cr		-25.4	8.0	3.5	H	Sub
HGA-12-30	Lp	75	-22.7	15.4	3.3	B	Sub
HGA-12-31	Wd	2145	-19.9	15.5	3.1	B	U
HGA-12-31	Wd	2145	-21.3	17.7	3.4	S	U
HGA-12-32	Cr		-23.6	8.6	3.3	B	Sub
HGA-12-33	Lp	75	-22.7	15.6	3.4	B	Sub
HGA-12-34	Wd	794	-19.7	16.9	3.2	B	U
HGA-12-35	Cr	1347	-23.7	9.9	3.4	B	U
HGA-12-36	Wd	920	-23.0	17.0	3.2	B	U
HGA-12-37	Unknown		-22.4	7.8	3.2	B	Sub
HGA-12-38	Wd	645	-21.0	16.5	3.3	B	U
HGA-12-39	Cr		-23.5	10.1	3.0	B	Sub
HGA-12-40	Cr		-24.7	8.4	3.3	B	Sub
HGA-12-41	Wd	1033	-20.0	17.1	3.2	B	U
HGA-12-42	Cr	162	-23.0	9.5	3.2	B	Sub
HGA-12-43	Cr		-23.4	8.7	3.4	B	Sub
HGA-12-44	Cr	2319	-22.1	7.2	3.2	B	U
HGA-12-45	Lp	278	-22.5	14.6	3.5	H	Sub
HGA-12-47	Cr	225	-23.7	5.9	3.2	B	U
HGA-12-48	Cr		-21.1	10.9	3.2	B	Sub

HGA-12-49	Cr		-22.9	8.9	3.2	B	Sub
HGA-12-50	Cr	75	-22.0	10.5	3.3	B	Sub
HGA-12-51	Cr		-24.0	10.4	3.4	S	Sub
HGA-12-51	Cr		-24.7	8.4	3.5	H	Sub
HGA-12-52	Unknown		-22.7	8.6	3.2	B	Sub
HGA-12-53	Cr		-23.0	6.9	3.2	B	U
HGA-12-54	Cr		-23.3	8.7	3.3	B	Sub
HGA-12-55	Cr	167	-23.0	11.1	3.2	B	Sub
HGA-12-56	Cr	618	-22.3	7.8	3.2	B	Sub
HGA-12-57	Cr		-22.7	8.7	3.2	B	Sub
HGA-12-58	Cr	567	-23.8	8.1	3.3	B	Sub
HGA-12-59	Cr		-23.4	8.1	3.2	B	Sub
HGA-12-60	Cr	152	-23.8	9.5	3.4	B	Sub
HGA-12-61	Cr		-22.2	7.4	2.9	B	U
HGB-12-01	Cr		-23.3	7.0	3.2	B	Pup
HGB-12-02	Cr	524	-21.7	10.1	3.2	B	Sub
HGB-12-04	Cr		-23.9	6.4	3.2	B	Sub
HGB-12-05	Wd	777	-21.1	15.6	3.2	B	Pup
HGB-12-06	Cr		-23.5	8.2	3.2	B	Sub
HGB-12-08	Wd	1035	-22.9	16.5	3.4	B	U
HGB-12-09	Cr	172	-24.0	6.5	3.2	B	Ad
HGB-12-10	Cr	935	-22.5	15.5	3.2	B	U
HGB-12-11	Cr		-21.3	7.7	3.1	B	Sub
HGB-12-12	Cr		-21.8	6.2	3.2	B	Sub
HGB-12-13	Cr		-22.3	7.0	3.1	B	U
HGB-12-14	Cr		-22.5	7.5	3.3	B	U
HGB-12-15	Unknown		-21.2	9.1	3.1	B	U
HGB-12-16	Wd	609	-21.2	14.5	3.1	B	Sub
HGB-12-18	Unknown		-21.0	7.1	3.2	B	Sub
HGB-12-19	Cr	723	-24.1	11.2	3.4	B	U
HGB-12-21	Cr		-24.9	6.0	3.3	B	Sub
HGB-12-23AandB	Cr		-23.9	7.0	3.2	B	U
HGB-12-24	Cr		-23.9	6.3	3.2	B	U
HGB-12-25	Cr		-22.8	9.0	3.4	B	Sub
HGB-12-26	Cr		-23.1	8.4	3.4	B	Sub
HGB-12-29	Cr	277	-23.3	5.6	3.2	B	Sub
HGB-12-30	Cr		-23.8	8.6	3.2	B	Sub
HGB-12-31	Cr		-22.7	6.8	3.4	B	Sub
HGB-12-32	Cr		-22.9	6.0	3.2	B	U
HGB-12-33	Cr		-22.9	6.6	3.3	B	Sub
HGB-12-35	Cr		-23.8	6.1	3.2	B	Sub
HGB-12-36	Wd	444	-23.9	15.3	3.3	B	Sub
HGB-12-37	Cr		-23.6	6.6	3.2	B	Sub
HGB-12-38	Cr		-24.2	8.4	3.3	B	Sub
HGB-12-39	Cr		-23.3	8.1	3.4	B	Sub
HGB-12-40	Cr		-22.1	7.1	3.2	B	Sub
HGB-12-41	Cr		-22.9	7.3	3.2	B	Sub
HGB-12-42	Cr		-22.7	7.7	3.2	B	Sub
HGB-12-44	Wd	1073	-22.6	16.5	3.2	B	U
HGB-12-46	Cr		-23.2	8.9	3.2	B	Sub
HGB-12-47	Cr	422	-22.3	10.2	3.2	B	Sub
HGB-12-48	Lp	670	-21.1	14.2	3.2	B	Sub
HGB-12-51,52,53	Cr		-22.4	6.9	3.2	B	U

HGB-12-52	Cr		-24.0	7.1	3.2	B	U
HGC-12-01	Lp	75	-22.8	16.0	3.4	B	Sub
HGC-12-02	Cr	409	-23.7	6.9	3.2	B	Sub
HGC-12-03	Cr		-23.1	9.7	3.0	B	U
HGC-12-04	Cr	75	-22.2	9.0	3.2	B	Sub
HGC-12-04	Cr	75	-24.6	9.5	3.5	H	Sub
HGC-12-05	Cr		-23.1	8.2	3.4	H	Sub
HGC-12-06	Cr		-23.6	7.9	3.3	B	Sub
HGC-12-07	Cr		-22.8	8.9	3.2	B	Sub
HGC-12-08	Cr	75	-23.7	10.9	3.2	B	Ad
HGC-12-09	Cr		-23.4	6.6	3.2	B	Sub
HGC-12-10	Cr		-22.9	8.2	3.2	B	Sub
HGC-12-11	Wd	752	-22.7	15.5	3.3	B	Sub
HGC-12-12	Cr		-22.9	7.1	3.4	B	Sub
HGC-12-13	Cr		-24.0	6.9	3.3	B	U
HGC-12-14	Wd	399	-23.9	15.4	3.3	B	Pup
HGC-12-15	Cr		-23.8	9.0	3.3	B	Sub
HGC-12-16	Cr		-23.2	7.0	3.1	B	Sub
HGC-12-17	Lp	75	-22.4	14.5	3.2	B	U
HGC-12-18	Cr	1787	-22.6	7.9	3.3	B	U
HGC-12-20	Cr	75	-24.1	5.5	3.4	B	Sub
HGC-12-21	Cr		-23.2	6.7	3.4	B	Sub
HGC-12-22	Cr		-23.1	8.2	3.0	B	U
HGC-12-23	Cr		-24.9	9.6	3.5	H	Sub
HGC-12-24	Unknown		-22.5	6.5	3.1	B	Sub
HGC-12-25	Cr		-22.7	6.8	3.3	B	U
HGC-12-26	Cr		-23.5	8.1	3.0	B	U
HGC-12-27	Cr		-21.6	13.2	3.4	S	Sub
HGC-12-27	Cr		-22.6	10.8	3.4	H	Sub
HGC-12-28	Unknown		-22.1	6.8	2.9	B	U
HGC-12-29	Cr		-25.3	8.4	3.3	B	Sub
HGC-12-30	Cr		-23.4	5.9	3.1	B	Sub
HGC-12-31	Cr	75	-22.4	7.4	3.2	B	U
HGC-12-32	Cr		-23.3	7.7	3.2	B	Sub
HGC-12-33	Cr		-21.6	9.9	3.2	B	U
HGC-12-34	Unknown		-22.6	9.7	3.2	B	U
HGC-12-35	Cr		-23.5	8.1	3.4	B	U
HGC-12-36	Wd	588	-22.2	16.4	3.2	B	Pup
HGC-12-38	Cr		-20.0	8.6	3.2	B	Sub
HGC-12-39	Cr		-23.5	7.1	3.2	B	Sub
HGC-12-40	Cr		-23.2	7.9	3.3	B	Sub
HGC-12-41	Unknown		-23.3	7.6	3.3	B	Ad
HGC-12-42	Cr		-21.1	7.1	3.3	B	U
HGC-12-43	Cr		-22.7	6.9	3.2	B	U
HGC-12-44	Wd	2300	-20.9	15.0	3.2	B	U
HGC-12-45	Cr		-24.1	6.6	3.4	B	Sub
HGC-12-46	Wd	436	-22.6	13.7	3.2	B	Sub
HGC-12-47	Cr		-22.3	8.3	3.1	B	Sub
HGC-12-48	Cr		-23.0	5.8	3.2	B	Sub
HGC-12-49	Wd	365	-22.4	15.3	3.2	B	Sub
HGC-12-49	Wd	365	-21.7	15.1	3.1	B	Sub
HGC-12-50	Cr		-22.4	6.0	3.1	B	U
HGC-12-51	Cr		-23.1	7.8	2.9	B	U

HGC-12-52	Cr		-23.9	8.5	3.3	B	Sub
HGC-12-53	Cr		-23.6	7.4	3.2	B	Sub
S-06-01	SES	968	-19.8	15.4	3.4	B	U
S-06-02	SES	767				B	U
S-06-03	SES	521	-20.2	14.4	3.2	B	U
S-06-04	SES	1622	-18.4	13.3	3.0	B	U
S-06-06	SES	3035				B	U
S-06-07	SES	521	-16.7	13.8	3.2	B	U
S-06-08	SES	3187	-21.8	16.1	3.4	B	U
S-06-09	SES	1070	-19.4	15.4	3.1	B	U
S-06-10	SES	416	-19.0	16.6	3.1	B	U
S-06-11	SES	756				B	U
S-06-12	SES	493	-18.1	14.2	3.2	B	U
S-06-13A	SES	513	-21.5	16.5	3.4	B	U
S-06-14	SES	506	-19.5	15.6	3.2	B	U
S-06-15	SES	647	-17.4	14.5	3.2	B	U
S-06-17	SES	1632				B	U
S-06-18	SES	2038	-20.0	14.8	3.2	B	U
S-06-19	SES	2997	-20.0	15.7	3.2	B	U
S-06-20	SES	1439	-16.6	14.9	3.1	B	U
S-06-21	SES	1082	-20.2	14.8	3.3	B	U
S-06-22	SES	1126	-19.7	15.9	3.2	B	U
S-06-23	SES	1854	-19.9	16.7	3.3	B	U
S-06-24	SES	245				B	U
S-06-25	SES		-19.1	15.3	3.1	B	U
S-06-31	SES	1677	-20.3	15.7	3.1	B	U
S-06-32	SES	3274				B	U
S-06-33	SES	3105				B	U
S-06-34	SES		-20.6	14.1	3.2	B	U
S-06-36	SES	1100				B	U
S-06-49	SES	3227				B	U
01-B2	SES	1126				B	U
01-B3	SES	1120				B	U
Cross	SES	4085				B	U
CRS-1	SES	773				B	U
CRS-5	SES	2568				B	U
CRS-7	SES	4945				B	U
DIS-01	SES	2964				B	U
00-54	SES	2162				B	U
MCZ-49641	SES	5088				B	U
II-06-03	SES		-22.7	13.5	3.4	B	U

Table 3.S4. Nitrogen isotope values of amino acids for subfossil specimens of crabeater, Weddell, and southern southern elephant seals. Values of $\delta^{15}N$ are reported for the following amino acids: alanine (Ala), glycine (Gly), serine (Ser), valine (Val), leucine (Leu), isoleucine (Ile), proline (Pro), aspartic acid + asparagine (Asp), glutamic acid + glutamine (Glu), phenylalanine (Phe), lysine (Lys), and threonine (Thr).

Species	Sample ID	Mean $\delta^{15}N$ (‰)	SD $\delta^{15}N$ (‰)	Injections	Amino Acid
Crabeater	ECC-12-17	22.8	0.2	3	Ala
	ECC-12-17	12.5	0	3	Gly
	ECC-12-17	17.3	0.4	3	Ser
	ECC-12-17	23.6	0.3	3	Val
	ECC-12-17	24.1	0.2	3	Leu
	ECC-12-17	24.6	0.8	3	Ile
	ECC-12-17	24.7	0.1	3	Pro
	ECC-12-17	21.7	0.3	3	Asp
	ECC-12-17	24.5	0.2	3	Glu
	ECC-12-17	5.8	0.3	3	Phe
	ECC-12-17	7.2	0.2	3	Lys
	ECC-12-17	-28	0.2	3	Thr
	HGA-12-35	18.7	0.1	3	Ala
	HGA-12-35	4.4	0.1	3	Gly
	HGA-12-35	7.9	0.1	3	Ser
	HGA-12-35	17.7	0.2	3	Val
	HGA-12-35	17.4	0.1	3	Leu
	HGA-12-35	16.7	0.1	3	Ile
	HGA-12-35	17.9	0.1	3	Pro
	HGA-12-35	14.1	0.1	3	Asp
	HGA-12-35	19	0.1	3	Glu
	HGA-12-35	5.3	0.5	3	Phe
	HGA-12-35	5.3	0.6	3	Lys
	HGA-12-35	-26.8	0.2	3	Thr
	HGA-12-56	14.8	0.2	3	Ala
	HGA-12-56	3.1	0	3	Gly
	HGA-12-56	7.3	0.6	3	Ser
	HGA-12-56	13.2	0.3	3	Val
	HGA-12-56	13.4	0.3	3	Leu
	HGA-12-56	10	0.2	3	Ile
	HGA-12-56	15.2	0.1	3	Pro
	HGA-12-56	11.9	0.7	3	Asp
	HGA-12-56	15.1	0.3	3	Glu
	HGA-12-56	4.1	0.3	3	Phe
	HGA-12-56	3.1	0.6	3	Lys
	HGA-12-56	-23.7	0.4	3	Thr
	LBB-13-01	13.5	0.2	4	Ala
	LBB-13-01	4.7	0.1	4	Gly
	LBB-13-01	8.6	0.4	4	Ser
	LBB-13-01	18.3	0.7	4	Val
	LBB-13-01	13.2	0.4	4	Leu
	LBB-13-01	7.9	0.3	4	Ile
	LBB-13-01	16.4	0.1	4	Pro
	LBB-13-01	12.3	0.2	4	Asp
	LBB-13-01	15.4	0.2	4	Glu

LBB-13-01	5.1	0.6	4	Phe
LBB-13-01	4.8	0.7	4	Lys
LBB-13-01	-22.7	0.3	4	Thr
LBB-13-23	15.4	0.2	3	Ala
LBB-13-23	4.2	0.1	3	Gly
LBB-13-23	8.9	0.5	3	Ser
LBB-13-23	16	1.2	3	Val
LBB-13-23	15.1	0	3	Leu
LBB-13-23	14.8	0.1	3	Ile
LBB-13-23	17.1	0	3	Pro
LBB-13-23	13.5	0.1	3	Asp
LBB-13-23	16.4	0.2	3	Glu
LBB-13-23	4.9	0.1	3	Phe
LBB-13-23	5.5	0.5	3	Lys
LBB-13-23	-26.8	0.8	3	Thr
LBB-13-29B	14	0.1	3	Ala
LBB-13-29B	2.7	0.2	3	Gly
LBB-13-29B	8	0.5	3	Ser
LBB-13-29B	15.3	0.2	3	Val
LBB-13-29B	13.6	0.4	3	Leu
LBB-13-29B	14.1	0.3	3	Ile
LBB-13-29B	15.3	0.2	3	Pro
LBB-13-29B	11.7	0.1	3	Asp
LBB-13-29B	15.2	0.1	3	Glu
LBB-13-29B	6.7	0.8	3	Phe
LBB-13-29B	5.4	0.2	3	Lys
LBB-13-29B	-14.8	0.6	3	Thr
LBC-13-17	13.8	0.3	3	Ala
LBC-13-17	3.2	0.2	3	Gly
LBC-13-17	6.6	0.7	3	Ser
LBC-13-17	12	0.7	3	Val
LBC-13-17	12.5	0.6	3	Leu
LBC-13-17	9.5	0.8	3	Ile
LBC-13-17	15.3	0.1	3	Pro
LBC-13-17	12	0.3	3	Asp
LBC-13-17	15.1	0.3	3	Glu
LBC-13-17	4.1	0.2	3	Phe
LBC-13-17	3.5	0.1	3	Lys
LBC-13-17	-22.6	0.2	3	Thr
LBC-13-24	23.2	0.1	3	Ala
LBC-13-24	13	0.3	3	Gly
LBC-13-24	17.6	0.1	3	Ser
LBC-13-24	23.7	0.3	3	Val
LBC-13-24	23.5	0.3	3	Leu
LBC-13-24	23.1	0.7	3	Ile
LBC-13-24	25.1	0.1	3	Pro
LBC-13-24	21.6	0.3	3	Asp
LBC-13-24	24.8	0	3	Glu
LBC-13-24	7.4	0.3	3	Phe
LBC-13-24	8	0.3	3	Lys
LBC-13-24	-26.7	0.6	3	Thr
LBC-13-52	14.2	0.1	3	Ala
LBC-13-52	0.9	0	3	Gly

	LBC-13-52	4.2	0.5	3	Ser
	LBC-13-52	12.8	0.6	3	Val
	LBC-13-52	11.4	0.3	3	Leu
	LBC-13-52	11.1	0.6	3	Ile
	LBC-13-52	13.7	0.1	3	Pro
	LBC-13-52	10.9	0.3	3	Asp
	LBC-13-52	14.4	0.1	3	Glu
	LBC-13-52	4	0.4	3	Phe
	LBC-13-52	3.9	0.7	3	Lys
	LBC-13-52	-20.4	0.5	3	Thr
	MVA-13-05	22.9	0.6	3	Ala
	MVA-13-05	9.9	0.4	3	Gly
	MVA-13-05	12.4	0.9	3	Ser
	MVA-13-05	22.9	0.6	3	Val
	MVA-13-05	22.5	0.2	3	Leu
	MVA-13-05	20.9	0.4	3	Ile
	MVA-13-05	23.1	0.2	3	Pro
	MVA-13-05	19.7	0.2	3	Asp
	MVA-13-05	24.2	0.2	3	Glu
	MVA-13-05	7	0.2	3	Phe
	MVA-13-05	6.8	0.2	2	Lys
	MVA-13-05	-28	0.8	3	Thr
	MVA-13-24	21.5	0.2	3	Ala
	MVA-13-24	8.6	0.2	3	Gly
	MVA-13-24	15.6	0.6	3	Ser
	MVA-13-24	22.4	0	3	Val
	MVA-13-24	22	0.4	3	Leu
	MVA-13-24	21.1	0.6	3	Ile
	MVA-13-24	22.8	0.1	3	Pro
	MVA-13-24	18.9	0.1	3	Asp
	MVA-13-24	23.1	0.3	3	Glu
	MVA-13-24	7.1	0.3	3	Phe
	MVA-13-24	7.1	0.2	3	Lys
	MVA-13-24	-28.7	0.8	3	Thr
	MVA-13-34	23	0.2	3	Ala
	MVA-13-34	10.5	0.1	3	Gly
	MVA-13-34	14.9	0.2	3	Ser
	MVA-13-34	21.9	0.2	3	Val
	MVA-13-34	22.3	0.1	3	Leu
	MVA-13-34	22.1	0.4	3	Ile
	MVA-13-34	23.6	0.1	3	Pro
	MVA-13-34	19.7	0.1	3	Asp
	MVA-13-34	23.4	0.2	3	Glu
	MVA-13-34	6.8	0.2	3	Phe
	MVA-13-34	6.8	0.2	3	Lys
	MVA-13-34	-27	0.7	3	Thr
Weddell	ECB-12-12	22.5	0.5	3	Ala
	ECB-12-12	11	0.1	3	Gly
	ECB-12-12	16.2	0.9	3	Ser
	ECB-12-12	27.7	0.8	3	Val
	ECB-12-12	20.9	0.7	3	Leu
	ECB-12-12	19.7	0.9	3	Ile
	ECB-12-12	23.5	0.1	3	Pro

ECB-12-12	20.2	0.2	3	Asp
ECB-12-12	23	0.4	3	Glu
ECB-12-12	6	0.4	3	Phe
ECB-12-12	5.7	0.2	3	Lys
ECB-12-12	-27.8	0.5	3	Thr
ECB-12-59	25.9	0	3	Ala
ECB-12-59	16	0.2	3	Gly
ECB-12-59	19.4	0.4	3	Ser
ECB-12-59	25.6	0.4	3	Val
ECB-12-59	26	0.2	3	Leu
ECB-12-59	25.4	0.8	3	Ile
ECB-12-59	26.6	0	3	Pro
ECB-12-59	23.5	0	3	Asp
ECB-12-59	27.5	0.4	3	Glu
ECB-12-59	9.2	0	3	Phe
ECB-12-59	9.1	0.6	3	Lys
ECB-12-59	-27.2	0.1	4	Thr
HGB-12-08	23.9	0	4	Ala
HGB-12-08	15.4	0.1	4	Gly
HGB-12-08	17	0.7	4	Ser
HGB-12-08	21.5	0.9	4	Val
HGB-12-08	22.8	0.3	4	Leu
HGB-12-08	22.2	0.9	4	Ile
HGB-12-08	24.2	0.1	4	Pro
HGB-12-08	20.7	0.1	4	Asp
HGB-12-08	24	0.1	4	Glu
HGB-12-08	9.4	0.6	4	Phe
HGB-12-08	9.1	0.5	4	Lys
HGB-12-08	-23.1	0.7	4	Thr
LBA-13-27	22.8	0.4	3	Ala
LBA-13-27	13.6	0.2	3	Gly
LBA-13-27	17.3	0.9	3	Ser
LBA-13-27	21.6	0.8	3	Val
LBA-13-27	22.4	0.7	3	Leu
LBA-13-27	20.4	0.6	3	Ile
LBA-13-27	24.9	0.2	3	Pro
LBA-13-27	22	0.2	3	Asp
LBA-13-27	24	0.6	3	Glu
LBA-13-27	8.2	0.6	3	Phe
LBA-13-27	7.4	0.1	3	Lys
LBA-13-27	-28.8	0.5	3	Thr
LBA-13-30	24.7	0.1	4	Ala
LBA-13-30	10.2	0.2	4	Gly
LBA-13-30	14.6	0.7	4	Ser
LBA-13-30	25.5	0.5	4	Val
LBA-13-30	24.7	0.3	4	Leu
LBA-13-30	23.5	0.7	4	Ile
LBA-13-30	24.1	0.1	4	Pro
LBA-13-30	21.6	0.4	4	Asp
LBA-13-30	25.6	0.2	4	Glu
LBA-13-30	9.6	0.5	4	Phe
LBA-13-30	8.4	0.2	3	Lys
LBA-13-30	-28.7	0.5	3	Thr

LBB-13-12	23.5	0.2	3	Ala
LBB-13-12	10.9	0.1	3	Gly
LBB-13-12	13.9	1	3	Ser
LBB-13-12	23	0.8	3	Val
LBB-13-12	24.1	0.3	3	Leu
LBB-13-12	23.5	0.6	3	Ile
LBB-13-12	23.7	0.3	3	Pro
LBB-13-12	21	0.4	3	Asp
LBB-13-12	24.8	0.3	3	Glu
LBB-13-12	9	0.3	3	Phe
LBB-13-12	9.3	0.6	3	Lys
LBB-13-12	-22.2	0.6	3	Thr
LBB-13-59	23.9	0.1	3	Ala
LBB-13-59	13.3	0.1	3	Gly
LBB-13-59	18.5	0.4	3	Ser
LBB-13-59	23	0.7	3	Val
LBB-13-59	24.6	0.5	3	Leu
LBB-13-59	23.8	0.3	3	Ile
LBB-13-59	25	0.1	3	Pro
LBB-13-59	22.7	0.1	3	Asp
LBB-13-59	25.6	0.3	3	Glu
LBB-13-59	10	0.2	3	Phe
LBB-13-59	9.5	0.3	3	Lys
LBB-13-59	-27.8	0.8	3	Thr
LBC-13-11F	24.2	0.2	3	Ala
LBC-13-11F	13.4	0.1	3	Gly
LBC-13-11F	14.3	0.9	3	Ser
LBC-13-11F	24	0	3	Val
LBC-13-11F	24.6	0.3	3	Leu
LBC-13-11F	24.4	0.1	3	Ile
LBC-13-11F	26.7	0.2	3	Pro
LBC-13-11F	22.5	0.1	3	Asp
LBC-13-11F	25.6	0.2	3	Glu
LBC-13-11F	8.2	0.6	3	Phe
LBC-13-11F	8.4	0.3	3	Lys
LBC-13-11F	-28.7	1	3	Thr
LBC-13-11G	24.1	0.2	3	Ala
LBC-13-11G	12.8	0.1	3	Gly
LBC-13-11G	18.1	0.6	3	Ser
LBC-13-11G	22.9	0.6	3	Val
LBC-13-11G	24.1	0.4	3	Leu
LBC-13-11G	23.5	0.4	3	Ile
LBC-13-11G	27	0.1	3	Pro
LBC-13-11G	22.9	0	3	Asp
LBC-13-11G	26.1	0.3	3	Glu
LBC-13-11G	9.6	0.3	3	Phe
LBC-13-11G	8.9	0.3	3	Lys
LBC-13-11G	-26.6	0.5	3	Thr
LBC-13-15	22	0.3	3	Ala
LBC-13-15	14.6	0.3	3	Gly
LBC-13-15	15.7	0.1	3	Ser
LBC-13-15	23.6	0.5	3	Val
LBC-13-15	23.1	0.4	3	Leu

LBC-13-15	20.3	0.1	3	Ile
LBC-13-15	24.7	0.4	3	Pro
LBC-13-15	21.1	0.7	3	Asp
LBC-13-15	24.1	0.1	3	Glu
LBC-13-15	7.6	0.1	3	Phe
LBC-13-15	7.5	0.9	3	Lys
LBC-13-15	-28.4	0.9	2	Thr
LBC-13-21	22.1	0.3	5	Ala
LBC-13-21	11.2	0.2	5	Gly
LBC-13-21	14	0.1	5	Ser
LBC-13-21	21.7	0.5	5	Val
LBC-13-21	23.1	0.1	5	Leu
LBC-13-21	21.4	0.8	5	Ile
LBC-13-21	22.1	0.2	5	Pro
LBC-13-21	20.2	0.4	5	Asp
LBC-13-21	23.2	0.3	5	Glu
LBC-13-21	5.1	0.5	5	Phe
LBC-13-21	5.8	0.3	5	Lys
LBC-13-21	-28	0.8	5	Thr
LBC-13-29	23.3	0.4	3	Ala
LBC-13-29	12.5	0.2	3	Gly
LBC-13-29	14.5	0.5	3	Ser
LBC-13-29	23.3	0.5	3	Val
LBC-13-29	23.4	0.3	3	Leu
LBC-13-29	23.3	0.8	3	Ile
LBC-13-29	23.1	0.1	3	Pro
LBC-13-29	21.3	0.1	3	Asp
LBC-13-29	24.6	0.1	3	Glu
LBC-13-29	9.1	0.1	3	Phe
LBC-13-29	9.2	0	3	Lys
LBC-13-29	-27.4	0.7	3	Thr
LBC-13-32	21.8	0.2	3	Ala
LBC-13-32	11.6	0.2	3	Gly
LBC-13-32	18.4	0.8	3	Ser
LBC-13-32	21.6	0.4	3	Val
LBC-13-32	22.2	0.6	3	Leu
LBC-13-32	19.1	0.9	3	Ile
LBC-13-32	23.1	0	3	Pro
LBC-13-32	20.7	0.3	3	Asp
LBC-13-32	24.2	0.3	3	Glu
LBC-13-32	6.2	0.4	3	Phe
LBC-13-32	6.2	0.6	2	Lys
LBC-13-32	-26.1	0.9	3	Thr
LBC-13-44	22.9	0.1	3	Ala
LBC-13-44	10.9	0.2	3	Gly
LBC-13-44	16.6	0.3	3	Ser
LBC-13-44	24	0.3	3	Val
LBC-13-44	24.4	0.3	3	Leu
LBC-13-44	25.1	0.6	3	Ile
LBC-13-44	23.4	0.1	3	Pro
LBC-13-44	21.6	0.1	3	Asp
LBC-13-44	24.5	0.4	3	Glu
LBC-13-44	7.4	0.2	3	Phe

LBC-13-44	7.9	0.5	3	Lys
LBC-13-44	-27.1	0.4	3	Thr
MVA-13-03 Affil	24	0.1	3	Ala
MVA-13-03 Affil	12.5	0.1	3	Gly
MVA-13-03 Affil	15.1	0.4	3	Ser
MVA-13-03 Affil	22.3	0.5	3	Val
MVA-13-03 Affil	24.9	0.1	3	Leu
MVA-13-03 Affil	24.3	0.8	3	Ile
MVA-13-03 Affil	25.5	0.1	3	Pro
MVA-13-03 Affil	22.9	0.3	3	Asp
MVA-13-03 Affil	25.8	0.3	3	Glu
MVA-13-03 Affil	8.1	0.2	3	Phe
MVA-13-03 Affil	8.5	0.2	3	Lys
MVA-13-03 Affil	-21.9	0.6	3	Thr
MVA-13-06	22.5	0.2	3	Ala
MVA-13-06	9.9	0.2	3	Gly
MVA-13-06	15.1	0.9	3	Ser
MVA-13-06	20.6	0.8	3	Val
MVA-13-06	22.5	0.7	3	Leu
MVA-13-06	21.9	0.4	3	Ile
MVA-13-06	22.3	0.2	3	Pro
MVA-13-06	19.6	0.4	3	Asp
MVA-13-06	23.9	0.3	3	Glu
MVA-13-06	6.8	0.9	3	Phe
MVA-13-06	7.3	1	3	Lys
MVA-13-06	-24	0.8	5	Thr
MVA-13-10	23.9	0.3	3	Ala
MVA-13-10	13.2	0.2	3	Gly
MVA-13-10	14.5	0.5	3	Ser
MVA-13-10	23.8	0.1	3	Val
MVA-13-10	24.9	0.2	3	Leu
MVA-13-10	24.1	0	3	Ile
MVA-13-10	25.4	0.3	3	Pro
MVA-13-10	23.3	0.3	3	Asp
MVA-13-10	26.2	0.3	3	Glu
MVA-13-10	7.6	0.3	3	Phe
MVA-13-10	8.4	0.1	3	Lys
MVA-13-10	-21.7	0.7	3	Thr
MVA-13-40	22.9	0.2	3	Ala
MVA-13-40	13.4	0.1	3	Gly
MVA-13-40	16.6	0.1	3	Ser
MVA-13-40	22.5	0.1	3	Val
MVA-13-40	22.8	0.4	3	Leu
MVA-13-40	21.7	0.5	3	Ile
MVA-13-40	24.6	0.1	3	Pro
MVA-13-40	21.7	0.2	3	Asp
MVA-13-40	24.1	0.2	3	Glu
MVA-13-40	9	0.2	3	Phe
MVA-13-40	9.7	0.2	2	Lys
MVA-13-40	-26.8	0.2	3	Thr
MVC-13-06	23.6	0.1	6	Ala
MVC-13-06	13.9	0.1	6	Gly
MVC-13-06	14.9	0.6	6	Ser

	MVC-13-06	22.9	1	6	Val
	MVC-13-06	23.2	0.3	6	Leu
	MVC-13-06	22.5	0.8	6	Ile
	MVC-13-06	25.9	0.1	6	Pro
	MVC-13-06	21.6	0.4	6	Asp
	MVC-13-06	24.3	0.2	6	Glu
	MVC-13-06	10.2	0.4	6	Phe
	MVC-13-06	9.8	0.3	6	Lys
	MVC-13-06	-25.6	0.8	6	Thr
	MVC-13-14	22.4	0.4	3	Ala
	MVC-13-14	10.8	0.6	3	Gly
	MVC-13-14	12.9	0.4	3	Ser
	MVC-13-14	21.5	0.4	3	Val
	MVC-13-14	22.4	0.3	3	Leu
	MVC-13-14	22.7	0.8	3	Ile
	MVC-13-14	23.9	0.3	3	Pro
	MVC-13-14	20.9	0.3	3	Asp
	MVC-13-14	23.7	0	3	Glu
	MVC-13-14	8.1	0.1	3	Phe
	MVC-13-14	8	0.4	3	Lys
	MVC-13-14	-26.7	0.8	3	Thr
	MVC-13-27	22.8	0.2	4	Ala
	MVC-13-27	15.3	0.2	4	Gly
	MVC-13-27	15.6	0.2	4	Ser
	MVC-13-27	23.5	0.4	4	Val
	MVC-13-27	22.5	0.3	4	Leu
	MVC-13-27	21.4	0.7	4	Ile
	MVC-13-27	25.4	0.3	4	Pro
	MVC-13-27	21.1	0.3	4	Asp
	MVC-13-27	24.1	0.2	4	Glu
	MVC-13-27	8.4	0.5	4	Phe
	MVC-13-27	9.7	0.6	4	Lys
	MVC-13-27	-26.2	0.8	4	Thr
	MVC-13-39	22.8	0.2	3	Ala
	MVC-13-39	11.2	0.1	3	Gly
	MVC-13-39	16.5	0.3	3	Ser
	MVC-13-39	23.6	0.5	3	Val
	MVC-13-39	23	0.1	3	Leu
	MVC-13-39	22.5	0.7	3	Ile
	MVC-13-39	23.9	0.1	3	Pro
	MVC-13-39	21.1	0.1	3	Asp
	MVC-13-39	24.1	0	3	Glu
	MVC-13-39	7	0.2	3	Phe
	MVC-13-39	7.6	0.1	3	Lys
	MVC-13-39	-27.2	0.4	3	Thr
Southern elephant	S-06-01	25.7	0.4	3	Ala
	S-06-01	7.5	0.1	3	Gly
	S-06-01	13.6	0.4	3	Ser
	S-06-01	25	0.7	3	Val
	S-06-01	25.7	0.4	3	Leu
	S-06-01	23.7	0.6	3	Ile
	S-06-01	25.4	0.2	3	Pro
	S-06-01	21.6	0.2	3	Asp

S-06-01	26.4	0.2	3	Glu
S-06-01	6.7	0.6	3	Phe
S-06-01	6.5	0.7	2	Lys
S-06-01	-35.4	0.7	3	Thr
S-06-04	24.4	0.1	3	Ala
S-06-04	8.5	0.1	3	Gly
S-06-04	9.3	0.6	3	Ser
S-06-04	25.3	0.2	3	Val
S-06-04	22.6	0.4	3	Leu
S-06-04	22.6	0.7	3	Ile
S-06-04	23.8	0.1	3	Pro
S-06-04	18.8	0.3	3	Asp
S-06-04	24.3	0.2	3	Glu
S-06-04	4.7	0.2	3	Phe
S-06-04	6	0.5	3	Lys
S-06-04	-32.7	0.8	3	Thr
S-06-08	22	0.4	3	Ala
S-06-08	8.4	0.2	3	Gly
S-06-08	12.3	0.5	3	Ser
S-06-08	22.3	0.8	3	Val
S-06-08	23.9	0.9	3	Leu
S-06-08	24.2	0.8	3	Ile
S-06-08	27.7	0.2	3	Pro
S-06-08	22.6	0	3	Asp
S-06-08	26	0.1	3	Glu
S-06-08	9.1	0.6	3	Phe
S-06-08	8.1	0.4	3	Lys
S-06-08	-37.3	0.6	3	Thr
S-06-09	25.3	0.1	3	Ala
S-06-09	9.9	0.1	3	Gly
S-06-09	12.3	0.2	3	Ser
S-06-09	22.5	0.1	2	Val
S-06-09	23.8	0.6	3	Leu
S-06-09	23.7	0.2	3	Ile
S-06-09	25.5	0.1	3	Pro
S-06-09	20.7	0.3	3	Asp
S-06-09	25	0.2	3	Glu
S-06-09	7	0.5	3	Phe
S-06-09	5.7	0.2	3	Lys
S-06-09	-33.5	0.8	3	Thr
S-06-12	22.3	0.1	3	Ala
S-06-12	8.1	0.2	3	Gly
S-06-12	12.6	0.8	3	Ser
S-06-12	21.9	0.4	3	Val
S-06-12	22.8	0.6	3	Leu
S-06-12	23.2	0.8	3	Ile
S-06-12	24.1	0.1	3	Pro
S-06-12	20.1	0.3	3	Asp
S-06-12	23.7	0.6	3	Glu
S-06-12	4.8	0.1	3	Phe
S-06-12	5.1	0.4	3	Lys
S-06-12	-34.3	0.7	3	Thr
S-06-13A	26.8	0	3	Ala

S-06-13A	9.9	0.2	3	Gly
S-06-13A	14.9	0.8	3	Ser
S-06-13A	25.5	0.2	3	Val
S-06-13A	27.1	0.4	3	Leu
S-06-13A	28.2	0.6	3	Ile
S-06-13A	28.8	0.1	3	Pro
S-06-13A	22.8	0.3	3	Asp
S-06-13A	28.6	0.2	3	Glu
S-06-13A	8	0.4	3	Phe
S-06-13A	7.9	0.2	3	Lys
S-06-13A	-34.3	1	3	Thr
S-06-15	24.2	0.2	3	Ala
S-06-15	10.6	0.2	3	Gly
S-06-15	11.3	1	3	Ser
S-06-15	21.5	0.4	3	Val
S-06-15	22.7	0.5	3	Leu
S-06-15	20.8	0.5	3	Ile
S-06-15	25.7	0.1	3	Pro
S-06-15	19.6	0.2	3	Asp
S-06-15	24.6	0.3	3	Glu
S-06-15	6	0.9	3	Phe
S-06-15	6.4	0.4	2	Lys
S-06-15	-31.5	0.7	3	Thr
S-06-18	24.1	0.3	3	Ala
S-06-18	6.9	0	3	Gly
S-06-18	13.1	1.2	3	Ser
S-06-18	28.8	0.4	2	Val
S-06-18	26	0.1	3	Leu
S-06-18	25.5	0.2	3	Ile
S-06-18	26.7	0.2	3	Pro
S-06-18	21.8	0.2	3	Asp
S-06-18	26.8	0.1	3	Glu
S-06-18	7.6	0.3	3	Phe
S-06-18	8.2	0.6	2	Lys
S-06-18	-31.6	0.9	3	Thr
S-06-19	26.3	0.2	4	Ala
S-06-19	7.5	0.1	4	Gly
S-06-19	15.9	0.9	4	Ser
S-06-19	25.7	1.2	4	Val
S-06-19	26.6	1	4	Leu
S-06-19	26.6	1.3	4	Ile
S-06-19	27	0.2	4	Pro
S-06-19	22.8	0.4	4	Asp
S-06-19	28.1	0.4	4	Glu
S-06-19	8.9	0.6	4	Phe
S-06-19	7.8	0.2	4	Lys
S-06-19	-35.5	0.6	4	Thr
S-06-21	24.8	0.2	4	Ala
S-06-21	7.2	0.2	4	Gly
S-06-21	12.2	0.8	4	Ser
S-06-21	23.4	0.2	3	Val
S-06-21	26	0.2	4	Leu
S-06-21	26.4	1	4	Ile

	S-06-21	25.8	0.2	4	Pro
	S-06-21	21	0.3	4	Asp
	S-06-21	26.4	0.2	4	Glu
	S-06-21	7.2	0.3	4	Phe
	S-06-21	6.8	0.3	4	Lys
	S-06-21	-33.2	0.8	4	Thr
	S-06-23	27.1	0.4	3	Ala
	S-06-23	10.4	0.1	3	Gly
	S-06-23	14.1	0.5	3	Ser
	S-06-23	24.8	0.9	3	Val
	S-06-23	26.9	0.8	3	Leu
	S-06-23	27	0.6	3	Ile
	S-06-23	29.3	0.1	3	Pro
	S-06-23	23.2	0.4	3	Asp
	S-06-23	28.6	0.8	3	Glu
	S-06-23	8.8	0.6	3	Phe
	S-06-23	8.3	0.4	3	Lys
	S-06-23	-33.8	0.9	3	Thr

Table 3.S5. Carbon isotope values of amino acids for subfossil specimens of crabeater, Weddell, and southern southern elephant seals. Values of $\delta^{13}C$ are reported for the following amino acids: alanine (Ala), glycine (Gly), serine (Ser), valine (Val), leucine (Leu), isoleucine (Ile), proline (Pro), aspartic acid + asparagine (Asp), glutamic acid + glutamine (Glu), phenylalanine (Phe), lysine (Lys), and threonine (Thr).

Species	Sample ID	Mean $\delta^{13}C$ (‰)	SD $\delta^{13}C$ (‰)	Injections	Amino Acid
Crabeater	HGA-12-56	-24.7	0.4	3	Ala
	HGA-12-56	-10.0	0.1	3	Gly
	HGA-12-56	-7.5	0.2	3	Ser
	HGA-12-56	-30.1	0.4	3	Val
	HGA-12-56	-34.7	0.4	3	Leu
	HGA-12-56	-22.1	0.4	3	Ile
	HGA-12-56	-22.1	0.3	3	Pro
	HGA-12-56	-21.1	0.1	3	Asp
	HGA-12-56	-27.2	0.5	3	Glu
	HGA-12-56	-27.5	0.6	3	Phe
	HGA-12-56	-14.6	0.5	3	Lys
	HGA-12-56	-11.7	0.8	3	Thr
	LBB-13-01	-28.8	0.2	3	Ala
	LBB-13-01	-16.5	0.3	3	Gly
	LBB-13-01	-12.8	0.7	3	Ser
	LBB-13-01	-32.2	0.6	3	Val
	LBB-13-01	-35.6	0.6	3	Leu
	LBB-13-01	-20.6	0.3	3	Ile
	LBB-13-01	-22.1	0.6	3	Pro
	LBB-13-01	-23.6	0.3	3	Asp
	LBB-13-01	-29.7	0.3	3	Glu
	LBB-13-01	-28.4	0.6	3	Phe
	LBB-13-01	-20.2	0.5	3	Lys
	LBB-13-01	-11.2	0.5	3	Thr
	LBC-13-24	-28.4	0.4	3	Ala
	LBC-13-24	-12.9	0.6	3	Gly
	LBC-13-24	-8.9	0.5	3	Ser
	LBC-13-24	-26.4	0.5	3	Val
	LBC-13-24	-29.9	0.1	3	Leu
	LBC-13-24	-15.3	0.2	3	Ile
	LBC-13-24	-20.9	0.6	3	Pro
	LBC-13-24	-21.3	0.5	3	Asp
	LBC-13-24	0.6	-25.2	3	Glu
	LBC-13-24	0.2	-28.8	3	Phe
	LBC-13-24	-16.9	0.9	3	Lys
	LBC-13-24	-7.6	0.6	3	Thr
	MVA-13-24	-22.7	0.5	3	Ala
	MVA-13-24	-9.7	0.4	3	Gly
	MVA-13-24	-4.9	0.6	3	Ser
	MVA-13-24	-26.7	0.7	3	Val
	MVA-13-24	-34.0	0.4	3	Leu
	MVA-13-24	-19.7	0.6	3	Ile
	MVA-13-24	-18.4	0.3	3	Pro
	MVA-13-24	-20.5	0.3	3	Asp
	MVA-13-24	-24.4	0.1	3	Glu

	MVA-13-24	-29.4	0.3	3	Phe
	MVA-13-24	-17.6	0.2	3	Lys
	MVA-13-24	-8.8	0.1	3	Thr
Weddell	LBB-13-59	-23.2	0.1	3	Ala
	LBB-13-59	-11.3	0.0	3	Gly
	LBB-13-59	-9.6	0.7	3	Ser
	LBB-13-59	-25.4	0.3	3	Val
	LBB-13-59	-30.4	0.8	3	Leu
	LBB-13-59	-17.7	0.2	3	Ile
	LBB-13-59	-18.7	0.1	3	Pro
	LBB-13-59	-22.2	0.6	3	Asp
	LBB-13-59	-20.5	0.0	3	Glu
	LBB-13-59	-30.4	0.4	3	Phe
	LBB-13-59	-15.9	–	1	Lys
	LBB-13-59	-3.3	0.3	3	Thr
	MVC-13-06	-27.7	0.8	3	Ala
	MVC-13-06	-11.9	0.6	3	Gly
	MVC-13-06	-7.5	0.4	3	Ser
	MVC-13-06	-27.9	0.5	3	Val
	MVC-13-06	-31.7	0.9	3	Leu
	MVC-13-06	-18.0	0.6	3	Ile
	MVC-13-06	-20.1	0.7	3	Pro
	MVC-13-06	-23.2	0.6	3	Asp
	MVC-13-06	-20.8	0.6	3	Glu
	MVC-13-06	-30.2	0.8	3	Phe
	MVC-13-06	-18.2	0.7	3	Lys
	MVC-13-06	-10.6	0.3	3	Thr
	MVC-13-27	-26.8	0.2	3	Ala
	MVC-13-27	-10.9	0.1	3	Gly
	MVC-13-27	-5.2	0.1	3	Ser
	MVC-13-27	-24.6	0.2	3	Val
	MVC-13-27	-32.4	0.6	3	Leu
	MVC-13-27	-16.4	0.6	3	Ile
	MVC-13-27	-20.5	0.2	3	Pro
	MVC-13-27	-22.3	0.3	3	Asp
	MVC-13-27	-25.4	0.2	3	Glu
	MVC-13-27	-29.4	0.4	3	Phe
	MVC-13-27	-18.4	0.5	3	Lys
	MVC-13-27	-9.9	0.5	3	Thr
Southern elephant	S-06-04	-21.1	0.3	3	Ala
	S-06-04	-4.7	0.2	3	Gly
	S-06-04	-1.7	0.6	3	Ser
	S-06-04	-22.2	0.9	3	Val
	S-06-04	-27.4	0.6	3	Leu
	S-06-04	-15.2	0.2	3	Ile
	S-06-04	-18.0	0.3	3	Pro
	S-06-04	-16.0	0.2	3	Asp
	S-06-04	-15.9	0.0	3	Glu
	S-06-04	-25.8	0.1	3	Phe
	S-06-04	-14.2	0.6	3	Lys
	S-06-04	-6.9	0.3	3	Thr
	S-06-08	-25.1	0.3	3	Ala
	S-06-08	-6.7	0.1	3	Gly

	S-06-08	-6.4	0.3	3	Ser
	S-06-08	-26.2	0.7	3	Val
	S-06-08	-31.4	0.3	3	Leu
	S-06-08	-17.0	0.4	3	Ile
	S-06-08	-19.2	0.7	3	Pro
	S-06-08	-23.4	0.4	3	Asp
	S-06-08	-22.1	0.7	3	Glu
	S-06-08	-28.5	0.8	3	Phe
	S-06-08	-18.8	0.4	3	Lys
	S-06-08	-8.5	0.1	3	Thr
	S-06-12	-18.0	0.3	3	Ala
	S-06-12	-3.1	0.6	3	Gly
	S-06-12	-2.5	0.3	3	Ser
	S-06-12	-19.0	0.5	3	Val
	S-06-12	-25.3	0.1	3	Leu
	S-06-12	-12.3	0.7	3	Ile
	S-06-12	-13.2	0.6	3	Pro
	S-06-12	-13.5	0.3	3	Asp
	S-06-12	-14.5	0.4	3	Glu
	S-06-12	-23.8	0.6	3	Phe
	S-06-12	-13.4	0.4	3	Lys
	S-06-12	-4.9	0.4	3	Thr
	S-06-13A	-25.9	0.2	4	Ala
	S-06-13A	-10.5	0.3	4	Gly
	S-06-13A	-6.5	0.3	4	Ser
	S-06-13A	-24.1	0.3	4	Val
	S-06-13A	-30.7	0.2	4	Leu
	S-06-13A	-14.7	0.6	4	Ile
	S-06-13A	-21.6	0.3	4	Pro
	S-06-13A	-20.5	0.6	4	Asp
	S-06-13A	-27.1	0.6	4	Glu
	S-06-13A	-29.5	0.4	4	Phe
	S-06-13A	-14.0	1.0	4	Lys
	S-06-13A	-9.4	0.4	4	Thr

REFERENCES

Hall-Aspland SA, Rogers TL, Canfield RB (2005). Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. Mar Ecol Prog Ser 305:249-259

Zhao L, Castellini MA, Mau TL, Trumble SJ (2004) Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biol 27:368-373

CONCLUSIONS

This dissertation research has provided considerable information on the environmental conditions and seal ecologies of the modern West Antarctic, as well as those of this region during the early Holocene. This information is particularly valuable given the rapid climate change occurring in West Antarctica today and its considerable effects on the physical environment, biogeochemical cycles, and food webs.

In Chapter 1, I presented the first empirically derived zooplankton isoscapes for West Antarctica, which appeared to reflect biogeochemical change across the region. The isoscapes revealed an approximately 3 ‰ increase in $\delta^{15}N$ values from the Polar Front Zone/ Subantarctic Zone (PFZ/SAZ) to the Amundsen and Ross Seas, which likely resulted from less productivity and nutrient utilization in the former than the latter region. Additionally, $\delta^{13}C$ values from the PFZ/SAZ to the Ross Sea decreased by about 3 ‰, which tracked a gradient sea surface temperature (SST) with lower SST in the Ross Sea than the PFZ/SAZ. The $\delta^{15}N$ and $\delta^{13}C$ isoscapes have provided critical data for accurate assessments of food web architecture, biogeochemical cycling, and animal migration in the Southern Ocean. They have also served as an anchor for future studies examining biogeochemical change in the West Antarctic, which has been rapidly changing in response to modern climate change.

I assessed the foraging regions and trophic positions of three Antarctic seal species in modern times via bulk and amino acid isotope analyses in Chapter 2. I

provided new information on the habitat preferences of these animals. Ross seals are foraging in a pelagic-based food web separate from that of Weddell and crabeater. Weddell and crabeater seals forage within similar food webs, but the former targets productive areas within the West Antarctic, while the latter likely follows sea ice to capture krill. Importantly, I showed that the bulk $\delta^{15}N$ data inaccurately estimated the trophic position of Ross seals due to the variation in baseline $\delta^{15}N$ values in West Antarctica. The amino acid $\delta^{15}N$ analysis accounted for this variation and redefined the trophic position of Ross seals as one equivalent to that of Weddell seals, which matched well with the findings of stomach content and dive depth analysis for this species. This study highlights the importance of understanding the baseline isotope values of a consumer's habitat before using bulk isotope analysis for examining its foraging ecology.

In my final chapter, I showed how four species of Antarctic seals and their habitats responded to past climate change in the Ross sea. I found that crabeater seals had diverse diets earlier in the Holocene and only recently shifted to diets consisting almost exclusively of krill. This finding suggests that this species can be a generalist and likely has a high adaptive capacity. In contrast, my results revealed that Weddell seals have experienced insignificant variation in their diets over the last 5,000 years despite their habitat substantially changing over this time, probably becoming less productive after about 800 YBP. Thus, the Weddell seal appears to have a low adaptive capacity. Lastly, my results have showed that southern elephant seals have been able to utilize a spectrum of habitats, ranging from the productive coastal

regions of the Ross Sea to the Antarctic Convergence region, for foraging throughout the Holocene, indicating that this species may have a fairly high adaptive capacity. Given the predicated changes in the environmental conditions of the Ross Sea from global warming, Weddell seals may experience population declines as they have not been able to respond to past environmental changes. Crabeater and southern elephant seals are likely to experience neutral or positive effects from anthropogenic climate change since they are capable of being generalist and shifting their foraging region, respectively. Overall, Chapter 3 has provided important information for predicting the responses of top predators in Antarctica to climate events, such as that occurring today.

BIBLIOGRAPHY

Abram NJ, Wolff EW, Curran MA (2013) A review of sea ice proxy information from polar ice cores. Quaternary Science Reviews 79:168-83

Ainley DG, Siniff DB (2009) The importance of Antarctic toothfish as prey of Weddell seals in the Ross Sea. Antarct Sci 21:317-327

Alderkamp AC, Mills MM, van Dijken GL, Laan P, Thuróczy CE, Gerringa LJA, de Baar HJW, Payne CD, Visser RJW, Buma AGJ, Arrigo KR (2012) Iron from melting glaciers fuels phytoplankton blooms in the Amundsen Sea (Southern Ocean): Phytoplankton characteristics and productivity. Deep-Sea Res Part II Top Stud Oceanogr 71-76:32-48

Altabet MA, Francois R (1994) Sedimentary nitrogen isotopic ratio as a recorder for surface ocean nitrate utilization. Global Biogeochem Cycles 8:103-116

Altabet MA, Francois R (2001) Nitrogen isotope biogeochemistry of the Antarctic Polar Frontal Zone at 170 W. Deep Sea Res Part II 48:4247-4273

Alter SE, Meyer M, Post K, Czechowski P, Gravlund P, Gaines C, Rosenbaum HC, Kaschner K, Turvey ST, Plicht J, Shapiro B (2015) Climate impacts on transocean dispersal and habitat in gray whales from the Pleistocene to 2100. Mol Ecol 24(7):1510-1522

Ambrose SH (1990) Preparation and characterization of bone and tooth collagen for isotopic analysis. J Archaeol Sci 17:431-451

Arcalís-Planas A, Sveegaard S, Karlsson O, Harding KC, Wåhlin A, Harkonen T, Teilmann J (2015) Limited use of sea ice by the Ross seal (*Ommatophoca rossii*), in Amundsen Sea, Antarctica, using telemetry and remote sensing data. Polar Biol 38:445-461

Arim M, Naya DE (2003) Pinniped diets inferred from scats: analysis of biases in prey occurrence. Can J Zool 81:67-73

Arrigo KR, Weiss AM, Smith WO (1998) Physical forcing of phytoplankton dynamics in the southwestern Ross Sea. J Geophys Res Oceans 103:1007-1021

Arrigo KR, DiTullio GR, Dunbar RB, Robinson DH, VanWoert M, Worthen DL, Lizotte MP (2000) Phytoplankton taxonomic variability in nutrient utilization and primary production in the Ross Sea. J Geophys Res, C, Oceans 105:8827-8846

Arrigo KR, van Dijken, GL (2003) Phytoplankton dynamics within 37 Antarctic coastal polynya systems. J Geophys Res Oceans 108:3271

Arrigo KR, van Dijken GL (2004) Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. Deep Sea Res II 51:117-138

Arrigo KR, van Dijken G, Long M (2008) Coastal Southern Ocean: A strong anthropogenic CO_2 sink. Geophys Res Lett 35(21):L21602

Arrigo KR, van Dijken GL, Bushinsky S (2008) Primary production in the Southern Ocean, 1997–2006. J Geophys Res Oceans 113:C08004

Arrigo KR, van Dijken GL, Strong AL (2015) Environmental controls of marine productivity hot spots around Antarctica. J Geophys Res, C, Oceans, 120:5545-5565

Atkinson A, Siegel V, Pakhomov E, Rothery P (2004) Long-term decline in krill stock and increase in salps within the southern ocean. Nature 432:100-103

Azzali M, Leonori I, De Felice A, Russo A (2006). Spatial–temporal relationships between two euphausiid species in the Ross Sea. Chem Ecol 22:S219-S233

Bamberg A (2007) Geologic and Biologic Indicators of Climate Change in the Ross Sea, Antarctica. M.S. thesis. The University of Maine, Orono, ME

Barth A, Alvera A, Troupin C, Ouberdous M, Beckers JM (2010) A web interface for griding arbitrarily distributed in situ data based on Data-Interpolating Variational Analysis (DIVA). Adv Geosci 28:29-37

Bengtson JL, Stewart BS (1997) Diving patterns of a Ross seal (*Ommatophoca rossii*) near the eastern coast of the Antarctic Peninsula. Polar Biol 18:214-218

Bengtson JL, Laake JL, Boveng PL, Cameron MF, Hanson MB, Stewart BS (2011) Distribution, density, and abundance of pack-ice seals in the Amundsen and Ross Seas, Antarctica. Deep Sea Res Pt II 58:1261-1276

Bertler NA, Mayewski PA, Carter L (2011) Cold conditions in Antarctica during the Little Ice Age—Implications for abrupt climate change mechanisms. Earth Planet Sci Lett. 308:41-51

Bidigare RR, Fluegge A, Freeman KH, Hanson KL, Hayes JM, Hollander D, Jasper JP, King LL, Laws EA, Milder J, Millero FJ, Pancost R, Popp BN, Steinberg PA, Wakeham SG (1997) Consistent fractionation of ^{13}C in nature and in the laboratory: Growth-rate effects in some haptophyte algae. Global Biogeochem

Cycles 11:279-292

Biuw M, Boehme L, Guinet C, Hindell M, Costa D, Charrassin JB, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y (2007) Variations in behavior and condition of a Southern Ocean top predator in relation to in situ oceanographic conditions. Proc Natl Acad Sci USA104:13705-10

Bligh EG, Dyer WJ (1959) A rapid method of total lipid extraction and purification. Can J Biochem Physiol 37:911-917

Blix AS, Nordøy ES (2007) Ross seal (*Ommatophoca rossii*) annual distribution, diving behaviour, breeding and moulting, off Queen Maud Land, Antarctica. Polar Biol 30:1449-1458

Boecklen, W.J., Yarnes, C.T., Cook, B.A. and James, A.C., 2011. On the use of stable isotopes in trophic ecology. Annu Rev Ecol Evol Syst 42:411-440

Bowen GJ (2010) Isoscapes: spatial pattern in isotopic biogeochemistry. Annu Rev Earth Planet Sci 38:161-187

Box GE, Cox DR (1964) An analysis of transformations. J R Stat Soc Series B Stat Methodol 26:211-252

Bracegirdle TJ, Connolley WM, Turner J (2008) Antarctic climate change over the twenty first century. J Geophys Res Atmos 113: D03103

Bracegirdle TJ, Stephenson DB (2012) Higher precision estimates of regional polar warming by ensemble regression of climate model projections. Clim Dynam 39:2805-2821

Brault EK (2012) Evaluating Persistent Organic Pollutants (POPs) and Mercury in the West Antarctic Peninsula (WAP) Food Web, with a Focus on Antarctic Fur Seals (*Arctocephalus gazella*). MS thesis, Virginia Institute of Marine Sciences, Gloucester Point, VA

Burns JM, Trumble SJ, Castellini MA, Testa JW (1998) The diet of Weddell seals in McMurdo Sound, Antarctica as determined from scat collections and stable isotope analysis. Polar Biol 19:272-282

Burns JM, Costa DP, Fedak MA, Hindell MA, Bradshaw CJ, Gales NJ, McDonald B, Trumble SJ, Crocker DE (2004) Winter habitat use and foraging behavior of crabeater seals along the Western Antarctic Peninsula. Deep Sea Res Pt II 51:2279-2303

Burns JM, Hindell MA, Bradshaw CJA, Costa DP (2008) Fine-scale habitat selection of crabeater seals as determined by diving behavior. Deep Sea Res Pt II 55:500-514

Casaux R, Baroni A, Carlini A (1997) The diet of the Weddell seal Leptonychotes weddelli at Harmony Point, South Shetland Islands. Polar Biol 18: 371-375

Casaux R, Baroni A, Ramón A (2006) The diet of the Weddell Seal *Leptonychotes weddellii* at the Danco Coast, Antarctic Peninsula. Polar Biol 29:257-262

Casaux R, Carlini A, Corbalán A, Bertolin L, DiPrinzio CY (2009) The diet of the Weddell seal *Leptonychotes weddellii* at Laurie Island, South Orkney Islands. Polar Biol 32:833-838

Cherel Y, Hobson KA (2007) Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. Mar Ecol Prog Ser 329:281-287

Chikaraishi Y, Ogawa NO, Kashiyama Y, Takano Y, Suga H, Tomitani A, Miyashita H, Kitazato H, Ohkouchi N (2009) Determination of aquatic food-web structure based on compound-specific nitrogen isotopic composition of amino acids. Limnol Oceanogr Methods 7:740-750

Cipro CV, Bustamante P, Taniguchi S, Montone RC (2012) Persistent organic pollutants and stable isotopes in pinnipeds from King George Island, Antarctica. Mar Pollut Bull 64:2650-2655

Clarke MR, Macleod N (1982) Cephalopod remains in the stomachs of eight Weddell seals. Br Antarct Surv Bull 57:33-40

Cloern, JE, Jassby AD (2010) Patterns and scales of phytoplankton variability in estuarine–coastal ecosystems. Estuar Coasts 33:230-241

Costa DP, Hückstädt LA, Crocker DE, McDonald BI, Goebel ME, Fedak MA (2010) Approaches to studying climatic change and its role on the habitat selection of Antarctic pinnipeds. Integr Comp Biol 50:1018-1030

Croxall JP, Nicol S (2004) Management of Southern Ocean fisheries: global forces and future sustainability. Antarct Sci 16:569-584

Curtis C, Stewart BS, Karl SA (2009) Pleistocene population expansions of Antarctic seals. Mol Ecol 18:2112-21

Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest2: more models, new heuristics, and parallel computing. Nature Methods 9:772-772

Dasmahapatra KK, Hoffman JI, Amos W (2009) Pinniped phylogenetic relationships inferred using AFLP markers. Heredity 103:168-177

Davis RW, Fuiman LA, Williams TM, Collier SO, Hagey WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. Science 283:993-996

DeNiro MJ (1987) Stable isotopy and archaeology. Am Sci 75:182-191

de Baar HJ, Buma AG, Nolting RF, Cadée GC, Jacques G, Tréguer PJ (1990) On iron limitation of the Southern Ocean: experimental observations in the Weddell and Scotia Seas. Mar Ecol Prog Ser 65:105-122

de Bruyn M, Hall BL, Chauke LF, Baroni C, Koch PL, Hoelzel AR (2009) Rapid response of a marine mammal species to Holocene climate and habitat change. PLoS Genet, 5:e1000554

de Bruyn M, Pinsky ML, Hall B, Koch P, Baroni C, Hoelzel AR (2014) Rapid increase in southern elephant seal genetic diversity after a founder event. Proc R Soc Lond B Biol Sci 281:20133078

Dellinger T, Trillmich F (1988) Estimating diet composition from scat analysis in otariid seals (Otariidae): is it reliable? Can J Zool 66:1865-1870

DiFiore PJ, Sigman DM, Trull TW, Lourey MJ, Karsh K, Cane G, Ho R (2006) Nitrogen isotope constraints on subantarctic biogeochemistry. J Geophys Res Oceans 111:C08016

DiFiore PJ, Sigman DM, Dunbar RB (2009) Upper ocean nitrogen fluxes in the Polar Antarctic Zone: Constraints from the nitrogen and oxygen isotopes of nitrate. Geochem Geophys Geosyst 10:Q11016

Dobush GR, Ankney CD, Krementz DG (1985) The effect of apparatus, extraction time, and solvent type on lipid extractions of snow geese. Can J Zool 63:1917-1920

Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, Smith RC, Stammerjohn SE, Vernet M, Fraser W (2007) Marine pelagic ecosystems: the west Antarctic Peninsula. Philos Trans R Soc Lond B Biol Sci 362:67-94

Ducklow HW, Clarke A, Dickhut R, Doney SC, Geisz H, Huang K, Martinson DG, Meredith MP, Moeller HV, Montes-Hugo M, Schofield O, Stammerjohn SE, Steinberg D, Fraser W (2012) The marine system of the Western Antarctic Peninsula. In: Rogers AD, Johnston NM, Murphy EJ, Clarke A (eds) Antarctic ecosystems: an extreme environment in a changing world, Blackwell Publishing LTD, Hoboken, New Jersey, USA, p 121-159

Eder EB, Lewis MN, Campagna C, Koch PL (2010) Evidence of demersal foraging from stable isotope analysis of juvenile elephant seals from Patagonia. Mar Mamm Sci 26:430-442

Emslie SD, Patterson WP (2007) Abrupt recent shift in $\delta^{13}C$ and $\delta^{15}N$ values in Adélie penguin eggshell in Antarctica. Proc Natl Acad Sci USA.104:11666-11669

Ernest SK, Enquist BJ, Brown JH, Charnov EL, Gillooly JF, Savage VM, White EP, Smith FA, Hadly EA, Haskell JP, Lyons SK (2003) Thermodynamic and metabolic effects on the scaling of production and population energy use. Ecol Lett 6:990-995

Falkowski PG, Barber RT, Smetacek V (1998) Biogeochemical controls and feedbacks on ocean primary production. Science 281:200-206

Forcada J, Trathan PN (2009) Penguin responses to climate change in the Southern Ocean. Glob Change Biol 15:1618-1630

Fraser WR, Trivelpiece WZ, Ainley DG, Trivelpiece SG (1992) Increases in Antarctic penguin populations: reduced competition with whales or a loss of sea ice due to environmental warming? Polar Biol 11:525-531

Fry (2006) Stable isotope ecology. Springer+Business Media, LLC, New York, p 145

Fuiman L, Davis R, Williams T (2002) Behavior of midwater fishes under the Antarctic ice: observations by a predator. Mar Biol 140:815-822

Fulton TL and Strobeck C (2010) Multiple markers and multiple individuals refine true seal phylogeny and bring molecules and morphology back in line. Proc R Soc Lond B Biol Sci 277:1065-1070

Gales NJ, Burton HR (1989) The past and present status of the southern elephant seal (*Mirounga leonina* Linn.) in Greater Antarctica. Mammalia 53:35-48

Germain LR, Koch PL, Harvey J, McCarthy MD (2013) Nitrogen isotope fractionation in amino acids from harbor seals: implications for compound-specific trophic position calcuations. Mar Ecol Prog Ser 482:265-277

Gille ST (2002) Warming of the Southern Ocean since the 1950s. Science 295:1275-1277

Goericke R, Fry B (1994) Variations in marine plankton $\delta^{13}C$ with latitude, temperature, and dissolved CO_2 in the world ocean. Global Biogeochem Cycles 8:85-90

Goetz KT, Burns JM, Hückstädt LA, Shero MR, Costa DP (2017) Temporal variation in isotopic composition and diet of Weddell seals in the western Ross Sea. Deep Sea Res II 140:36-44

González-Bergonzoni I, Vidal N, Wang B, Ning D, Liu Z, Jeppesen E, Meerhoff M (2015) General validation of formalin-preserved fish samples in food web studies using stable isotopes. Methods Ecol Evol 6:307-314

Gordon LI, Codispoti LA, Jennings JC, Millero FJ, Morrison JM, Sweeney C (2000) Seasonal evolution of hydrographic properties in the Ross Sea, Antarctica, 1996–1997. Deep Sea Res II 47:3095-3117

Gouretski VV, Koltermann KP (2004) WOCE global hydrographic climatology. Berichte des Bundesamtes für Seeschifffahrt und Hydrographie Tech Rep 35:1-52

Graham BS, Koch PL, Newsome SD, McMahon KW, Aurioles D (2010) Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West JB, Bowen GJ, Dawson TE, Tu KP (eds) Isoscapes. Springer, Netherlands, p 299-318

Hall BL, Denton GH (2002) Holocene history of the Wilson Piedmont Glacier along the southern Scott Coast, Antarctica. The Holocene12:619-627

Hall BL, Hoelzel AR, Baroni C, Denton GH, Le Boeuf BJ, Overturf B, Töpf A (2006). Holocene elephant seal distribution implies warmer-than-present climate in the Ross Sea. Proc Natl Acad Sci USA 103:10213-10217

Hall BL, Henderson GM, Baroni C, Kellogg TB (2010) Constant Holocene Southern-Ocean 14 C reservoir ages and ice-shelf flow rates. Earth Planet Sci Lett 296:115-123

Hall-Aspland SA, Rogers TL, Canfield RB (2005). Stable carbon and nitrogen isotope analysis reveals seasonal variation in the diet of leopard seals. Mar Ecol Prog Ser 305:249-259

Hannides C, Popp BN, Landry MR, Graham BS (2009) Quantification of zooplankton trophic position in the North Pacific Subtropical Gyre using stable nitrogen isotopes. Limnol Oceanogr 54:50-61

Hayes, JM (2001) Fractionation of carbon and hydrogen isotopes in biosynthetic processes. Rev Mineral Geochem 43:225-277

Higgins DG, Sharp PM (1988) CLUSTAL: a package for performing multiple sequence alignment on a microcomputer Gene 73:237-244

Hoffman, R (2017) Sealing, whaling and krill fishing in the Southern Ocean: past and possible future effects on catch regulations. Polar Rec 53:88-99

Hopkins TL (1987) Midwater food web in McMurdo Sound, Ross Sea, Antarctica. Mar Biol 96:93-106

Howland MR, Corr LT, Young SM, Jones V, Jim S, Van Der Merwe NJ, Mitchell AD, Evershed RP (2003) Expression of the dietary isotope signal in the compound-specific $\delta^{13}C$ values of pig bone lipids and amino acids. Int J Osteoarchaeol 13:54-65

Hückstädt LA, Burns JM, Koch PL, McDonald BI, Crocker DE, Costa DP (2012) Diet of a specialist in a changing environment: the crabeater seal along the western Antarctic Peninsula. Mar Ecol Prog Ser 455:287-301

Hückstädt LA, Koch PL, McDonald BI, Goebel ME, Crocker DE, Costa DP (2012) Stable isotope analyses reveal individual variability in the trophic ecology of a top marine predator, the southern elephant seal. Oecologia 169:395-406

Hückstädt LA, McCarthy MD, Koch PL, Costa DP (2017) 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 284:20170927

Jacobs SS, Giulivi CF, Mele PA (2002) Freshening of the Ross Sea during the late 20th century. Science 297:386-389

Jaeger A, Connan M, Richard P, Cherel Y (2010) Use of stable isotopes to quantify seasonal changes of trophic niche and levels of population and individual specialization in seabirds. Mar Ecol Prog Ser 401:269-277

Katoh K, Misawa K, Kuma KI, Miyata T (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Res 29:4793-4799

Kattner G, Hagen W, Graeve M, Albers C (1998) Exceptional lipids and fatty acids in the pteropod Clione limacina (Gastropoda) from both polar oceans. Mar Chem 61:219-228

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28:1647-1649

Kim SZ, Ainley DG, Pennycook J, Eastman JT (2011) Short Note: Antarctic toothfish heads found along tide cracks of the McMurdo Ice Shelf. Antarct Sci 23:469-470

Klunder MB, Laan P, Middag R, De Baar HJW, Van Ooijen JC (2011) Dissolved iron in the Southern Ocean (Atlantic sector). Deep Sea Res II 58:2678-2694

Koressaar T, Remm M (2007) Enhancements and modifications of primer design program Primer3. Bioinformatics 23:1289-1291

Kurle CM, Worthy GA (2002) Stable nitrogen and carbon isotope ratios in multiple tissues of the northern fur seal Callorhinus ursinus: implications for dietary and migratory reconstructions. Mar Ecol Prog Ser 236:289-300

Kwok R, Comiso JC (2002) Southern Ocean climate and sea ice anomalies associated with the Southern Oscillation. J Clim 15:487-501

Lake S, Burton H, van den Hoff J (2003) Regional, temporal and fine-scale spatial variation in Weddell seal diet at four coastal locations in east Antarctica. Mar Ecol Prog Ser 254:293-305

Lake S, Burton H, Wotherspoon S (2006) Movements of adult female Weddell seals during the winter months. Polar Biol 29:270-279

Lannuzel D, Schoemann V, De Jong J, Pasquer B, Van der Merwe P, Masson F, Tison JL, Bowie A (2010) Distribution of dissolved iron in Antarctic sea ice: Spatial, seasonal, and inter-annual variability. J Geophys Res Biogeosci115:G03022

Larsen T, Taylor DL, Leigh MB, O'Brien DM (2009) Stable isotope fingerprinting: a novel method for identifying plant, fungal, or bacterial origins of amino acids. Ecology 90:3526-3535

Laws R (1960) The southern elephant seal (*Mirounga leonine* Linn.) at South Georgia. Norsk Hvalfangst 49:466-476

Laws RM (1977) Seals and whales of the Southern Ocean. Philos Trans R Soc Lond B Biol Sci 279:81-96

Laws RM (1985) The ecology of the Southern Ocean: The Antarctic ecosystem, based on krill, appears to be moving toward a new balance of species in its recovery from the inroads of whaling. Am Sci 73:26-40

Le Boeuf BJ, Laws RM (1994) Elephant seals: An introduction to the genus. In: Le Boeuf BJ, Laws RM (eds) Elephant Seals: Population Ecology, Behavior, and Physiology. University of California Press, Berkley, CA, p 1-26

Lee RF, Hagen W, Kattner G (2006) Lipid storage in marine zooplankton. Mar Ecol Prog Ser 307:273-306

Leventer A, Dunbar RB (1988) Recent diatom record of McMurdo Sound, Antarctica: Implications for history of sea ice extent. Paleoceanography 3:259-274

Lewis R, O'Connell TC, Lewis M, Campagna C, Hoelzel AR (2006) Sex-specific foraging strategies and resource partitioning in the southern elephant seal (Mirounga leonina). Proc R Soc Lond B Biol Sci 273:2901-2907

Loeb VA, Puglise KI, Outram DA (1997) AMLR program: salps and other macrozooplankton collected from January to March 1997. Ant J US 32:131-134

Loeb VJ, Hofmann EE, Klinck JM, Holm-Hansen O (2009) White WB. ENSO and variability of the Antarctic Peninsula pelagic marine ecosystem. Antarct Sci 21:135-148

Lorenzen ED, Nogués-Bravo D, Orlando L, Weinstock J, Binladen J, Marske KA, Ugan A, Borregaard MK, Gilbert MT, Nielsen R, Ho SY (2011) Species-specific responses of Late Quaternary megafauna to climate and humans. Nature 479:359-364

Lorrain A, Graham B, Ménard F, Popp B, Bouillon S, Van Breugel P, Cherel Y (2009) Nitrogen and carbon isotope values of individual amino acids: a tool to study foraging ecology of penguins in the Southern Ocean. Mar Ecol Prog Ser 391:293-306

MacAvoy SE, Arneson LS, Bassett E (2006) Correlation of metabolism with tissue carbon and nitrogen turnover rate in small mammals. Oecologia 150:190-201

MacFadden BJ, Solounias N, Cerling TE (1999) Ancient Diets, Ecology, and Extinction of 5-Million-Year-Old Horses from Florida. Science 283:824-827

Marinov I, Gnanadesikan A, Toggweiler JR, Sarmiento JL (2006) The southern ocean biogeochemical divide. Nature 441:964-967

Martin JH, Gordon RM, Fitzwater SE (1990) Iron in Antarctic waters. Nature 345:156-158

Martin C, Bentaleb I, Steelandt S, Guinet C (2011) Stable carbon and nitrogen isotope variations in canine dentine growth layers of Kerguelen southern elephant seals. Mar Ecol Prog Ser 439:295-305

Masson V, Vimeux F, Jouzel J, Morgan V, Delmotte M, Ciais P, Hammer C, Johnsen S, Lipenkov VY, Mosley-Thompson E, Petit JR (2000) Holocene climate variability in Antarctica based on 11 ice-core isotopic records. Quaternary Res 54:348-358

Mayewski PA, Carleton AM, Birkel SD, Dixon D, Kurbatov AV, Korotkikh E, McConnell J, Curran M, Cole-Dai J, Jiang S, Plummer C (2017) Ice core and climate reanalysis analogs to predict Antarctic and Southern Hemisphere climate changes. Quaternary Sci Rev 155:50-66

McCarthy MD, Benner R, Lee C, Fogel ML (2007) Amino acid nitrogen isotopic fractionation patterns as indicators of heterotrophy in plankton, particulate, and dissolved organic matter. Geochim Cosmochim Ac 71:4727-4744

McCarthy MD, Lehman J, Kudela R (2013) Compound-specific amino acid $\delta^{15}N$ patterns in marine algae: Tracer potential for cyanobacterial vs. eukaryotic organic nitrogen sources in the ocean. Geochim Cosmochim Ac 103:104-120

McClelland JW, Montoya JP (2002) Trophic relationships and the nitrogen isotopic composition of amino acids in plankton. Ecology 83:2173-2180

McIntyre T, Ansorge IJ, Bornemann H, Plötz J, Tosh CA, Bester MN (2011) Elephant seal dive behaviour is influenced by ocean temperature: implications for climate change impacts on an ocean predator. Mar Ecol Prog Ser 441:257-272

McMahon KW, Fogel ML, Elsdon TS, Thorrold SR (2010) Carbon isotope fractionation of amino acids in fish muscle reflects biosynthesis and isotopic routing from dietary protein. J Anim Ecol 79:1132-1141

McMahon KW, Hamady LL, Thorrold SR (2013) A review of ecogeochemistry approaches to estimating movements of marine animals. Limnol Oceanogr 58:697-714

McMahon KW, Hamady LL, Thorrold SR (2013) Ocean ecogeochemistry: a review. Oceanogr Mar Biol 51:327-374

McMahon KW, Polito MJ, Abel S, McCarthy MD, Thorrold SR (2015) Carbon and nitrogen isotope fractionation of amino acids in an avian marine predator, the gentoo penguin (Pygoscelis papua). Ecol Evol 5:1278-1290

McMahon KW, McCarthy MD (2016) Embracing variability in amino acid δ15N fractionation: mechanisms, implications, and applications for trophic ecology. Ecosphere 7:e01511

Meredith MP, King JC (2005) Rapid climate change in the ocean west of the Antarctic Peninsula during the second half of the 20th century. Geophys Res Lett 32:L19604

Mihlbachler MC, Rivals F, Solounias N, Semprebon GM (2011) Dietary change and evolution of horses in North America. Science 331:1178-1181

Minagawa M, Wada E (1984) Stepwise enrichment of 15N along food chains: further evidence and the relation between δ15N and animal age. Geochim Cosmochim Ac 48:1135-1140

Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western western Antarctic Peninsula. Science 323:1470-1473

Mullin MM, Rau GH, Eppley RW (1984). Stable nitrogen isotopes in zooplankton: some geographic and temporal variations in the North Pacific. Limnol Oceanogr 29:1267-1273

New LF, Clark JS, Costa DP, Fleishman E, Hindell MA, Klanjšček T, Lusseau D, Kraus S, McMahon CR, Robinson PW, Schick RS (2014) Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. Mar Ecol Prog Ser 496:99-108

Newland C, Field IC, Cherel Y, Guinet C, Bradshaw CJ, McMahon CR, Hindell MA (2011) Diet of juvenile southern elephant seals reappraised by stable isotopes in whiskers. Mar Ecol Prog Ser 424:247-258

Nicol S (2006) Krill, currents, and sea ice: Euphausia superba and its changing environment. Bioscience 56:111-120

Nicol S, Worby A, Leaper R (2008) Changes in the Antarctic sea ice ecosystem: potential effects on krill and baleen whales. Mar Freshw Res 59:361-382

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

Paolo FS, Fricker HA, Padman L (2015) Volume loss from Antarctic ice shelves is accelerating. Science 348:327-331

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol Syst 37:637-669

Parkinson CL (2002) Trends in the length of the Southern Ocean sea-ice season, 1979-99. Ann Glaciol 34:435-440

Peakall ROD and Smouse PE (2006) GENALEX 6: Genetic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288-295

Peakall ROD and Smouse PE (2012) GENALEX 6.5: Genetic analysis in Excel. Population genetic software for teaching and research, an update. Bioinformatics 28:2537-2539

Peterson BJ, Fry B (1987) Stable isotopes in ecosystem studies. Annu Rev Ecol Syst 18:293-320

Pinkerton MH, Forman J, Bury SJ, Brown J, Horn P, O'Driscoll RL (2013) Diet and trophic niche of Antarctic silverfish Pleuragramma antarcticum in the Ross Sea, Antarctica. J Fish Biol 82:141-164

Plötz J, Ekau W, Reijnders PJ (1991). Diet of Weddell seals *Leptonychotes weddellii* at Vestkapp, eastern Weddell Sea (Antarctica), in relation to local food supply. Mar Mam Sci 7:136-144

Plötz J, Bornemann H, Bornemann H, Knust R, Schröder A, Bester M (2001) foraging behaviour of weddell seals and its ecological implications. Polar Biol 24:901-909

Ponganis PJ, Stockard TK (2007) Short Note: The Antarctic toothfish: how common a prey for Weddell seals? Antarct Sci 19:441-442

Popp BN, Graham BS, Olson RJ, Hannides CCS, Lott MJ, López-Ibarra GA, Galván-Magaña F, Fry B (2007) Insight into the trophic ecology of the yellowfin tuna, *Thunnus albacares*, from compound-specific nitrogen isotope analysis of

proteinaceous amino acids. In: Dawson T, Siegwolf R (eds) Stable Isotopes as Indicators of Ecological Change. Elsevier, New York, p 173-190

Quillfeldt P, Masello JF, McGill RA, Adams M, Furness RW (2010) Moving polewards in winter: a recent change in the migratory strategy of a pelagic seabird? Front Zool 7:1-11

Quillfeldt P, Ekschmitt K, Brickle P, McGill RA, Wolters V, Dehnhard N, Masello JF (2015) Variability of higher trophic level stable isotope data in space and time–a case study in a marine ecosystem. Rapid Commun Mass Spectrom 7:667-674

R Core Team (2014). R: A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria

Raiswell R, Tranter M, Benning LG, Siegert M, De'ath R, Huybrechts P, Payne T (2006) Contributions from glacially derived sediment to the global iron (oxyhydr) oxide cycle: implications for iron delivery to the oceans. Geochim Cosmochim Ac 70:2765-2780

Raiswell R, Benning LG, Tranter M, Tulaczyk S (2008) Bioavailable iron in the Southern Ocean: the significance of the iceberg conveyor belt. Geochem Trans 9:7

Raiswell R (2011) Iceberg-hosted nanoparticulate Fe in the Southern Ocean: Mineralogy, origin, dissolution kinetics and source of bioavailable Fe. Deep Sea Res II 58:1364-1375

Rankin AM, Wolff EW, Martin S (2002) Frost flowers: Implications for tropospheric chemistry and ice core interpretation. J Geophys Res Atmos 107:4683

Rankin, A.M., Wolff, E.W. and Mulvaney, R (2004) A reinterpretation of sea-salt records in Greenland and Antarctic ice cores? Ann Glaciol 39:276-282

Rau GH, Sweeney RE, Kaplan IR (1982) Plankton 13C: 12C ratio changes with latitude: differences between northern and southern oceans. Deep Sea Res Pt I 29:1035-1039

Rau GH, Takahashi T, Des Marais DJ (1989) Latitudinal variations in plankton $\delta^{13}C$: implications for CO_2 and productivity in past oceans. Nature 341:516-518

Rau GH, Ainley DG, Bengtson JL, Torres JJ, Hopkins TL (1992) $^{15}N/^{14}N$ and $^{13}C/^{12}C$ in Weddell Sea birds, seals, and fish: implications for diet and trophic structure. Mar Ecol Prog Ser 84:1-8

Reeves RR (2008) Guide to marine mammals of the world. Knopf Doubleday Publishing Group, New York

Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Ramsey CB, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM (2013). IntCal13 and Marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1869-1887

Reiss CS, Cossio AM, Loeb V, Demer DA (2008) Variations in the biomass of Antarctic krill (Euphausia superba) around the South Shetland Islands, 1996–2006. ICES J Mar Sci 65:497-508

Rhodes RH, Bertler NA, Baker JA, Steen-Larsen HC, Sneed SB, Morgenstern U, Johnsen SJ (2012) Little Ice Age climate and oceanic conditions of the Ross Sea, Antarctica from a coastal ice core record. Climat Past 8:1223-1238

Sarakinos HC, Johnson ML, Zanden MJV (2002) A synthesis of tissue-preservation effects on carbon and nitrogen stable isotope signatures. Can J Zool 80:381-387

Schell DM, Barnett BA, Vinette KA (1998) Carbon and nitrogen isotope ratios in zooplankton of the Bering, Chukchi and Beaufort seas. Mar Ecol Prog Ser 162:11-23

Schlitzer R (2015) Ocean Data View (ODV) version (4.7.4). http://odv.awi.de

Schmidt K, Atkinson A, Stübing D, McClelland JW, Montoya J P, Voss M (2003) Trophic relationships among Southern Ocean copepods and krill: some uses and limitations of a stable isotope approach. Limnol Oceanogr 48:277-289

Schmidt K, Atkinson A, Petzke KJ, Voss M, Pond DW (2006) Protozoans as a food source for Antarctic krill, Euphausia superba: Complementary insights from stomach content, fatty acids, and stable isotopes. Limnol Oceanogr 51:2409-2427

Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR (2010) How do polar marine ecosystems respond to rapid climate change? Science 328:1520-1523

Scott JH, O'Brien DM, Emerson D, Sun H, McDonald GD, Salgado A, Fogel ML (2006) An examination of the carbon isotope effects associated with amino acid biosynthesis. Astrobiology 6:867-880

Sedwick PN, DiTullio GR (1997) Regulation of algal blooms in Antarctic shelf waters by the release of iron from melting sea ice. Geophys Res Lett 24:2515-2518

Siegel V, Loeb V (1995) Recruitment of Antarctic krill Euphausia superba and possible causes for its variability. Mar Ecol Prog Ser 123:45-56

Shaw TJ, Raiswell R, Hexel CR, Vu HP, Moore WS, Dudgeon R, Smith KL (2011) Input, composition, and potential impact of terrigenous material from free-drifting icebergs in the Weddell Sea. Deep Sea Res II 58:1376-1383

Sherwood OA, Lehmann MF, Schubert CJ, Scott DB, McCarthy MD (2011) Nutrient regime shift in the western North Atlantic indicated by compound-specific $\delta^{15}N$ of deep-sea gorgonian corals. P Natl Acad Sci USA 108:1011-1015

Siniff DB (1991) An overview of the ecology of Antarctic seals. Am Zool 31:143-149

Siniff DB, Garrott RA, Rotella JJ, Fraser WR, Ainley DG (2008) Opinion: Projecting the effects of environmental change on Antarctic seals. Antarct Sci 20:425-435

Silfer JA, Engel MH, Macko SA, Jumeau EJ (1991) Stable carbon isotope analysis of amino acid enantiomers by conventional isotope ratio mass spectrometry and combined gas chromatography/isotope ratio mass spectrometry. Anal Chem 63:370-374

Skinner JD, Klages NTW (1994) On some aspects of the biology of the Ross seal *Ommatophoca rossii* from King Haakon VII Sea, Antarctica. Polar Biol 14:467-472

Smetacek V, Nicol S (2005) Polar ocean ecosystems in a changing world. Nature 437:362-368

Smith RC, Baker KS, Vernet M (1998) Seasonal and interannual variability of phytoplankton biomass west of the Antarctic Peninsula. J Mar Syst 17:229-243

Smith WO, Ainley DG, Cattaneo-Vietti R (2007) Trophic interactions within the Ross Sea continental shelf ecosystem. Philos Trans R Soc Lond B Biol Sci 362:95-111

Smith WO, Comiso JC (2008). Influence of sea ice on primary production in the Southern Ocean: A satellite perspective. J Geophys Res Oceans 113:C05S93

Smith WO, Dinniman MS, Hofmann EE, Klinck JM (2014) The effects of changing winds and temperatures on the oceanography of the Ross Sea in the 21st century. Geophys Res Lett 41:1624-1631

Smith Jr WO, Ainley DG, Arrigo KR, Dinniman MS (2014) The Oceanography and Ecology of the Ross Sea. Annu Rev Mar Sci 6:469-487

Sneed SB, Mayewski PA, Dixon DA (2011) An emerging technique: multi-ice-core multi-parameter correlations with Antarctic sea-ice extent. Ann Glaciol 52:347-354

Somes CJ, Schmittner A, Galbraith ED, Lehmann MF, Altabet MA, Montoya JP, Letelier RM, Mix AC, Bourbonnais A, Eby M (2010) Simulating the global distribution of nitrogen isotopes in the ocean. Global Biogeochem Cycles 24:16

Stammerjohn S, Massom R, Rind D, Martinson D (2012) Regions of rapid sea ice change: An inter-hemispheric seasonal comparison. Geophys Res Lett 39: L06501

Staniland IJ (2002) Investigating the biases in the use of hard prey remains to identify diet composition using Antarctic fur seals (*Arctocephalus gazella*) in captive feeding trials. Mar Mamm Sci 18:223-243

Steig EJ, Hart CP, White JW, Cunningham WL, Davis MD, Saltzman ES (1998) Changes in climate, ocean and ice-sheet conditions in the Ross embayment, Antarctica, at 6 ka. Ann Glaciol 27:305-310

Steig EJ, Morse DL, Waddington ED, Stuiver M, Grootes PM, Mayewski PA, Twickler MS, Whitlow SI (2000) Wisconsinan and Holocene climate history from an ice core at Taylor Dome, western Ross Embayment, Antarctica. Geogr Ann A 82:213-235

Stenni B, Proposito M, Gragnani R, Flora O, Jouzel J, Falourd S, Frezzotti M (2002) Eight centuries of volcanic signal and climate change at Talos Dome (East Antarctica). J Geophys Res Atmos 107:4076

Surma S, Pakhomov EA, Pitcher TJ (2014) Effects of whaling on the structure of the southern ocean food web: insights on the "Krill Surplus" from ecosystem modelling. PLoS One 9:e114978

Sweeting CJ, Polunin NVC, Jennings S (2006) Effects of chemical lipid extraction and arithmetic lipid correction on stable isotope ratios of fish tissues. Rapid Commun Mass Spectrom 20:595-601

Swofford DL (1998) PAUP 4.0: Phylogenic analysis using parsimony (and other methods). 4.0b10 ed. Sinauer Associates, Inc., Sunderland, MA

Tortell PD, Payne CD, Li Y, Trimborn S, Rost B, Smith WO, Riesselman C, Dunbar RB, Sedwick P, DiTullio GR (2008) CO_2 sensitivity of Southern Ocean phytoplankton. Geophys Res Lett 35:L04605

Trathan PN, Forcada J, Murphy EJ (2007) Environmental forcing and Southern Ocean marine predator populations: effects of climate change and variability. Philos Trans R Soc Lond B Biol Sci 362:2351-2365

Trathan PN, Ratcliffe N, Masden EA (2012) Ecological drivers of change at South Georgia: the krill surplus, or climate variability. Ecography 35:983-993

Trivelpiece WZ, Hinke JT, Miller AK, Reiss CS, Trivelpiece SG, Watters GM (2011)Variability in krill biomass links harvesting and climate warming to penguin population changes in Antarctica. Proc Natl Acad Sci USA 108:7625-7628

Untergasser A, Cutcutache I, Koressaar T, Ye J, Faircloth BC, Remm M, Rozen SG (2012) Primer3--new capabilities and interfaces. Nucleic Acids Res 40:e115

Vaughan DG, Marshall GJ, Connolley WM, Parkinson C, Mulvaney R, Hodgson DA, King JC, Pudsey CJ, Turner J (2003) Recent rapid regional climate warming on the Antarctic Peninsula. Clim Change 60:243-274

Vokhshoori NL, Larsen T, McCarthy MD (2014) Reconstructing $\delta^{13}C$ isoscapes of phytoplankton production in a coastal upwelling system with amino acid isotope values of littoral mussels. Mar Ecol Prog Ser 504:59-72

Vokhshoori NL, McCarthy MD (2014) Compound-specific $\delta^{15}N$ amino acid measurements in littoral mussels in the California upwelling ecosystem: a new approach to generating baseline $\delta^{15}N$ isoscapes for coastal ecosystems. PLOS ONE 9:e98087

Wada E, Terazaki M, Kabaya Y, Nemoto T (1987) 15N and 13C abundances in the Antartic Ocean with emphasis on the biogeochemical structure of the food web. Deep Sea Res I 34:829-841

Walker MJC, Berkelhammer M, Björck S, Cwynar LC, Fisher DA, Long AJ, Lowe JJ, Newnham RM, Rasmussen SO, Weiss H (2012), Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). J Quaternary Sci 27:649-659

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416:389-395

West JB, Bowen GJ, Dawson TE, Tu KP (2010) Isoscapes. Springer, Netherlands

Yonezaki S, Kiyota M, Baba N, Koido T, Takemura A (2003) Size distribution of the hard remains of prey in the digestive tract of northern fur seal (*Callorhinus ursinus*) and related biases in diet estimation by scat analyses. Mamm Study 28:97-102

Zhao L, Castellini MA, Mau TL, Trumble SJ (2004) Trophic interactions of Antarctic seals as determined by stable isotope signatures. Polar Biol 27:368-373

Zingone A, Phlips EJ, Harrison PJ (2010) Multiscale variability of twenty-two coastal phytoplankton time series: a global scale comparison. Estuar Coasts 33:224-229